

1 **Manuscript title**

2 Coffee and shade trees show complementary use of soil water in a traditional agroforestry  
3 ecosystem

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19

20 **Abstract**

21 Globally, coffee has become one of the most sensitive commercial crops being affected by climate  
22 change. Arabica coffee (*Coffea arabica*) grows in traditionally shaded agroforestry systems in  
23 tropical regions and accounts for ~70% of the coffee production worldwide. Nevertheless, the  
24 interaction between plant and soil water sources in these coffee plantations remains poorly  
25 understood. To investigate the functional response of dominant shade trees species and coffee (*C.*  
26 *arabica* var. *typica*) plants to different soil water availability conditions, we conducted a study during  
27 a near normal and a more pronounced dry season (2014 and 2017, respectively) and a wet season  
28 (2017) in a traditional coffee plantation in central Veracruz, Mexico. For the different periods, we  
29 specifically investigated the variations in water sources and root water uptake via MixSIAR mixing  
30 models that use  $\delta^{18}\text{O}$  and  $\delta^2\text{H}$  stable isotope composition of rainfall, plant xylem and soil water. To  
31 further increase our mechanistic understanding about root activity, the distribution of belowground  
32 biomass and soil macronutrients were also examined and considered in the model as prior  
33 information. Results showed that, over the course of the two dry seasons investigated, all shade tree  
34 species (*Lonchocarpus guatemalensis*, *Inga vera* and *Trema micrantha*) relied on average, on water

35 sources from intermediate (>15 to 30 cm depth:  $58 \pm 18\%$  (SD)) and deep soil layers (> 30 to 120 cm  
36 depth:  $34 \pm 21\%$ ), while coffee plants used much shallower water sources (< 5 cm depth:  $42 \pm 37\%$   
37 and 5-15 cm depth:  $52 \pm 35\%$ ). In addition, in these same periods, coffee water uptake was influenced  
38 by antecedent precipitation, whereas trees showed little sensitiveness to antecedent wetness. Our  
39 findings also showed that during the wet season coffee plants substantially increased the use of near  
40 surface water (+56% from < 5 cm depth), while shade trees extended the water acquisition to much  
41 shallower soil layers (+19% from < 15 cm depth) in comparison to drier periods. Despite the plasticity  
42 in root water uptake observed between canopy trees and coffee plants, a complementary use of soil  
43 water prevailed during the dry and wet seasons investigated. However, more variability in plant water  
44 sources was observed among species in the rainy season when higher soil moisture conditions were  
45 present and water stress was largely absent.

46

47 *Key words: Coffea arabica; water stable isotopes, roots, nutrients, clay-rich soils, MixSIAR,*

48 *Mexico*

## 49 **1. Introduction**

50 Coffee agroforestry systems are highly valued because of their ecological, environmental,  
51 economic and social benefits (Mas and Dietsch, 2004; Perfecto et al., 2007; Tschardt et al., 2011).  
52 Moreover, shade coffee of the species Arabica (*Coffea arabica*) accounts for ~ 70% of the total coffee  
53 production (USDA, 2017). Although Arabica coffee is mainly grown in tropical montane regions, it  
54 is cultivated under a wide range of climatic and soil conditions (Jha et al., 2014). Coffee Arabica  
55 plantations can be broadly classified as traditional or modern coffee systems, according to vegetation  
56 composition and structure and management practices (Moguel and Toledo, 1999). In the traditional  
57 systems, coffee plants are cultivated under a diverse canopy of native and/or introduced shade tree  
58 species. In contrast, monoculture coffee plantations exemplify the modern cultivation scheme, in  
59 which the shade is provided by a single commercial tree species. The use of agrochemicals is also  
60 typically required in this type of plantation (Moguel and Toledo, 1999).

61 Until recently, the vast majority of Arabica coffee was cultivated in traditionally managed  
62 shaded coffee plantations, which have lower production costs and enhanced biodiversity, carbon  
63 sequestration, soil fertility and biological pest control in comparison to modern systems (Greenberg  
64 et al., 1997; Perfecto et al., 2002; Kellermann et al., 2008). However, coffee management practices  
65 have become more intensive promoting the replacement of native trees with fast-growing  
66 monospecific timber species (i.e. *Cedrela odorata*, *Eucalyptus deplupta*, *Hevea brasiliensis*) (Nath et  
67 al., 2011).

68 Growing a crop in association with shade trees inevitably leads to some degree of competition  
69 for the above-ground (light) and below-ground (water and nutrients) resources (Monteith et al., 1991).  
70 In an agroforestry system, the outcome of competition for light is relatively predictable due to the  
71 hierarchical structure of the canopy (i.e., shade trees intercept part of the sunlight, thereby reducing  
72 the amount available for the understory crop). Conversely, competitive interactions for below-ground  
73 resources can be much more diverse and complex. The central hypothesis of agroforestry underscores  
74 that crops and trees are complementary in their use of soil water (Cannell et al., 1996), however the  
75 degree to which this occurs will be largely controlled by the spatial and temporal patterns of resource  
76 availability, root distribution and root activity, which in turn depend on factors such as climate, soil  
77 conditions, crop and tree species, and plantation age, density and management practices (Beer et al.,  
78 1998; Lehmann, 2003; van Noordwijk et al., 2015). In addition, below-ground competitive  
79 interactions for water and/or nutrients are much more difficult to elucidate than above-ground  
80 relationships. So far, the most common approach is to measure the distribution of root abundance of  
81 crops and trees, and examine to what extent they overlap or are separated (e.g., Schaller et al., 2003;  
82 van Kanten et al., 2005). An important limitation of this method is, however, that the spatial

