

Water Use Characteristics of the Common Tree Species in Rock-dominated and Thin-soil Environments in Subtropical Monsoon Climate Region

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1 **Water use characteristics of the common tree species in**
2 **rock-dominated and thin-soil environments in subtropical monsoon**
3 **climate region**

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18

19 **Abstract**

20 Variations in precipitation pattern under climate changes influence water availability that have
21 important implications for plants water use and vegetation sustainability. However, the water use
22 characteristic of the main tree species under different temporal-spatial of water availability remain
23 poorly understood, especially in high temporal-spatial heterogeneity area, such as subtropical
24 monsoon climate region of China. We investigated water use characteristics of the most widely
25 and common natural trees, *Mallotus philippensis* and *Celtis biondii*, in edaphic and rocky habitats.
26 We measured the δD and $\delta^{18}O$ values of xylem and soil water and water potential of plant leaves
27 during the wet season in 2020. The results showed that the two species mainly absorbed soil water
28 from shallow layers and switched for deeper layers during the late of the wet season in both
29 habitats. But the plant water sources were different in edaphic and rocky habitats when the
30 antecedent precipitation was much high, deep layers soil water in the former and still shallow
31 layers in the latter. The two species had no significant differences in water uptake depth, but
32 notably distinction in the diurnal water potential ranges. *M. philippensis* maintained less negative
33 predawn and midday water potential, whereas *C. biondii* showed higher diurnal water potential
34 ranges. Besides, the water potential of *C. biondii* were negatively associated with antecedent
35 precipitation amount. These results indicate that there is significant eco-physiological niche
36 segregation but no ecohydrological segregation co-existing species in communities. Besides,
37 antecedent precipitation amount and habitat differences were the main factors influencing the
38 plant water uptake depth. While the relationship between leaf physiological traits and water
39 availability was affected by the species types, rather than the habitats. Furthermore, during the
40 long drought in growing season, there are probable divergent responses of *M. philippensis* and *C.*

41 *biondii*, such as growth restriction and hydraulic failure. But when the precipitation is heavy and
42 long, these natural species could increase the ecohydrological linkages between ecosystem and the
43 deep-layer system in edaphic habitat.

44 **Key words**

45 Plant water source; Habitat; Stable isotope; Leaf water potential; Water use efficiency

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48 **1 Introduction**

49 Increases in vegetation greenness have been reported around the world over the last three
50 decades, manifested as the expanding of afforestation and reforestation (Forzieri et al., 2020; Piao
51 et al., 2015; Zhu et al., 2016). While the forests maybe vulnerable to degradation due to global
52 climate changes with new precipitation patterns (Aguirre et al., 2019; Gu et al., 2016; Malhi et al.,
53 2008). Changes in characteristics of precipitation may result in changes in water availability that
54 have implications for plants water use in ecosystem (Dietrich and Kahmen, 2019; Konapala et al.,
55 2020). The variation of plants water use response to precipitation and water availability plays an
56 important role in the sustainability of the restored vegetation and promotion of water cycle in
57 critical zone (Anderegg et al., 2018; Chen et al., 2019; Macias, 2018).

58 The temporal-spatial heterogeneity of precipitation and water availability affect plant water use
59 strategies (Liang et al., 2019; Zhao and Wang, 2018). At the point scale, the water source
60 variability along soil profile is one of the most important factors for plants water uptake
61 (Kuhnhammer et al., 2020). At the surface scale, the aquifer storage is distinct in different habitats,
62 such as deep soil habitat (Wang et al., 2020a), outcrop habitat (Deng et al., 2020), soil with rock
63 fragments habitat (Ceacero et al., 2020), which is related with the soil properties and plant water
64 consuming. At different stages of the season, the plant water uptake depth maybe also divergent
65 with the changes of rhizosphere water availability (Nie et al., 2012; Wang et al., 2020a). Some tree
66 species may switch their water sources from shallow layers to stable layers from wet season with
67 sufficient precipitation to dry season (Drake and Franks, 2003; Yang et al., 2015; Yang et al.,
68 2017). Meanwhile, the amount of precipitation may be a critical factor affecting the water sources
69 of trees. Liu et al. (2019b) found that following the rainfall events, *Platyclus orientalis* with

70 dense and shallow fine root system absorbed more water from the soil surface layers and
71 precipitation. While, other plants mostly take up water from deep and stable layers regardless of
72 seasonal changes or precipitation events (Deng et al., 2020; Zunzunegui et al., 2018).

73 The divergent response of plant water uptake to the changes in precipitation and water
74 availability was related with physiological characteristic. It has been suggested that the predawn
75 and midday leaf water potential was used to describe the daily patterns of plant-water relations,
76 coupling water among root zone, plant itself and atmosphere (Hochberg et al., 2018). Previous
77 studies found that the plants relying on shallower water sources exhibited a larger diurnal range of
78 leaf water potential, on the contrary, the narrower diurnal ranges usually linking with the deep and
79 stable water sources (Ding et al., 2020; Eggemeyer et al., 2009; Liu et al., 2021). Moreover, the
80 plant water efficiency (WUE_i) has been drawn attention to reflect plant water use characteristic
81 together with plant water uptake (Craven et al., 2013; Hasselquist et al., 2010). Nie et al. (2014)
82 explored the leaf WUE based on $\delta^{13}C$ values and found that the high WUE was corresponding
83 with the deep water sources, indicating more conservative water-use strategies in subtropical
84 monsoon climate region. Whereas, Wang et al. (2021) found that plantation trees increased water
85 availability by increasing WUE_i instead of switching water sources responses to variations in
86 precipitation on the Loess Plateau. The plant water uptake pattern was influenced by water
87 availability and physiological traits in different ecosystems (Volkman et al., 2016). However, the
88 relationship between two factors affecting plant water uptake is unclear, especially in complex and
89 fragile forest ecosystem, such as subtropical monsoon climate region, which limits the
90 understanding of restored vegetation adaptability and rock-soil-water-plant-atmosphere
91 interactions in critical zone.

92 Subtropical areas in China with a monsoon climate are ecologically sensitive areas of global
93 change (Bruehlheide and others 2014). At the same time, the subtropical monsoon climate region of
94 China is suffering from rocky desertification. The ecological conservation projects facilitate to the
95 subtropical monsoon climate region of tree cover in the globe now (Brandt et al., 2018; Delang
96 and Zhen, 2015; Tong et al., 2020). The distribution of natural restored vegetation was fragmented
97 with the heterogeneous habitats (Liu et al., 2019a). Plant water use strategies in different habitats
98 is critical important for the evaluation of vegetation adaptation and the implementation of the next
99 comprehensive treatment of rocky desertification. A number of previous studies were primarily
100 focused on the water source of different types of plantation or natural vegetation in one certain
101 habitat in the subtropical monsoon climate region (Deng et al., 2020; Ding et al., 2018). Few
102 attached attentions to the common tree species in different habitats (Nie et al., 2012). Besides,
103 rainwater and spring was treated as a potential water source for plants growing on outcrops
104 assuming that they can use them stored in crevices/cracks directly (Nie et al., 2012). Actually, in
105 most rocky habitat, there are lumps of relative thick soil surrounded by outcrops with substantial
106 fine root where maybe the important water sources for tree species. However, previous studies
107 failed to focus on the soil water availability for the plants due to the narrow distribution of soil
108 than the continuous outcrops. With the global precipitation pattern changes, short-term drought or
109 rainstorm was more frequent especially in the wet/growing season. However, it is unclear how the
110 water uptake of common plants in the different habitats responds during the wet season with
111 precipitation changes.

112 Based on the above analysis, we applied isotope techniques (δD , $\delta^{18}O$, and $\delta^{13}C$) and leaf water
113 potential to determine the plant water use strategies of natural restoration in edaphic and rocky

114 habitat with seasonal sampling during the growing season on the subtropical monsoon climate
115 region of China. The primary objectives of the study were to (i) evaluate the water uptake pattern
116 of species in two habitats for the temporal-spatial heterogeneity of water availability; (ii)
117 investigate how the leaf water potential and water use efficiency of species responds to season
118 variation with different precipitation; (iii) explore the relationship between plant physiological
119 traits and water uptake pattern. The first hypothesis is that the plant water use pattern varies in the
120 seasonal changes with different precipitation in two habitats, and the second is that the plant water
121 uptake would coordinate with physiological characteristic of species, coupling with water
122 availability.

123

124 **2 Materials and methods**

125 **2.1 Study area and sampling sites characteristics**

126 The study site is located in a small catchment (area = 1.14 km²) in the Lutou Observation and
127 Research Station for north Luoxiao national forest park (28°31'7"-28°38'N,
128 113°51'52"-113°58'24"E), which is situated in the northeast of Hunan Province, China. Along the
129 part of the slope, the soil is mainly thin with a depth of 10-30 cm. At the foot of the slope and in
130 the depression, the soil is relatively thick of 70-90 cm with amounts of rock fragments. The other
131 part of the slope has a high exposed dolomite ratio, while the soil occurs discontinuous only in
132 carbonate rock gaps. Thus, the habitats were variable with the different outcrop ratio, such as
133 edaphic habitat with low outcrop ratio, continuous broken rock habitat with patches of soil,
134 isolated outcrops habitat, and so on. Springs sometimes appear at the bottom of hillslopes during
135 the rainy season or after rains in the drought season. The region has a subtropical mountainous

136 monsoon climate, with mean annual precipitation of 1450.8 mm and an annual temperature of
137 18.5°C. The wet season lasts from late April to the end of September and provides >60% of total
138 annual rainfall, while the dry season extends from December to February (Nie et al., 2012). The
139 growing season spans from April to October.

140 The area was undergone dramatic deforestation caused by farming, grazing, and burning, then
141 under natural restoration and reforestation for almost 21 years (Jiang et al., 2014; Moore et al.,
142 2016; Zhang et al., 2016). The distribution of natural restored vegetation was fragmented with the
143 heterogeneous habitats. The secondary forest is usually found on dolomite outcrops and soil
144 habitat at the foot of the slope (Nie et al., 2012). Plant species growing on outcrops usually emerge
145 from cracks or crevices, or grow on protuberant rocks with their roots ultimately penetrating into
146 cracks. Tree species are usually random growth on soil habitat with the long laterally extend of
147 taproot.

148 According to the distribution of these typical habitats, thick soil with rock fragments habitat
149 (edaphic habitat for short) and one continuous stone outcrops with soil fragments (rocky habitat
150 for short) were chosen at the foot of the Northwest-facing hillslope in two 20×20m sample plots
151 (Fig. 1). The two habitats are 50 meters apart, while the elevation difference was about 5 meters.
152 In the edaphic habitat, the soil is relatively thick (about 90cm deep), horizontally interrupted by
153 small outcrops, and vertically interrupted by small rocks. At the soil profile, the upper layer soil
154 (0-30 cm) is well-drained, while the lower layers (30-70 cm) are sticky with a low soil saturated
155 hydraulic conductivity (Ks) (Fu et al., 2015). Underneath the soil is a high-weathered dolomite
156 bedrock zone (70-90cm). The outcrop ratio is about 20% in this habitat. This habitat is covered by
157 dense vegetation, with *Mallotus philippensis*, *Rhus chinensis*, and *Celtis biondii* dominating the

158 tree layer. *Vitex negundo* and *Pyracantha fortuneana* dominate the shrub layer. In the rocky habitat,
159 the outcrop ratio is more than 80%, and the range of height from the top of the outcrop to the soil
160 in the rock gaps is from 0.3m to 3m. The soil inlaid in the rock in a spotty pattern and is
161 discontinuous (average 30cm deep). Similarly, high-weathered dolomite bedrock zone is under the
162 soil. The vegetation is sparse in this habitat. The tree layer is dominated by *M. philippensis*, *Ficus*
163 *tinctoria*, and *C. biondii*, and the shrub layer is dominated by *V. negundo*. There is a intermittent
164 spring outflow near the two habitats at the bottom of the hillslope.

165 **2.2 Plant and soil sampling**

166 Plant and soil sampling were conducted simultaneously at the two habitats bimonthly on Jun 12
167 (middle wet season with high antecedent precipitation), August 5 (middle wet season with low
168 antecedent precipitation) and October 18 (early dry season) 2020. Besides, we also sampled on
169 May 18 in early wet season with 20-day drought. Two common species, adult *M. philippensis*
170 (DBH of from 5 to 11cm) and *C. biondii* (DBH of from 6 to 12cm) at each of the habitats, were
171 selected for the study. We selected four individuals per species for analysis. The leaf and plant
172 xylem samples from every selected plant were collected in each habitat. every selected plant was
173 collected in each stand-age tree per month. The fully sun-exposed, mature and healthy leaves in
174 the upper canopy from each selected plant were collected in different directions on each sampling
175 date. The leaves were mixed and packed into craft paper bags and brought them back to the
176 laboratory for measuring the plant leaves $\delta^{13}\text{C}$. Shoots ranging from 0.3 to 0.5 cm in diameter and
177 3 to 5cm in length were collected at mid-day from stems more than 2 years old; the outer bark and
178 phloem of the shoots were removed to obtain the xylem sample.

179 Soil samples were obtained in two habitats from six depth intervals (0-10, 10-20, 20-30, 30-50,

180 50-70, 70-90 cm) with an auger (sampling only at 70cm deep in the rocky habitat); and, five
181 replicates were collected at each layer. Among them, the high-weathered bedrock samples were
182 collected between 70-90cm in the edaphic habitat and 50-70cm in the rocky habitat. A subsample
183 of the soil samples was stored at -20 °C for isotopic analysis, whereas the remainder of the
184 samples were sealed for measurement of gravimetric soil water content, obtained by oven drying
185 for one day. The volumetric water content (VWC) was converted according to gravimetric water
186 content and bulk density of each layer.

187 **2.3 Precipitation and spring sampling**

188 Rainwater samples were routinely collected for each rain event above 5mm from May 2020 to
189 December 2020. The isotopic values of precipitation were not collected from January to April due
190 to the COVID-19 pandemic impacting. The collection equipment was designed based on the new
191 device for monthly rainfall sampling for the Global Network of Isotopes in Precipitation (Agency,
192 2002). The rainwater samples were stored in cap vials, wrapped in parafilm and stored in a freezer
193 until the analysis of stable isotopes. Temporal distribution of rainfall data and other meteorological
194 data were collected at a meteorological station located in the middle of the same small catchment.
195 Spring water discharged from June 1 to November 29, but cutoff between July 25 to August 29.
196 The spring was sampled regularly during the outflow period. Both rainwater and spring water
197 were stored in cap vials, wrapped in parafilm, and frozen until stable isotope analysis.

198 **2.4 Isotopic analyses**

199 The water was extracted from xylem and soil using automatic cryogenic vacuum distillation
200 water extraction system (LI-2100, LICA, Beijing, China) (Ehleringer et al., 2000; Li et al., 2007).
201 The δD and $\delta^{18}O$ in xylem and soil water samples were measured with liquid water isotope ratio

202 infrared spectroscopy (IRIS, DLT- 100, Los Gatos Research, Mountain View, CA, USA) at the
203 Key Laboratory for Agro-ecological Processes in Subtropical Region, Chinese Academy of
204 Sciences. The $\delta^{13}\text{C}$ in the plant leaves were analyzed using an isotope ratio mass spectrometer
205 (IRMS, MAT253, Thermo Fisher Scientific, Bremen, Germany).