83 distribution of roots does not always mirror the actual resource capture along the soil profile (Dawson  
84 et al., 2002; Lehmann, 2003). Another approach is to examine the vertical patterns of soil water  
85 (Cannavo et al., 2011; Padovan et al., 2015) or nutrient (Schroth et al., 2000, cited in Lehmann, 2003)  
86 depletion. However, these methods are problematic because they cannot provide information on  
87 whether resource depletion is caused by the crop, the trees, or both (Cannavo et al., 2011; Padovan et  
88 al., 2015). Recently, the use of hydrogen ( $\delta^2\text{H}$ ) and oxygen ( $\delta^{18}\text{O}$ ) water stable isotope techniques in  
89 combination with mixing models based on Bayesian theory has proved to be a powerful tool for  
90 quantifying the proportions and probability distributions of different water sources to plant uptake  
91 across different ecosystems and regions (Barbeta et al., 2015; Beyer et al., 2018; Penna et al., 2018),  
92 with the potential to largely overcome the above-mentioned limitations (Dawson et al., 2002;  
93 Lehmann, 2003; van Noordwijk et al., 2015). Although rarely implemented, including nutrient and  
94 root distribution data along the soil profile to inform these models could provide more comprehensive  
95 insights into depth of plant water uptake (cf. Muñoz-Villers et al., 2018).

96 To date, research into plant-soil interactions and plant water source partitioning in coffee  
97 agroforestry systems is extremely scarce. To our knowledge, only five studies have investigated the  
98 water sources of shade trees and coffee shrubs using either information on the isotopic composition  
99 of plant xylem and bulk soil water (Wu et al., 2016), soil water depletion (Cannavo et al., 2011;  
100 Padovan et al., 2015) or root distribution (Schaller et al., 2003; van Kanten et al., 2005). Moreover,  
101 all these studies have been carried out in intensive monospecific plantations characterized by high  
102 coffee planting densities ( $\sim 4000\text{--}5000$  shrubs  $\text{ha}^{-1}$ ), low density ( $\sim 150\text{--}280$  trees  $\text{ha}^{-1}$ ) and very  
103 low diversity (1-2 species) of shade trees. While recognizing the limitations of some of the methods  
104 used in these previous studies, the available information suggests that competition for water between  
105 coffee and trees can be strong at sites with a pronounced seasonal dry period (Wu et al., 2016;  
106 Padovan et al., 2015), while it seems to be virtually absent at sites with no or a relatively short dry  
107 season (Schaller et al., 2003; Cannavo et al., 2011). Further, although most coffee roots are usually  
108 located in the upper soil layers ( $< 30$  cm depth; van Kanten et al., 2005, and references therein), the  
109 plant and soil interactions for water during the dry season seem to occur below the main crop rooting  
110 zone ( $> 30$  cm depth) (Wu et al., 2016). The latter reflects the ability of coffee to develop an extensive  
111 root system, and to increase the root water uptake at greater soil depths once the available water has  
112 been depleted in shallower layers (Huxley et al., 1974, cited in Lehmann, 2003).

113 Currently, we lack of information on plant water sources in traditional shade coffee  
114 plantations. In these agroforestry systems, the higher density and diversity of shade trees could  
115 potentially lead to stronger and more diverse tree-crop interactions (van Noordwijk et al., 2015). On  
116 the other hand, the dense tree canopy reduces light availability and hence limits coffee water use. This

117 could lead to a lower soil water demand and thus increased plant water availability during the dry  
118 season.

119 Further, ecohydrological research in these shade coffee systems is becoming increasingly  
120 important since trees have been promoted as a strategy for mitigating and adapting to future climate  
121 (Schroth et al., 2009; Vaast et al., 2016; Rice, 2018). Shaded coffee plantations store more carbon  
122 than sun-grown coffee systems, thereby contributing to the reduction of greenhouse gases (Vaast et  
123 al., 2016; Rice, 2018, and references therein). In addition, the tree canopy provides some level of  
124 protection against the rising mean and maximum air temperatures (Baker and Hagggar, 2007; Schroth  
125 et al., 2009; Vaast et al., 2016), which in recent modeling studies have been pointed out as the key  
126 climatic changes affecting coffee growth, yield and quality (Schroth et al., 2009; Baca et al., 2014;  
127 Bunn et al., 2015). Although there are important differences across sites, rainfall is also predicted to  
128 decrease and become more variable in many of the world's coffee-growing regions. For example,  
129 Giorgi (2006) estimated that rainfall will decrease by about 17% (per 100 years) during the dry season  
130 and by about 9% during the wet season in Mexico and Central America. Similarly, predictions by  
131 Karmalkar et al. (2011) for the same regions pointed out changes in rainfall of -24% to +8% (per 100  
132 years) during the dry season and of -39% to -1% during the wet season. As such, if warming is  
133 accompanied by decreases in rainfall, this could lead to, or exacerbate, competition for water sources  
134 between coffee shrubs and shade trees (Baker and Hagggar, 2007), which in turn could affect the long-  
135 term sustainability of these agroecosystems.

136 Mexico is among the largest shade coffee producers in the world, and the central region of  
137 Veracruz constitutes the second most important coffee zone in the country. In this area, we selected  
138 a representative traditional shade coffee plantation to investigate plant water sources of dominant  
139 shade trees species and coffee (*C. arabica* var. *typica*) shrubs under different conditions of soil water  
140 availability. During a near normal and a more pronounced dry season (2014 and 2017, respectively)  
141 and a wet season (2017), variations in depth of plant water uptake were examined using the stable  
142 isotopic composition ( $\delta^{18}\text{O}$  and  $\delta^2\text{H}$ ) of rainfall, plant xylem and soil water in combination with a  
143 Bayesian mixing model (MixSIAR), along with microclimatic and soil moisture measurements. To  
144 further increase our understanding about root activity and water uptake, the distribution of roots and  
145 macronutrients along the soil profile were also examined and considered in the mixing model as prior  
146 information. Specifically, we addressed the following questions:

147

- 148 1. Does a complementary water use strategy between shade trees and coffee shrubs prevail  
149 over competition in a traditional shaded agroforestry system?

- 150 2. Does competition exist for water sources among tree and coffee species during more  
151 pronounced dry periods?  
152 3. What are the seasonal patterns in plant-water source partitioning?  
153

## 154 **2. Materials and methods**

### 155 *2.1 Study site*

156 The research was carried out in the “La Orduña” coffee plantation (~100 ha) located on a flat  
157 plateau at an elevation of 1210 m a.s.l. on the eastern slopes of the Cofre de Perote mountain (19°28'  
158 N, 96°56' W) in central Veracruz State, Mexico (Fig. 1). The coffee plantations in this region occur  
159 between elevations of 1000 and 1350 m a.s.l. (Hernández-Martínez et al., 2013; Marchal and Palma,  
160 1985).

161 The climate is classified as temperate humid with abundant rains during the summer (García,  
162 1988). Two distinct seasons can be distinguished: (1) a wet season (May–October), during which  
163 rainfall is associated primarily with cumulus and cumulonimbus clouds formed during convective  
164 and orographic uplift of the moist maritime air masses brought in by the easterly trade winds; and (2)  
165 a (relatively) dry season (November–April), during which most rainfall falls from stratus clouds  
166 associated with the passage of cold fronts (Báez et al., 1997). Mean annual rainfall measured nearby  
167 the study site during the period 1971–2000 was 1765 mm, with on average 389 mm falling during  
168 the dry season and 1376 mm falling during the wet season (SMN, 2018). Mean annual temperature  
169 over this period was 19.5 °C, with a minimum and maximum monthly average value of 15.5 and  
170 22.5°C observed in January and May, respectively (SMN, 2018). Annual potential evapotranspiration  
171 (ET<sub>0</sub>) is about 1120 mm (Holwerda et al., 2013).

172 The investigated shade coffee plantation is a so-called traditional commercial polyculture  
173 system (*sensu* Moguel and Toledo, 1999), which was established more than 80 years ago. The tree  
174 canopy was diverse and consisted predominantly of the species *Inga spp.*, *Citrus spp.*, *Lonchocarpus*  
175 *guatemalensis*, *Trema micrantha* and *Enterolobium cyclocarpum* (Holwerda et al., 2016). The shade  
176 trees were planted at a density of ca. 500 ha<sup>-1</sup>, and currently form a canopy of about 14 m high. The  
177 Arabica coffee plants were of the variety *typica*. *Typica* –a tall cultivar of *Coffea arabica*– was the  
178 first coffee variety that arrived from Ethiopia to Mexico (Renard, 2010); it has bronze-tipped young  
179 leaves and the berries are large. Plants of *typica* variety are tolerant to conditions of low soil fertility  
180 and drought, but vulnerable to most pests and diseases (Escamilla et al., 2005). In the study site, this  
181 cultivar was planted approximately 20 years ago at a density of about 1700 shrubs ha<sup>-1</sup>, currently  
182 having an average height of ~ 2 m. In this region, the coffee flowering occurs in March or April, fruit  
183 development between May and October, and ripening and harvest between October and February

184 (Villers et al., 2009). The management of the plantation involves weed control practices and selective  
185 pruning of mature coffee plants and shade trees at irregular times once every ~ 7 years (cf. Hernández-  
186 Martínez et al., 2009). No pruning activities occurred during or in between our study periods. A  
187 photograph of the coffee plantation is provided in the Supplementary Material.

188 The soil type is an Andic Acrisol derived from volcanic ashes. Soil profiles (~150 cm) are  
189 multilayered (A, B1/BT and BC) and have clay (~ 65%) as the dominant texture across all layers. A  
190 general description of the soil profile showed a dark brown to dark yellowish brown, clay silty organic  
191 A horizon (0–20 cm) overlying a dark yellowish brown, clay silty sand B1/BT horizon (20–135 cm),  
192 followed by a dark yellowish brown, clay sandy BC horizon (>135 cm). Average soil bulk densities  
193 and porosities were 1.2 gr cm<sup>-3</sup> and 63%, respectively, along the A and B horizons (Holwerda et al.,  
194 2013). The underlying material consists of deeply weathered old lava and sandy-gravelly pyroclastic  
195 flow deposits (Rodríguez et al., 2010). Soils were mostly covered by a thin (1-2 cm) but continuous  
196 layer of litter.

197

## 198 **2.2 Hydrometeorological measurements**

199 During the study period, rainfall and microclimate conditions were continuously monitored  
200 above the canopy in an 18 m high tower, located in the southwestern part of the coffee plantation.  
201 Rainfall ( $P$ , mm) was measured using a TR-525 M tipping bucket rain gauge (Texas Electronics,  
202 USA). Temperature ( $T$ , °C) and relative humidity (RH, %) were measured using a HC2-S3 probe  
203 (Rotronic, USA). Data were recorded every 30 s, accumulated ( $P$ ) or averaged values (all other  
204 parameters) were stored at 5-min intervals using a CR1000 datalogger (Campbell Scientific Ltd.,  
205 USA).

206

## 207 **2.3 Isotope sampling**

208 To examine the water sources of overstory shade trees and understory coffee shrubs, plant  
209 tissue and soil samples were collected for isotope analysis at the middle (Jan. 23) and end (Apr. 11  
210 and 26) of the 2014 dry season. In 2017, the dry season was warmer and drier offering the opportunity  
211 to examine the vegetation responses to more pronounced dry conditions. Therefore, a second  
212 sampling campaign was carried out to collect plant and bulk soil samples at the middle (Feb. 27), end  
213 (Apr. 5) and late end (May. 20) of the 2017 dry season. Another sampling was carried out in the  
214 middle of the 2017 wet season (Aug. 4) to evaluate plant-soil water uptake patterns at higher soil  
215 water availability conditions.