206 The isotope composition is reported in δ notation relative to V-SMOW as

$$207 \quad \delta X = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000 \quad (1)$$

208 Where X represents D, ^{18}O , or ^{13}C . R_{sample} and R_{standard} are the ratio D/H, $^{18}\text{O}/^{16}\text{O}$, or $^{13}\text{C}/^{12}\text{C}$ ratio
209 of a measured sample and a standard sample, respectively. The standard deviation for repeat
210 measurements was $\pm 1\%$ for δD , $\pm 0.2\%$ for $\delta^{18}\text{O}$ and $\pm 0.15\%$ for $\delta^{13}\text{C}$.

211 Extracting water from plant xylem using cryogenic vacuum distillation can mix organic
212 materials (e.g., methanol and ethanol) that may affect the spectroscopy and lead to erroneous
213 stable isotope values when analyzing with IRIS (Liu et al., 2013; Schultz et al., 2011). We have
214 corrected the isotopic values of xylem according to Liu et al. (2021).

215 **2.5 Leaf water potential**

216 Predawn and midday water potentials (Ψ_{pd} and Ψ_{md} , respectively) of leaves were measured in
217 the wet seasons (simultaneously with isotope sampling) with a pressure chamber (PMS
218 Instruments Co., Corvallis, OR, USA). Samples (n= 5 per species) were collected from branches
219 that were fully exposed to the sun, 2/3 of the way up of the canopy, at least 2 m above ground and
220 for predawn water potential between 4:00 to 6:00 h and midday measurements were subsequently
221 conducted between 12:00 and 14:00 h on the same day.

222 **2.6 Data analysis**

223 Soil water is the primary vegetation water source on the subtropical monsoon climate region,

224 and spring as the potential deep water sources. Plant water source partitioning was determined by
225 the Bayesian mixing model MixSIAR (version 3.1.7) (Stock and Semmens, 2013). The raw
226 isotopic ratios of the xylem water were input into MixSIAR as the mixture data. The averages and
227 standard deviations of the soil water isotopes in the different soil layers were the source data. The
228 discrimination was set to zero for both δD and $\delta^{18}O$ because there is generally no isotopic
229 discrimination of water during plant water uptake by roots (Ehleringer and Dawson, 2010).

230 For the subsequent analysis and comparison, the plant water sources were divided into shallow
231 (0-30 cm), middle (30-70 cm in the edaphic habitat and 30-50 cm in the rocky habitat), deep
232 (70-90 cm in the edaphic habitat and 50-70 cm in the rocky habitat) layers and spring according to
233 the soil texture and fluctuations and patterns of isotopic ratios in the soil water, VWC and the
234 impact of rainfall pulse. (1) shallow soil layer: The variability of soil water isotopic compositions
235 and VWC in this layer were larger, and was vulnerable to rainfall pulse and evaporation with
236 seasons. (2) middle soil layer: The variability of soil water isotopic compositions and SWC in this
237 layer were lower than that of 0-30 cm soil layer. The impact of rainfall pulse and evaporation were
238 moderate. Both the clay content and soil bulk density were higher than the shallow layers. (3) deep
239 soil layer: This layer was high-weathered bedrock with high leakage and low water holding
240 capacity in the rocky habitat and high water moisture in the edaphic habitat, respectively.

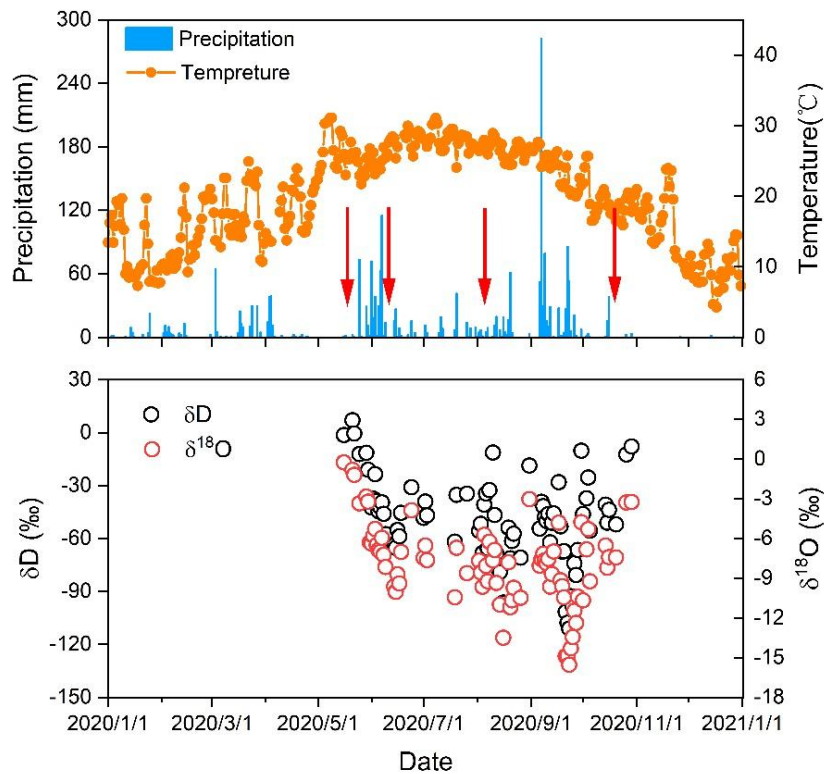
241 Independent-samples T test and One-way ANOVA were used to detect the differences in plant
242 water sources and water potential among the species, habitats and their seasonal differences. Post
243 hoc comparisons were based on Tukey's HSD. Moreover, Pearson correlation was used to conduct
244 the correlation analysis, and the figures were plotted with Origin software version 9.0.

245 **3 Results**

246 3.1 Meteorological factors and isotopic compositions of precipitation

247 The total precipitation was approximately 2121 mm in 2020 (Fig. 1), 52.69% higher than the
248 multiyear mean (1961- 2017) precipitation (1450.8 mm) (Ding et al., 2020). While the distribution
249 of rainfall was temporally uneven (Fig. 1), 79.32% of the rainfall occurred during the wet season.
250 It was noted that there are two extreme precipitation events in Sep. 7 (282.2mm) and Jun. 7
251 (115.2mm). On the other hand, no effective rainfall records were collected in the 20 days from Apr.
252 to May in the wet season. The first sampling took place after the 20-day drought. The other three
253 samplings were conducted in the sunny day after 1-2 days of rainfalls. The accumulated
254 precipitation amount ten days before the last three samplings were 283.6mm, 49.4mm, and
255 55.4mm, respectively.

256 The isotopic compositions of the precipitation showed a large fluctuation during the study
257 period (Fig. 1). The mean δD of the precipitation was -48.69 ‰, the mean $\delta^{18}O$ of the
258 precipitation -7.88 ‰. The relatively depleted isotopic values of precipitation occurred when it
259 rains continuously for a long time with high precipitation. The δD of ten days precipitation before
260 three samplings in middle and late wet season were ranging from -23.55 to -57.52 ‰, -34.54 to
261 -68.36 ‰, -40.76 to -51.02 ‰, respectively. The $\delta^{18}O$ of precipitation before three samplings were
262 ranging from -5.27 ‰ to -8.15 ‰, -7.68 ‰ to -9.65 ‰, -6.54 ‰ to -7.4 ‰, respectively.