216 In all seven samplings, xylem samples were obtained from three individuals of each of the  
217 three dominant shade tree species (*Lonchocarpus guatemalensis*, *Inga vera* and *Trema micrantha*) by

218 extracting ~5-6 cm cores using a Pressler increment borer inserted at 1.2 m above ground ( $n = 60$   
219 samples of trees in total). On each occasion, xylem samples were taken from the same individuals but  
220 from various aspects of the trunk. The bark was immediately removed after core extraction to avoid  
221 contamination of phloem water. For the coffee plants, samples were obtained from ~6 cm segments  
222 of mature suberized branches that were cut near the main stem of several shrubs each time. The bark  
223 (~1mm thick) and cambium were not stripped from the coffee branches, to avoid exposure of the  
224 samples to evaporation. All coffee plants were sampled randomly ( $n = 40$  samples of coffee shrubs  
225 in total). During the 2014 and 2017 dry seasons, sampling of coffee shrubs involved 5-6 individuals  
226 each time. Since only one sampling occasion was performed during the 2017 wet season, a larger  
227 number of individuals (10) was sampled to reduce the uncertainties associated with different sampling  
228 sizes between wet and dry seasons respectively. For each tree, we measured diameter at breast height  
229 (DBH) and height, and for the coffee plants the diameter of the main stem was measured below its  
230 bifurcation in small branches (Table 1).

231 Bulk soil samples were collected at three locations and at depths of 5, 15, 30, 60, 90 and 120  
232 cm, using a hand auger ( $n = 126$  samples of soil in total). Auger sampling points were located so that  
233 each of the sampled shade trees and coffee plants had one soil sampling point within a 3 m radius.

234 Samples of xylem and bulk soil were collected during the morning and early afternoon  
235 (between 8:30 to 13:30 hrs), and each sampling campaign was preceded by at least 6 days up to 22  
236 days without or with minimum accumulated rainfall ( $< 5$  mm). All xylem and soil samples were  
237 collected quickly and carefully and stored in water-tight vials to avoid any evaporation (see section  
238 below).

239 To establish the local meteoric water line and compare soil water sources with recent rainfall,  
240 bulk samples of rainfall ( $n = 80$  in total) were collected weekly at a nearby (~ 5 km) meteorological  
241 station over the course of the two years studied (Nov. 2013 – Oct. 2014 and Nov. 2016 – Oct. 2017)  
242 as part of a long-term isotope sampling of precipitation (cf. Muñoz-Villers et al., 2018).

243

#### 244 ***2.4 Isotope collection and analysis***

245 Samples of precipitation, plant xylem and bulk soil for isotope analysis were collected in 30-  
246 ml borosilicate glass vials sealed with polycone caps to prevent evaporation. All samples were  
247 refrigerated until extraction and analysis at the Center of Stable Isotope Biogeochemistry (CSIB) at  
248 the University of California-Berkeley, USA.

249 Xylem and soil samples were extracted using cryogenic vacuum distillation (temperature:  
250  $100 \pm 1.1^\circ\text{C}$ , vacuum:  $3 \pm 1.5$  Pa and time: 60-70 min) following the method of West et al. (2006).  
251 The  $\delta^2\text{H}$  and  $\delta^{18}\text{O}$  isotopic compositions of extracted water samples were then determined using an



252 isotope-ratio mass spectrometer (Thermo Delta Plus XL, Thermo Fisher Scientific, USA). The  
253 analytical precision of the instrument was  $\pm 0.60\text{‰}$  (1 SD) for  $\delta^2\text{H}$  and  $\pm 0.12\text{‰}$  (1 SD) for  $\delta^{18}\text{O}$ .  
254 Samples of precipitation were analyzed for  $\delta^2\text{H}$  and  $\delta^{18}\text{O}$  using a laser water isotope analyzer (L2140-  
255 i) from Picarro Inc. (Santa Clara, CA, USA) in high precision and without Micro-Combustion Module  
256 mode. The analytical precision was  $\pm 0.65\text{‰}$  (1 SD) and  $\pm 0.20\text{‰}$  (1 SD) for  $\delta^2\text{H}$  and  $\delta^{18}\text{O}$ ,  
257 respectively.

258 The isotope values are expressed in delta notation (‰) relative to Vienna Standard Mean  
259 Ocean Water (VSMOW). To evaluate evaporative enrichment in the soil and xylem water isotopes  
260 relative to rainfall, we calculated the deuterium-excess parameter ( $d = \delta^2\text{H} - 8 * \delta^{18}\text{O}$ ; Dansgaard,  
261 1964).

262

### 263 ***2.5 Soil sampling and laboratory determinations***

264 To determine volumetric soil water content (SWC), samples were collected at 5, 15, 30, 60,  
265 90 and 120 cm depth from each of the three boreholes excavated during the soil isotope samplings.  
266 Soil moisture content was determined gravimetrically and converted to volumetric values by using  
267 bulk density of the soil sample. In addition, to determine the antecedent moisture conditions for the  
268 15 days prior to each sampling date, an antecedent precipitation index (API) was calculated following  
269 Viessman et al. (1989).

270 To examine pH and N, P and K macronutrient concentrations along the soil profile, soil  
271 samples were collected at 5, 15, 30, 60, 90 and 120 cm depth from each borehole ( $n = 3$  samples per  
272 soil depth) during three isotope sampling campaigns: Apr. 11, 2014 (dry season), Feb. 27, 2017 (dry  
273 season) and Aug. 4, 2017 (wet season). Samples ( $n = 18$ ) for determining other chemical properties  
274 were collected at the same depths in soil profiles. All samples were first air-dried and then sieved  
275 using 2 mm screens. Soil pH was determined using a glass electrode pH meter in a 1:2 soil: water  
276 ratio. Organic matter (OM) was determined by the Walkley-Black method. Total carbon (C) and total  
277 nitrogen (N) were measured using a TruSpec dry combustion CN analyzer (LECO, USA). Extractable  
278 phosphorus (P) was determined by the Bray I method (Bray and Kurtz, 1945). Exchangeable cations  
279 ( $\text{Ca}^+$ ,  $\text{Mg}^+$ ,  $\text{K}^+$ ,  $\text{Na}^+$ ) were determined by extracting soil with 1 M  $\text{NH}_4\text{OAc}$  (pH 7.0).  $\text{Ca}^+$  and  $\text{Mg}^+$   
280 were analyzed using atomic absorption spectrometry and  $\text{K}^+$  and  $\text{Na}^+$  were analyzed using flame  
281 photometry. Soil cation exchange capacity (CEC) was determined by the ammonium acetate 1N (pH  
282 7.0) method (Van Reeuwijk, 2002) and base saturation (BS) was calculated as the portion of CEC  
283 that is occupied by exchangeable bases:  $(\text{Ca}^+, \text{Mg}^+, \text{K}^+, \text{Na}^+)/\text{CEC}$ .

284

### 285 ***2.6 Root biomass***

286 To examine the root biomass distribution along the soil profile in the study plot, 33 soil cores  
287 were collected using 5 cm diameter and 10 cm long samplers. Soil cores were extracted at 5, 20, 40,  
288 60 and 90 cm depth (from 5 to 40 cm:  $n = 9$  for each depth, and from 60 to 90 cm:  $n = 3$  for each  
289 depth). All cores were processed immediately in the laboratory. Soil samples were first sieved using  
290 2 mm screens to separate the bigger roots. Next, the samples were washed using a fine nylon mesh  
291 sieve, and then separated into diameter classes ( $< 1$  mm, 1–2 mm and  $> 2$  mm) and dried at 70 °C for  
292 48 hours. Root biomass ( $\text{g m}^{-3}$ ) was calculated from the dry weight of the roots and the volume of  
293 the core sampler for each class and soil depth. No differentiation between roots of coffee shrubs and  
294 shade trees was made.

295

## 296 ***2.7 Plant water uptake sources and temporal patterns***

297 The MixSIAR Bayesian mixing model framework (Moore and Semmens, 2008; Stock et al.,  
298 2018) was used to determine the most likely contributions of water sources for the shade tree species  
299 and coffee shrubs sampled over the course of the 2014 (Jan. 23, Apr. 11 and 26) and 2017 (Feb. 27,  
300 Apr. 5, May. 20) dry seasons and the 2017 wet season (Aug. 4). To assess temporal changes of the  
301 different plant water sources, the seven sampling occasions were modeled separately. The mixture  
302 data for the model was the mean xylem water isotopic ( $\delta^2\text{H}$  and  $\delta^{18}\text{O}$ ) composition of the shade tree  
303 species and coffee shrubs, changing accordingly with the sampling date. Based on statistical tests, the  
304 relative contributions of four potential plant water sources were evaluated and restricted to the  
305 following soil groups: near surface water ( $< 5$  cm), shallow (5 to 15 cm), intermediate ( $> 15$  to 30 cm)  
306 and deep soil water ( $> 30$  to 120 cm). For each sampling date, the mean and standard deviation of the  
307 soil water isotope ( $\delta^2\text{H}$  and  $\delta^{18}\text{O}$ ) signatures from the four different grouped soil depths were  
308 introduced into the model, all corresponding to the date of xylem tissue collection.

309 Further, we also considered the use of additional data such as soil macronutrients (N, P, K)  
310 and root biomass information to constrain model estimates by specifying an ‘informative’ prior  
311 distribution of the soil source proportions (Stock et al., 2018). These data were also grouped into four  
312 classes based on the depth of the soil samplings and corresponding largely with the grouping for soil  
313 water: near surface ( $< 5$  cm) shallow (5 to 20 cm), intermediate ( $> 20$  to 40 cm) and deep ( $> 40$  to  
314 120 cm). In addition, the nearest corresponding dry or wet season dataset of soil macronutrients were  
315 used according to the date of sampling. More details on the informative prior parametrization are  
316 provided in the Supplementary Materials. The effect of using these priors (i.e. a weight proportion  
317 before considering the isotope data) on the water sources distribution was then examined by  
318 comparing these with the results of ‘non-informative’ (i.e. all the combinations of proportions of  
319 water sources were equally likely) simulations. The results of each of these model runs were accepted

320 based on the examination of Markov Chain Monte Carlo convergence using the Gelman-Rubin and  
321 Geweke diagnostic tests (Gelman et al., 2014).

322 Furthermore, the effect of isotope fractionation on the quantification of plant water sources  
323 was specifically explored by comparing the results of the informed two-isotope mixing model with  
324 those from a mixing model using only one water stable isotope ratio in the MixSIAR Bayesian  
325 framework. This approach has been used elsewhere (e.g. Evaristo et al., 2017; Barbeta et al., 2019)  
326 to provide some initial insights. Nevertheless, we are aware that the use of a single isotope ratio  
327 approach in a multiple water source model could lead to erroneous results due to the overlap of  
328 feasible solutions with poor constrained of uncertainties (see Parnell et al., 2010).

329 Lastly, the relative contributions of the water sources were compared among shade trees and  
330 coffee shrubs across all sampling dates using factorial ANOVA and Tukey's HSD post-hoc tests. The  
331 analyses were carried out in R Statistical Software version 3.2.4 (R Core Development Team, 2016).