263

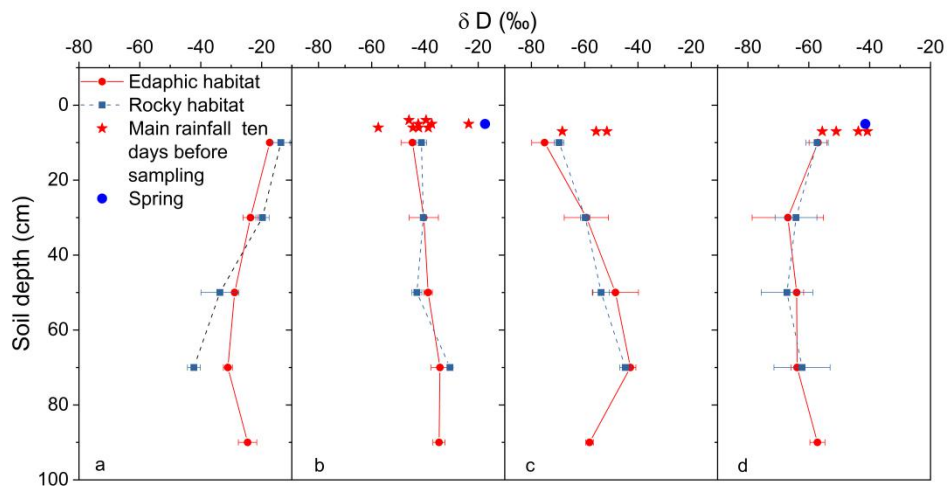
264 **Fig. 1 Variations in precipitation, mean air temperature, and isotopic values (δD , $\delta^{18}\text{O}$) in precipitation at a**
 265 **daily timescale in 2020. Arrows indicate sampling dates. (The isotopic values of precipitation were not**
 266 **collected from Jan. to Apr. due to the COVID-19 pandemic impacting.)**

267

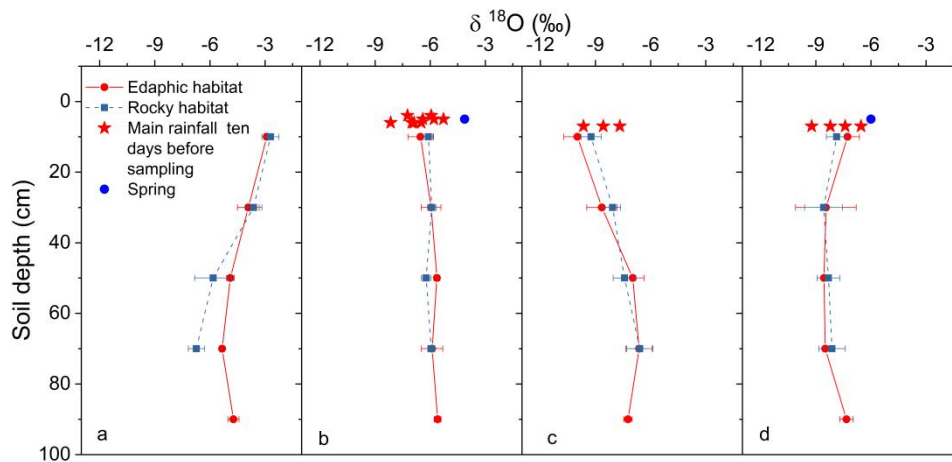
268 **3.2 Variation in isotopic composition of soil water and spring**

269 The δD and $\delta^{18}\text{O}$ values of soil water in the different habitat varied with soil depth and season
 270 (Fig. 2, Fig. 3). In edaphic habitat, the average δD value of soil water was $-45.56 \pm 16.05 \text{ ‰}$
 271 (mean \pm S.D.), and average $\delta^{18}\text{O}$ value was $-6.55 \pm 1.73 \text{ ‰}$. The average δD and $\delta^{18}\text{O}$ values of
 272 soil water in rocky habitat were $-44.6 \pm 16.58 \text{ ‰}$ and $-6.7 \pm 1.96 \text{ ‰}$, respectively. There were no
 273 significant differences ($p=0.84$ for δD , $p= 0.79$ for $\delta^{18}\text{O}$) in the soil isotopic compositions in the
 274 different habitats. In the early wet season with 20-day drought, the soil water isotopes displayed
 275 depleted with soil depth (Fig. 2a, Fig. 3a). In the middle wet season with high precipitation before

276 sampling, δD and $\delta^{18}O$ values of water at soil profile were consistent with recent rainfall values
 277 (Fig. 2b, Fig. 3b). In late two sampling, the soil water isotope composition converged at the top
 278 and bottom layers, which were similar to recent rainfall values (Fig. 2c, d). While the middle layer
 279 soil water showed more enriched isotopic values in the middle wet season or depleted in the late
 280 wet season and less variation with soil depth. The isotopic composition of spring changed across
 281 the sampling time. The isotopic values were less negative in the middle wet season than those in
 282 the late wet season.



283
 284 **Fig. 2** Variation in mean (\pm S.D.) δD along the soil profile during the wet season (a, May sampling; b, Jun.
 285 sampling; c, Aug. sampling; d, Oct. sampling)



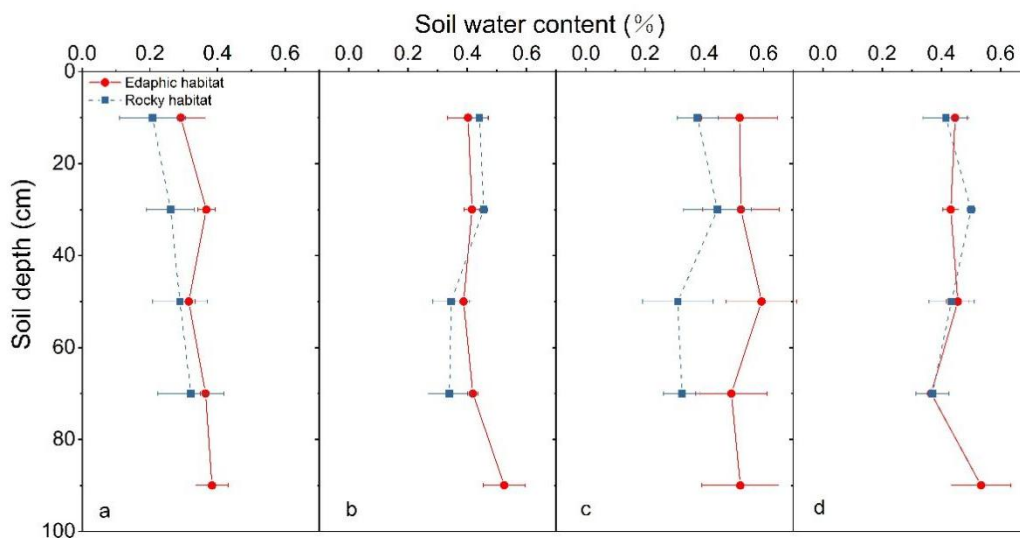
286
 287 **Fig. 3** Variation in mean (\pm S.D.) $\delta^{18}O$ along the soil profile during the wet season. (a, May sampling; b, Jun.
 288 sampling; c, Aug. sampling; d, Oct. sampling)

289

290 3.3. Variations in soil water content and water uptake patterns

291 The VWCs of the two habitats displayed clear vertical and seasonal variations (Fig. 4). The
292 average VWCs were $43.42 \pm 7.68\%$ in edaphic habitat and $38.24 \pm 8.42\%$ in rocky habitat during
293 the study periods. The VWCs of shallow soil layers in the two habitats differed significantly
294 ($p < 0.001$). However, the middle and deep soil moisture showed no significant differences in the
295 two habitats. In the early wet season with 20-day drought, the VWC of the shallow layer was
296 lowest in the two habitats and the soil moisture increased with depth (Fig. 4a). In the middle and
297 late wet season, the VWC exhibited slightly increasing tendency along the soil profile in the
298 edaphic habitat but decreasing tendency in the rocky habitat. Among them, the soil moisture in
299 edaphic habitat had the highest values in middle wet season (Fig. 4c).

300

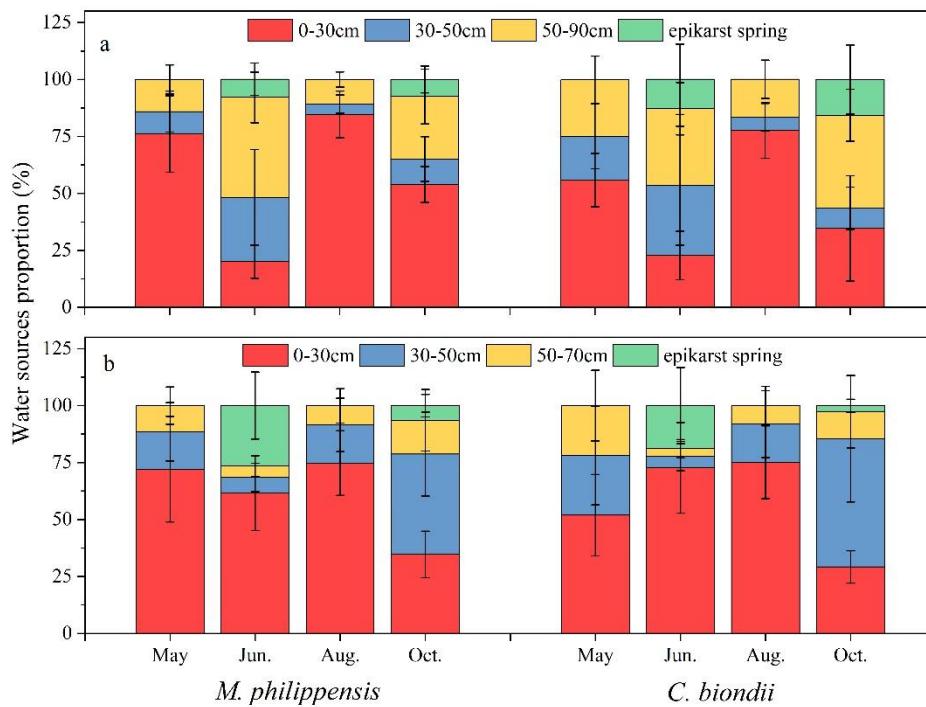


301

302 **Fig. 4 Variation in mean (\pm S.D.) soil water content along the soil profile during the wet season. (a, May**
303 **sampling; b, Jun. sampling; c, Aug. sampling; d, Oct. sampling)**

304 The two tree species mainly took up soil moisture throughout the wet season in two habitats
305 (Fig. 5). While the plants used different layers soil water in seasonal variation with no significant

306 species differences ($p>0.05$). In the early wet season with 20-day drought and middle wet season
 307 with low precipitation before sampling, both *M. philippensis* and *C. biondii* in two habitats
 308 utilized the largest proportion of shallow soil water (64.97%, 0-30cm). In the middle wet season
 309 with high precipitation before sampling, two species in rocky habitat also absorbed more than
 310 67.14% of its water from shallow soil layers. While the mean water uptake fractions of the two
 311 tree species in edaphic habitat were 64.45% for middle and deep soil layers (50-90cm.). In the late
 312 wet season, the *M. philippensis* and *C. biondii* in edaphic habitat obtained more than 74.82% of its
 313 water from the shallow and deep soil layers. While in rocky habitat, the two species mainly
 314 extracted soil water from shallow and middle layers (82.13%).



315
 316 **Fig. 5 Variation in mean (\pm S.D.) water source proportion for *M. philippensis* and *C. biondii* during the wet**
 317 **season. (a, Edaphic habitat; b, Rocky habitat)**

318

319 **3.4. Variations in water potential of plant leaves and its linkage water uptake depth**

320 The ψ_{pd} and ψ_{md} of the two species exhibited profoundly seasonal variation during the sampling
 321 period ($p<0.01$), which were less negative in the middle wet season than those in the early and late
 322 wet season (Table 1). *C. biondii* had significant variation of leaf water potential in two habitats in
 323 the sampling period ($p<0.05$), but the leaf water potential of *M. philippensis* only showed
 324 significant different between two habitats in the early and late wet season ($p<0.05$). In addition, in
 325 the edaphic habitat, both values of ψ_{pd} and ψ_{md} for *M. philippensis* were significant different from
 326 *C. biondii* ($p<0.05$) in the early and late wet season. In the rocky habitat, the variation in ψ_{md} for *C.*
 327 *biondii* ($-1.51\pm 0.49\text{MPa}$) showed significantly lower than *M. philippensis* ($-0.52\pm 0.26\text{MPa}$) in the
 328 rocky habitat in the sampling period, while the ψ_{pd} for the two species had no significant variation
 329 ($p>0.05$).

330

331 **Table 1 Comparisons of predawn water potential (ψ_{pd}) and midday water potential (ψ_{md}) (\pm SD) for *M.***

332 ***philippensis* and *C. biondii* between edaphic and rocky habitats**

		Edaphic habitat (-MPa)		Rocky habitat (-MPa)	
		<i>M. philippensis</i>	<i>C. biondii</i>	<i>M. philippensis</i>	<i>C. biondii</i>
May	ψ_{pd}	-0.74 \pm 0.05Ba	-0.46 \pm 0.05Bb	-0.51 \pm 0.09Aa	-0.30 \pm 0.05Aa
	ψ_{md}	-1.29 \pm 0.14Ba	-2.47 \pm 0.19Bb	-0.93 \pm 0.05Aa	-2.04 \pm 0.15Ab
Jun.	ψ_{pd}	-0.23 \pm 0.05Aa	-0.24 \pm 0.02Aa	-0.20 \pm 0.05Aa	-0.26 \pm 0.02Aa
	ψ_{md}	-0.57 \pm 0.17Aa	-0.50 \pm 0.18Ba	-0.49 \pm 0.13Aa	-0.96 \pm 0.02Ab
Aug.	ψ_{pd}	-0.17 \pm 0.04Aa	-0.15 \pm 0.02Aa	-0.20 \pm 0.06Aa	-0.27 \pm 0.05Aa
	ψ_{md}	-0.29 \pm 0.08Aa	-1.53 \pm 0.06Bb	-0.21 \pm 0.02Aa	-1.07 \pm 0.55Ab
Oct.	ψ_{pd}	-0.39 \pm 0.11Aa	-0.74 \pm 0.31Bb	-0.31 \pm 0.1Aa	-0.44 \pm 0.08Aa
	ψ_{md}	-1.12 \pm 0.15Ba	-1.77 \pm 0.34Ab	-0.45 \pm 0.14Aa	-1.97 \pm 0.52Ab

333 Note: Capital letters within a column indicate significant differences of the same tree species between edaphic and
 334 rocky habitats at the 0.05 level; lowercase letters indicate significant differences between *M. philippensis* and *C.*
 335 *biondii* in the same habitat at the 0.05 level.

336

337 The diurnal ranges of water potential ($\Delta\psi$) exhibited significant variation in different species with

338 seasonal changes ($p < 0.01$). *M. philippensis* showed significant lower $\Delta\psi$ than *C. biondii* ($p < 0.001$).