332

### 333 **3. Results**

#### 334 **3.1 Hydrometeorological conditions**

335 Precipitation ( $P$ ) was 1650 mm in the first study year (Nov. 2013 – Oct. 2014) and 1423 mm  
336 in the second study year (Nov. 2016 – Oct. 2017). During the 2013-2014 dry season (Nov – Apr.),  
337 rainfall was 323 mm, and mean daily values of temperature ( $T$ ) and vapor pressure deficit (VPD)  
338 were  $17.6 \pm 3.0^\circ\text{C}$  and  $0.65 \pm 0.39$  kPa, respectively. The lowest monthly  $P$  and the highest  $T$  and  
339 VPD were observed in April at the end of the dry season (Fig. 2a,b). During the 2016-2017 dry season,  
340 rainfall amounted to 235 mm, with lowest monthly values registered in January and February at the  
341 middle of the season (Fig. 2b). Mean daily  $T$  was  $18.3 \pm 2.6^\circ\text{C}$ , with the highest values observed at  
342 the end of the dry period. Generally, VPD was high during the entire dry season ( $0.78 \pm 0.46$  kPa on  
343 average), and reached maximum values in February and May.

344 Compared to long-term (1971–2000) climatic records of the region, rainfall in the first study  
345 year was very close to the mean annual precipitation of 1765 mm (SMN, 2018). In contrast, the second  
346 year was drier ( $\sim 300$  mm less;  $-20\%$ ), especially during the dry season, which had about 40% lower  
347 precipitation than the average value of 389 mm. Also, higher mean monthly temperatures ( $+ 0.54^\circ\text{C}$ )  
348 prevailed across the 2017 dry season in comparison with the 1971–2000 period. Although rainfall  
349 during the 2013-2014 dry season was also about 20% lower than normal, this season was considered  
350 as near average.

351 Rainfall during the 2017 wet season (May – Oct.) was lower in comparison to 2014 (1188  
352 mm vs. 1326 mm, respectively) (Fig. 2b). Further, the mean air temperature and vapor pressure deficit

353 were slightly higher in the 2017 wet season than in the 2014 wet season ( $20.7 \pm 1.6^\circ\text{C}$  and  $0.67 \pm$   
354  $0.25$  kPa vs.  $20.1 \pm 1.5^\circ\text{C}$  and  $0.60 \pm 0.21$  kPa, respectively) (Fig. 2a).

355

### 356 ***3.2 Soil moisture and antecedent precipitation during sampling campaigns***

357 During the 2014 dry season campaign (Jan. – Apr.), mean soil water content (SWC) was on  
358 average  $33.8 \pm 1.7\%$  at 5 cm depth,  $40.2 \pm 14.5\%$  at 15 cm depth,  $38.9 \pm 6.4\%$  at 30 cm depth and  
359  $48.3 \pm 1.4\%$  at 60 to 120 cm depth (Fig. 2b). In comparison, SWC in the 2017 dry season campaign  
360 (Feb. – May.) was lower in the first 30 cm ( $32.5 \pm 3.9\%$ ), meanwhile water content in the deeper  
361 layers was similar ( $49.0 \pm 2.9\%$ ) with respect to the 2014 dry period. In 2014, lowest SWC values  
362 were observed at the end of the dry season (April), whereas the greatest soil moisture depletion in  
363 2017 was registered at the middle of the dry season (February) (Fig. 2b).

364 During the wet season sampling in August 2017, SWC values at 5 cm ( $28.2 \pm 2.6\%$ ), 15 cm  
365 ( $30.9 \pm 4.3\%$ ), 30 cm ( $38.4 \pm 4.8\%$ ) and 60 to 120 cm ( $49.0 \pm 2.9\%$ ) depths were generally higher in  
366 comparison to the 2017 dry period (Fig. 2b). Although the 2017 wet season sampling showed slightly  
367 lower SWC values in the shallower soil layers in comparison to the 2014 dry season, the SWC values  
368 in the deeper layers were higher. For the different samplings, antecedent precipitation conditions  
369 (API) were, respectively, 4, 30 and 13 mm for Jan. 23, Apr. 11 and 26, 2014 and 1, 12, 9 and 43 mm  
370 for Feb. 27, Apr. 5, May. 20 and Aug. 4, 2017.

371

### 372 ***3.3 Stable isotope composition of waters***

373 Over the study periods, a greater range of variation was found in the rainfall isotope  
374 composition of the 2013-2014-year (from  $-126.7$  to  $14.4\%$  for  $\delta^2\text{H}$ ; from  $-17.7$  to  $0.0\%$  for  $\delta^{18}\text{O}$ ) in  
375 comparison to the 2016-2017-year (from  $-113.3$  to  $15.5\%$  for  $\delta^2\text{H}$ ; from  $-15.9$  to  $0.0\%$  for  $\delta^{18}\text{O}$ ) ( $p$   
376  $> 0.05$ ) (Fig. 3). Overall, mean dry season rainfall was significantly more enriched than the mean wet  
377 season rainfall in  $\delta^2\text{H}$  and  $\delta^{18}\text{O}$  ( $p \leq 0.001$ ) (Table 2 and 3). On average, the isotopic compositions of  
378 the dry and wet season rainfall were both more depleted during the second study year than during the  
379 first study year; thus, the local meteoric water line of 2016-2017 had a slightly steeper slope in  
380 comparison to the one for 2013-2014 (Fig. 3). Nevertheless, the range of variation of deuterium excess  
381 values was similar between years ( $9$ – $29\%$  for the first year vs.  $9$ – $31\%$  for the second year; Fig. 3),  
382 and deuterium excess values of rainfall within the dry and wet seasons were not statistically different  
383 ( $p \geq 0.05$ ).

384 For all sampling dates, hydrogen and oxygen isotope composition of bulk soil water showed  
385 a consistent pattern of increasing isotope depletion with soil depth (Supplementary Materials), in  
386 which shallower (5-15 cm) soil water was significantly more enriched than intermediate (15-30 cm)

387 and deeper (30-120 cm) soil water layers ( $p \leq 0.001$ ) (Table 2 and 3; Fig. 3). In correspondence,  
388 lowest values of deuterium excess generally characterized the near surface soil water pool.

389 For the 2014 dry season samplings, bulk soil ranged from  $-83.3$  to  $-11.9\text{‰}$  for  $\delta^2\text{H}$  and from  
390  $-11.1$  to  $-0.9\text{‰}$  for  $\delta^{18}\text{O}$  (Fig. 3a). For the 2017 dry season samplings, bulk soil water showed a  
391 narrower range of variation and more enriched isotope values (from  $-54.8$  to  $-19.1\text{‰}$   $\delta^2\text{H}$  and from  
392  $-7.5$  to  $-1.5\text{‰}$   $\delta^{18}\text{O}$ ) in comparison to 2014 (Fig. 3b). However, statistical differences were only  
393 suggested for the intermediate and deeper soil layers in both water isotopes between the two dry  
394 seasons investigated ( $p \leq 0.001$ ).

395 In the 2017 wet season sampling, bulk soil isotope composition ranged from  $-70.5$  to  $-37.5\text{‰}$   
396 for  $\delta^2\text{H}$  and from  $-8.4$  to  $-4.1\text{‰}$  for  $\delta^{18}\text{O}$  (Fig. 3c), showing significant differences in the shallow,  
397 intermediate and deep soil water pools in comparison to the 2017 dry season ( $p \leq 0.001$ ). In all  
398 sampling periods, bulk soil water across the different depth groups was isotopically distinct from  
399 rainfall during the 2014 and the 2017 dry seasons ( $p \leq 0.001$  for both water isotopes).

400 Across all sampling periods, xylem water of coffee shrubs was more enriched than that of  
401 shade trees ( $p \leq 0.001$ ) (Table 2 and 3; Figure 3). In the 2014 dry season, xylem water isotope values  
402 of shade trees ranged from  $-65.5$  to  $-32.1\text{‰}$  for  $\delta^2\text{H}$  and from  $-7.6$  to  $-3.6\text{‰}$  for  $\delta^{18}\text{O}$ , meanwhile a  
403 larger variation was observed in the xylem water of coffee shrubs (from  $-46.5$  to  $-9.6\text{‰}$   $\delta^2\text{H}$  and  
404 from  $-6.3$  to  $-0.6\text{‰}$   $\delta^{18}\text{O}$ ) ( $p \leq 0.001$ ) (Fig. 3a). Among tree species, *Lonchocarpus guatemalensis*  
405 showed the most depleted xylem water isotope signature ( $-58.1 \pm 4.8\text{‰}$   $\delta^2\text{H}$  and  $-6.8 \pm 0.5\text{‰}$   $\delta^{18}\text{O}$ ),  
406 whereas *Inga vera* had the most enriched values with a greater range of variation ( $-51.0 \pm 10.2\text{‰}$   $\delta^2\text{H}$   
407 and  $-5.3 \pm 1.1\text{‰}$   $\delta^{18}\text{O}$ ). Statistical tests showed that *Inga vera* was different from the other tree species  
408 in  $\delta^{18}\text{O}$  ( $p < 0.05$ ).

409 In the 2017 dry season, the isotopic composition of shade trees varied from  $-56.7$  to  $-34.5\text{‰}$   
410 for  $\delta^2\text{H}$  and from  $-6.0$  to  $-3.2\text{‰}$  for  $\delta^{18}\text{O}$ ; corresponding values for coffee shrubs varied from  $-39.6$   
411 to  $-7.8\text{‰}$  for  $\delta^2\text{H}$  and from  $-4.4$  to  $-1.1\text{‰}$  for  $\delta^{18}\text{O}$  ( $p \leq 0.001$ ) (Fig. 3b). Contrary to 2014, *L.*  
412 *guatemalensis* showed the most enriched isotope value ( $-41.3 \pm 5.7\text{‰}$  for  $\delta^2\text{H}$  and  $-4.6 \pm 0.5\text{‰}$  for  
413  $\delta^{18}\text{O}$ ), and *I. vera* had the most depleted values ( $-48.5 \pm 5.1\text{‰}$  for  $\delta^2\text{H}$  and  $-4.8 \pm 0.8\text{‰}$  for  $\delta^{18}\text{O}$ ),  
414 with differences being statistically significant for  $\delta^2\text{H}$  ( $p < 0.05$ ).

415 Overall, isotope values of plant xylem water were more enriched during the 2017 dry season  
416 than during the 2014 dry season ( $p \leq 0.001$ ) (Fig. 3a,b; Fig. 4). Deuterium excess values were also  
417 lower in shade trees and coffee shrubs during 2017, indicating a more evaporative signature (Table 2  
418 and 3; Fig. 3). Plots of  $\delta^2\text{H}$  xylem water against height for the individual shade trees and coffee shrubs  
419 sampled in both dry seasons are shown in Figure 4, in which a similar  $\delta^2\text{H}$  pattern was displayed  
420 between trees and coffee shrubs in the 2014 and 2017 years.

421 During the 2017 wet season sampling,  $\delta^2\text{H}$  and  $\delta^{18}\text{O}$  values in xylem water of trees and coffee  
422 shrubs were more depleted in comparison to the 2017 dry season ( $p < 0.05$ ) (Fig. 3c). The range of  
423 variation was from  $-60.6$  to  $-45.6$  ‰  $\delta^2\text{H}$  and  $-6.2$  to  $-5.4$ ‰  $\delta^{18}\text{O}$  for trees, and from  $-42.2$  to  $-34.4$   
424 ‰  $\delta^2\text{H}$  and  $-5.4$  to  $-4.4$ ‰  $\delta^{18}\text{O}$  for coffee shrubs ( $p \leq 0.001$ ).