339 The $\Delta\psi_{\max}$ was in the early wet season for *C. biondii* (-1.84 ± 0.19 MPa) and in the late wet season

340 for *M. philippensis* (-0.45 ± 0.34 MPa). And both two tree species displayed the minimum $\Delta\psi$

341 (-0.48 ± 0.11 MPa and 0.09 ± 0.06 MPa, respectively) in the middle wet season. Both two species had

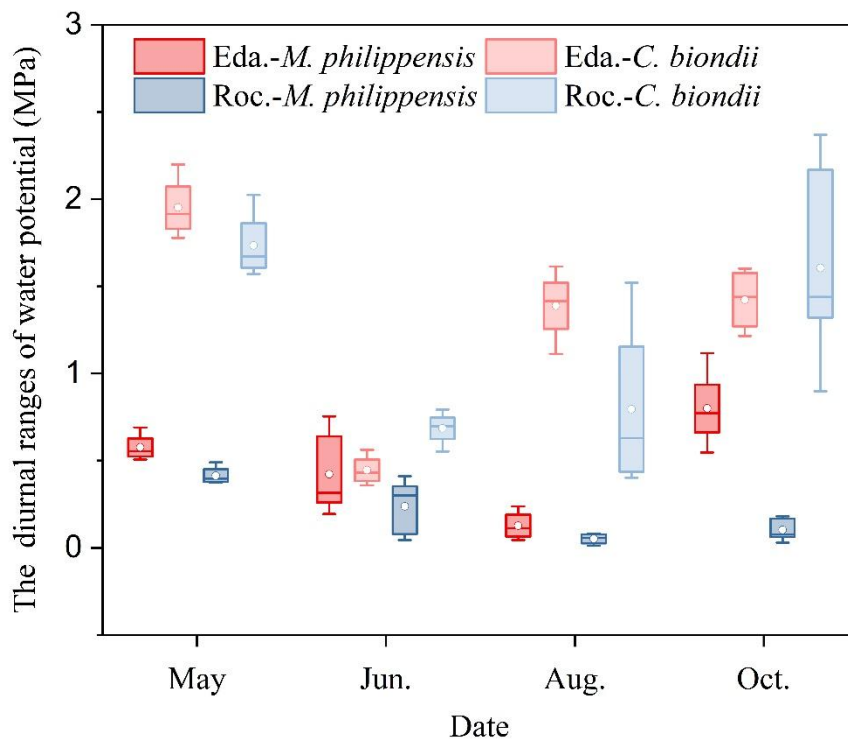
342 significant higher diurnal ranges of water potential in edaphic habitat than those in rocky habitat

343 ($p < 0.001$) during the sampling period, except for *C. biondii* in the middle wet season with low

344 precipitation and late wet season. Furthermore, it was not significant correlation between the $\Delta\psi$

345 and water uptake depth for *M. philippensis* and *C. biondii* in two habitats.

346



347

348 **Fig. 6 Variation in mean (\pm S.D.) diurnal ranges of water potential for *M. philippensis* and *C. biondii* during**

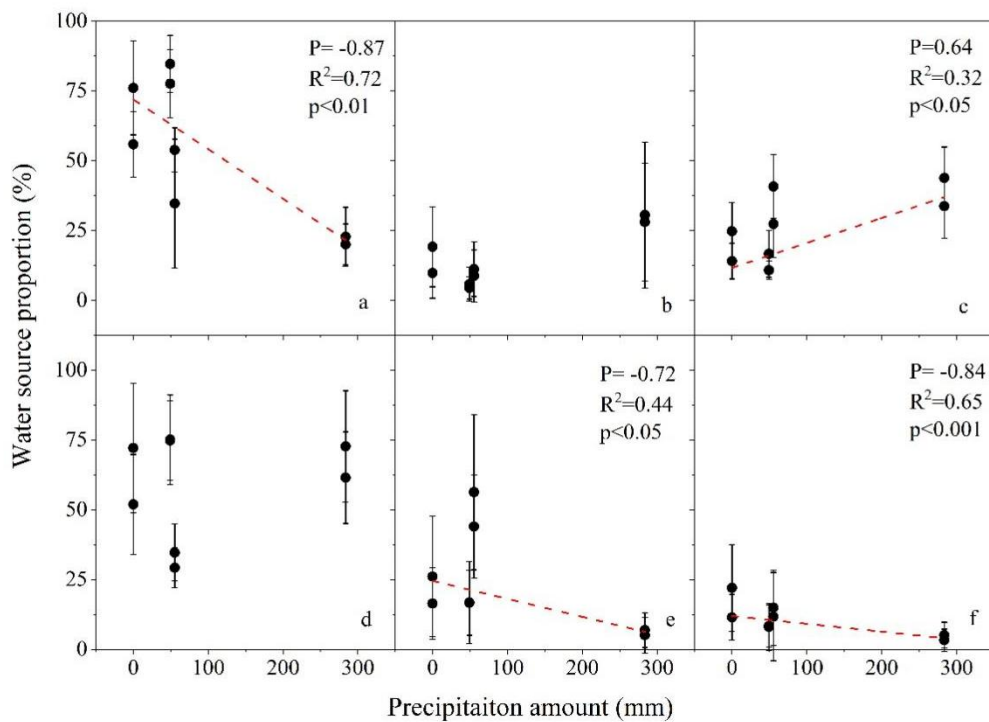
349 **the wet season.**

350

351 **3.5 Changes in plant uptake depth in response to precipitation amount in two habitats**

352 The response of plant water source proportion in each soil layers to precipitation amount ten
 353 days before sampling were distinct in two habitats (Fig. 7). In the edaphic habitat, tree species
 354 absorbed less water from shallow layers and more deep soil water with the precipitation increases
 355 (Fig. 7a, c). While the trees maintained high water uptake from shallow layers in the rocky habitat
 356 whatever precipitation variations (Fig. 7d). Meanwhile, there were significant negative linear
 357 relationships between the water source proportion of middle and deep soil layers and precipitation
 358 (Fig. 7e, f).

359



360

361 **Fig. 7 Relationships between water source proportion for each soil layers (mean \pm S.D.) and precipitation**

362 **amount ten days before sampling. P is Pearson correlation, R² represents fitting degree of the relationship**

363 **between water source proportion and precipitation amount; p is p-value of the fitting (a, b, c, plant water**

364 **sources from shallow, middle, deep layers in edaphic habitat, respectively; d, e, f, plant water sources from**

365 shallow, middle, deep layers in rocky habitat, respectively)

366

367 3.6 Contrasting leaf water potential responses to precipitation amount between two species

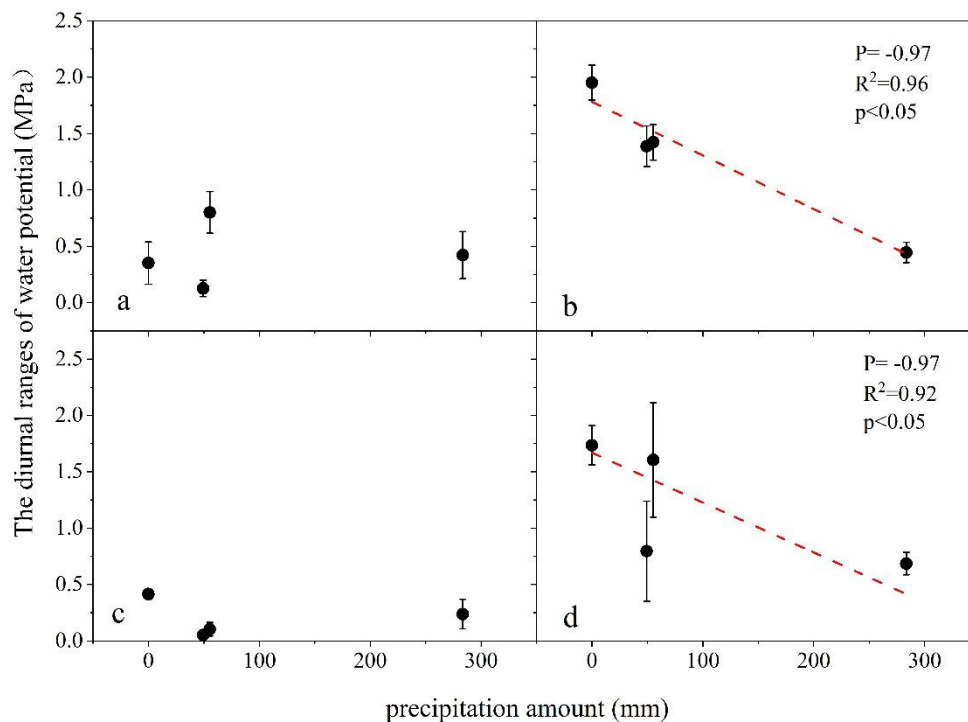
368 The response of the diurnal ranges of water potential to precipitation amount ten days before

369 sampling were different in two tree species (Fig. 8). The $\Delta\psi$ of *M. philippensis* did not increase

370 from no rain to high rainfall with relatively low values in two habitats. However, the diurnal

371 ranges of water potential for *C. biondii* showed lower values with the precipitation increases in the

372 edaphic and rocky habitat.



373

374 **Fig. 8 Relationships between the diurnal ranges of water potential (mean \pm S.D.) and precipitation amount ten days before**

375 **sampling. P is Pearson correlation, R² represents fitting degree of the relationship between the diurnal ranges of water potential**

376 **and precipitation amount; p is p-value of the fitting (a, *M. philippensis* in edaphic habitat; b, *C. biondii* in edaphic habitat; c, *M.***

377 ***philippensis* in rocky habitat; b, *C. biondii* in rocky habitat)**

378

379 **4 Discussion**

380 **4.1 Water uptake of tree species in two habitats**

381 The variation of plant water uptake depth in two habitats was consistent, except the Jun.
382 sampling with high antecedent precipitation. These two natural species, growing at the foot of the
383 slope, mainly absorbed soil water from shallow layers in the early and middle wet season, and
384 switched for deeper layers in the late wet season. This water use pattern has also been found in
385 other natural species and plantations in the similar study area (Deng et al., 2020; Liu et al., 2021).
386 But it was noted that the plants utilized shallow soil water rather than deep or water (no spring
387 flowing) in the early wet season with 20-day drought, which was inconsistent with other studies in
388 climate region (Deng et al., 2020; Liu et al., 2019b). For one thing, although the mean soil
389 moisture was lower compared to other sampling, the VWC is still higher than that in semiarid
390 climate region in the wet season (Tokumoto et al., 2014; Wang et al., 2020a). Meanwhile, with
391 relatively lower wilting coefficient and high spatial heterogeneity (Fu et al., 2016), the shallow
392 layers could also provide enough available water for plants. For another, this water use
393 characteristics is adaptation for plants to save more energy for growth in the early wet season.
394 Both *M. philippensis* and *C. biondii* grow quickly with high energy consuming in May as well as
395 the early growing season. Although the deep soil layer has higher VWC, the energy required to
396 take up water from the deep layer is greater than that of the upper layers (Liu et al., 2020a;
397 Williams and Ehleringer, 2000). Thus, the trees extracted shallow soil water to relieve excessive
398 energy consumption through physiological adjustments (Li et al., 2021; Moreno-Gutiérrez et al.,
399 2012; Renninger et al., 2014). Previous studies showed that the plant species adjusted their
400 hydraulic strategies, such as diurnal ranges of water potential, water use efficiency, in response of

401 the environment changes (Hochberg et al., 2018; Liu et al., 2012; Nie et al., 2019a). In our study,
402 *M. philippensis* and *C. biondii* exhibited the highest diurnal ranges of leaf water potential and leaf
403 $\delta^{13}\text{C}$ in the early wet season with 20-day droughts, indicating that they tried their best to absorbed
404 enough shallow soil water to balance carbon-water relations in tandem with high leaf-level
405 intrinsic water use efficiency (WUEi) (Table S2). In the middle and late wet season, plants water
406 uptake depth was from shallow to deeper layers. Soil water available may be the mainly reasons
407 for the water use pattern (Gaines et al., 2016; Zhan et al., 2019).

408 When the antecedent precipitation was much high in the middle wet season, the plants still
409 absorbed water from shallow layers in rocky habitat, but in edaphic habitat, they switched to deep
410 layers soil water. These results suggested that the response of plant water source proportion in
411 each soil layers to antecedent precipitation amount were distinct in two habitats. Water availability
412 is the most important factor influencing the plants water uptake depth (Ding et al., 2020;
413 Sanchez-Costa et al., 2015). Soil variabilities such as soil texture, bulk density, affected water
414 holding capacity and migration along with soil profiles, and then regulated plant water use (Liu et
415 al., 2021; Yang et al., 2019). The bulk density in the rocky habitat is lower than that in edaphic
416 habitat, promoting the high water holding capacity. While in the thin deep layers with large cracks
417 and crevices in the rocky habitat, moisture leaks into the layer flowing through the spring. The
418 thick deep layer with fine cracks in the edaphic habitat, the storage water was higher than shallow
419 layer after large and continuous precipitation. Therefore, the soil properties discrepancies are the
420 main reasons for the different soil water available along the profile in two habitats. In addition,
421 plant attributes also play critical role in affecting plant water use pattern in community scale.
422 Many researchers found that the plants species in a certain community had overlapping water

423 sources and enhanced water competition (Magh et al., 2020; Querejeta et al., 2007; Wolf et al.,
424 2016). In edaphic habitat, the plant water competition will aggravate especially for the shallow
425 water sources. Because the biodiversity and abundance will increase after high and continuous
426 precipitation in the middle wet season, exhibiting the herbaceous and undershrub growing crazy
427 and absorbing for shallow soil water (Jiang et al., 2020; Moran et al., 2009). Hence, the tree
428 species would switch to the deep and stable water sources to reduce the competition and risky and
429 maintain high transpiration demand. While in the rocky habitats with low biodiversity and
430 abundance for herbaceous (Nie et al., 2019b), the shallow layers water was enough for their
431 transpiration. Furthermore, the low diurnal ranges of water potential of *M. philippensis* and *C.*
432 *biondii* also demonstrated that they were both in sufficient water supply in the two habitats (Fig.
433 6).

434 **4.2 Water use characteristics and physiological changes in the different tree species**

435 The two coexisting plants either in the edaphic or rocky habitat exhibited no significant
436 differences in water uptake pattern with seasonal changes, indicating that they had the same
437 eco-hydrological niche and no water source segregation. This result was inconsistent with a
438 previous study in the similar study area, which found that the tree and shrub had different water
439 use sources in the dry season (Nie et al., 2012). But other studies showed that the coexisting
440 species usually had water competition in mixed stand in non-karst regions (Liu et al., 2020b;
441 Magh et al., 2020). Nie et al. (2018) investigated three communities on adjacent rocky karst hill
442 slopes, and found that different species within each community all exhibited a similar water
443 source. Du et al. (2021) studied three karstic climax forest communities of a typical karst hill, also
444 came to the same results. The similar root distribution of *M. philippensis* and *C. biondii* maybe the

445 main reason for the same water uptake pattern (Ellsworth and Sternberg, 2015; Schwinning, 2010).
446 Hence, the interspecific different in community was relatively low in subtropical monsoon climate
447 region. However, as the above analysis, the water use pattern was different between the edaphic
448 and rocky habitats for the same species. This suggested that the habitats may cause more influence
449 for plant water use than the interspecific difference in community, especially when the antecedent
450 precipitation was high.

451 Although the water uptake depth was similar for the two species, the two species had different
452 physiological response to the water uptake. In our study, *M. philippensis* maintain the little diurnal
453 ranges of water potential, high leaf $\delta^{13}\text{C}$ values, and much branching from the base of the trunk,
454 while *C. biondii* had the inverse characteristics. Meanwhile, the $\Delta\psi$ of *C. biondii* under two
455 habitats were negatively associated with antecedent precipitation amount, but the significant
456 relationship was not observed in *M. philippensis*. Wang et al. (2020a) also found the same results
457 of two species in the mixed plantation in the Loess Plateau. While Moreno-Gutiérrez et al. (2012)
458 found the existence of species-specific eco-physiological niche segregation in dryland plant
459 communities. A possible explanation was that the interspecific competition in the same habitat
460 makes each tree species establish different hydrological niches for water uptake (González de
461 Andrés et al., 2018; Williams and Ehleringer, 2000). However, in our study, there are significant
462 eco-physiological niche segregation but no ecohydrological segregation for two species in the
463 same habitat. This discrepancy may be attributed to sufficient precipitation and soil water
464 availability for ecohydrological non-segregation (Asbjornsen et al., 2011) and interspecific
465 different for eco-physiological segregation (Sánchez-Costa et al., 2015).

466 **4.3 Implications for plant water adaptation under precipitation changes**

467 With the increasing temperatures, precipitation patterns change seasonally and become more
468 variable (Konapala et al., 2020), which could lead to the increase in either the severity of drought
469 or extreme precipitation, especially in the growing season (Allen et al., 2010; Fan and Thomas,
470 2013; Messmer and Simmonds, 2021). When the drought or extreme precipitation occurs, soil
471 water availability may influence the plants water use strategies.

472 In our study, plants absorbed shallow layers soil water by increasing the diurnal ranges of water
473 potential for relieving the energy consumption to supply leaf rapid growth in the early wet season
474 with 20-day drought. The tree species seek for the balance of water uptake and growth through the
475 relatively high water use efficiency (Keep et al., 2021). However, if the drought is prolonged, soil
476 moisture declines and fails to supply water for plants. Ding et al. (2020) conducted a 135-day
477 rainfall exclusion experiment in the same catchment, and found two adverse responses along with
478 different physiological characteristic to the severe water limitation: canopy defoliation and/or
479 mortality and survive. In our study, *C. biondii*, as the profligate water use species, will exhibited
480 larger $\Delta\psi$ and lower ψ_{md} for absorbing water sources (Ding et al., 2020). Once the ψ_{md} is lower
481 than the hydraulic trait values, the species may suffer from hydraulic risky for xylem-cavitation
482 and leaf turgor loss (Choat et al., 2012; Magh et al., 2020). On the contrary, *M. philippensis*
483 displayed stable $\Delta\psi$ in the sampling period, indicating the rigorous stomatal control (Renninger et
484 al., 2015). The tree growth rate of *M. philippensis* may slow due to the reduction in shallow soil
485 water sources and the stoma close advanced.

486 Except for the drought in growing season, the frequency of rainstorm and extreme precipitation
487 also has been increasing recently (Berg et al., 2013; Min et al., 2011). The heavy rainfall with long
488 period caused the surface and subsurface runoff along the slope (Wang et al., 2020b) and flood in

489 the depression in subtropical region (Chen et al., 2017). Plants are the main conduit for returning
490 terrestrial water to the atmosphere, thereby exerting a strong effect on hydrologic fluxes of the
491 terrestrial-atmospheric system (Asbjornsen et al., 2011). Hence, the vegetation ecohydrological
492 functions and physiological responses raised more and more concerned in the extreme climate
493 (Geekiyanaage et al., 2019). In our study, the plants mainly utilized for deep layer soil water in the
494 edaphic habitat and the diurnal ranges of water potential of *C. biondii* were shrunken when the
495 precipitation was extreme high before ten days sampling. These results illustrated that the tree
496 species could adjust their water use strategies and increase the ecohydrological linkages between
497 ecosystem and the deep-layer system (Du et al., 2021).

498 **5 Conclusions**

499 In this study, stable isotope technique and pressure chamber were applied to detect the seasonal
500 water use characteristic of two common tree species in edaphic and rocky habitats on the
501 subtropical monsoon climate region. The results showed that the two species mainly absorbed soil
502 water from shallow layers and switched for deeper layers during the late of the wet season in both
503 habitats. But the plant water sources were different in edaphic and rocky habitats when the
504 antecedent precipitation was much high, deep layers soil water in the former and still shallow
505 layers in the latter. The two species had no significant differences in water uptake depth, but
506 notably distinction in the diurnal water potential ranges in the same habitat. These results indicate
507 that there is significant eco-physiological niche segregation but no ecohydrological segregation for
508 co-existing species in communities. Besides, antecedent precipitation amount and habitat
509 differences were the main factors influencing the plant water uptake depth. While the relationship
510 between leaf physiological traits and water availability was affected by the species types, rather

511 than the habitats. Thus, during the long drought in growing season, there are probable divergent
 512 responses of *M. philippensis* and *C. biondii*, such as growth restriction and hydraulic failure. But
 513 when the precipitation is heavy and long, these natural species could increase the ecohydrological
 514 linkages between ecosystem and the deep-layer system in edaphic habitat.

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520 **Declarations of interest**

521 We declare that we have no financial and personal relationships with other people or
 522 organizations that can inappropriately influence our work, there is no professional or other
 523 personal interest of any nature or kind in any product, service and/or company that could be
 524 construed as influencing the position presented in, or the review of, the manuscript entitled “Water
 525 use characteristics of the common tree species in rock-dominated and thin-soil environments in
 526 subtropical monsoon climate region”.

527 **Supplementary Material**

528

529 **Table S1 Relationship between water uptake depth and the diurnal ranges of water potential for *M.***

530 ***philippensis* and *C. biondii* in edaphic and rocky habitats.**

Pearson Correlation	Edaphic habitat (-MPa)		Rocky habitat (-MPa)	
	<i>M. philippensis</i>	<i>C. biondii</i>	<i>M. philippensis</i>	<i>C. biondii</i>
Shallow layer	-0.41, p>0.05	0.77, p>0.05	0.328, p>0.05	-0.825, p>0.05
Middle layer	0.152, p>0.05	-0.837, p>0.05	-0.411, p>0.05	-0.78, p>0.05
Deep layer	0.441, p>0.05	-0.562, p>0.05	-0.064, p>0.05	-0.886, p>0.05

531

532 **Table S2 Comparisons of $\delta^{13}\text{C}$ isotopic values for *M. philippensis* and *C. biondii* in edaphic and rocky**
 533 **habitats.**

Pearson Correlation	Edaphic habitat (-MPa)		Rocky habitat (-MPa)	
	<i>M. philippensis</i>	<i>C. biondii</i>	<i>M. philippensis</i>	<i>C. biondii</i>
May	-25.78±0.85Aa	-26.67±0.73Aa	-25.66±0.57Aa	-26.93±0.05Aa
Jun.	-27.07±0.41Ba	-27.75±0.85Ba	-27.95±1.26Ba	-28.31±0.18Aa
Aug.	-27.65±0.69Ba	-28.8±0.42Ba	-27.43±0.18Ba	-29.51±0.27Bb
Oct.	-27.22±0.47Ba	-28.23±0.18Bb	-27.86±0.64Ba	-28.86±0.25Ba

534 Note: Capital letters within a column indicate significant differences of the same tree species among different
 535 seasons at the 0.05 level; lowercase letters indicate significant differences between *M. philippensis* and *C. biondii*
 536 in the same habitat at the 0.05 level.

537

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