425 It was observed that the xylem isotopic composition of all shade trees and coffee plants fell  
426 within the range of the soil water sources during the 2014 dry season samplings (Fig. 3a). For the  
427 2017 dry season, we again observed a good isotopic match between the shade tree xylem water and  
428 soil water. However, for the coffee plants, the xylem water was more enriched in  $\delta^2\text{H}$  in comparison  
429 to soil water (Fig. 3b). During the 2017 wet season sampling, a slight enrichment in  $\delta^2\text{H}$  was again  
430 observed in the xylem water of coffee, while trees showed a good overlap with soil water (Fig. 3c).  
431 Based on these results, tests were carried out to specifically evaluate the effects of deuterium  
432 fractionation on coffee water sources by running a simple mixing model using only hydrogen isotope  
433 ratios in the MixSIAR framework.

434

### 435 **3.4 Root biomass and macronutrients along soils profile**

436 Overall, most roots were concentrated in the first 5 cm of soil with a sharp decline in biomass  
437 at 20 cm depth (Fig. 5a). Fine roots ( $< 1\text{mm}$ ) followed by bigger roots ( $> 2\text{mm}$ ) dominated the  
438 shallower soil layers ( $< 20\text{cm}$ ), meanwhile roots in general were scarce at deeper depths ( $> 60\text{cm}$ ).  
439 Soil acidity was highest near the surface and decreased gradually with depth (Table 4). Organic matter  
440 (OM) and total carbon were also greatest between 5 and 15 cm depth, while values decreased rapidly  
441 below  $\sim 30$  to  $60\text{cm}$  depth. Although highest concentrations of nitrogen were found in the first 15 cm  
442 of soil, values remained relatively high and constant at deeper layers (Fig. 5b). Phosphorus showed  
443 its highest concentration at the topsoil with values decreasing sharply below 30 cm depth. In contrast,  
444 concentrations of potassium, sodium and magnesium were lowest in the first 15 cm, while maximum  
445 values were observed below 90 cm depth. Base saturation (BS) was very low along the soil profile,  
446 indicating poor availability of soil macronutrients. Soil cation exchange capacity (CEC) was generally  
447 low across depths, indicating little potential for interaction between clay particles and cations.

448

### 449 **3.5 Plant water sources**

450 We found a good agreement between the MixSIAR Bayesian mixing model results using a  
451 non-informative and an informative prior distribution (on average 5% difference across all xylem  
452 water contributing sources;  $p > 0.05$ ). This indicates that the independent distribution (soil  
453 macronutrients and root data) set a *priori* to optimize source proportion estimates (informative  
454 approach) in the model was not influential enough to significantly modify the results obtained using

455 the isotope signatures of the xylem water sources alone (non-informative approach). Having this  
456 agreement between models, we present the results of the water source contribution based on the  
457 informative model runs. Results of the non-informative approach are provided in the Supplementary  
458 Materials.

459 The model results showed that the intermediate and deep soil water pools (> 15 to 120 cm  
460 soil depth) were the main sources for the shade trees over the course of the 2014 dry season ( $91 \pm$   
461  $37\%$  on average; Fig. 6 and Supplementary Materials). Across this period, *L. guatemalensis* showed  
462 on average the highest proportion of water uptake between 30 and 120 cm soil depth ( $49 \pm 26\%$ ),  
463 while *T. micrantha* and *I. vera* depended strongly on soil water sources between 15 and 30 cm ( $54 \pm$   
464  $18\%$  and  $67 \pm 6\%$ ) ( $p < 0.001$ ). In contrast, the water uptake of coffee plants was mainly sustained by  
465 sources from the first 15 cm of soil ( $94 \pm 27\%$  on average; Fig. 6 and Supplementary Materials),  
466 having significant differences with all shade tree species ( $p < 0.001$ ).

467 During the 2017 dry season, the same trend with most water extracted from intermediate and  
468 deep soil layers was observed in the shade trees ( $91 \pm 39\%$  on average; Fig. 7a,b,c and Supplementary  
469 Materials). Among samplings dates, differences between tree species only appeared to occur at the  
470 end of the dry period (Apr. 5) ( $p < 0.05$ ). Coffee water sources were again restricted to much shallower  
471 soil layers (0–5cm:  $53 \pm 44\%$  and 5–15 cm:  $42 \pm 41\%$ ; Fig. 7a,b,c and Supplementary Materials)  
472 compared to shade trees.

473 Overall, we did not find any statistically significant difference among main plant water  
474 sources between the dry periods investigated ( $p > 0.05$ ). Across the individual samplings throughout  
475 the two dry seasons, we observed that antecedent precipitation had a stronger effect on the water  
476 uptake sources of coffee plants than trees (Fig. 8). For example, when dry antecedent wetness  
477 prevailed ( $API_{15} < 5$  mm; Fig. 2b) coffee water sources were mainly composed of soil water from >  
478 5 to 15 cm depth ( $91 \pm 3\%$ ). Alternatively, when wetter antecedent conditions were present ( $API_{15} >$   
479 10 mm), the near surface soil water layer ( $58 \pm 31\%$ ) was the main contributing source. On the  
480 contrary, tree water uptake was essentially sustained by deeper soil water sources at low and relatively  
481 high antecedent wetness conditions ( $94 \pm 23\%$  and  $87 \pm 23\%$ , respectively) (Fig. 8). Nevertheless, for  
482 all species investigated, the relationships between API and the contribution of near surface soil water  
483 sources were not statistically significant ( $p > 0.05$ ).

484 During the 2017 wet season, water source partitioning differed among shade tree species  
485 (Fig. 7d and Supplementary Materials). During this period, *L. guatemalensis* and *I. vera* showed the  
486 greatest use of deep soil water ( $74 \pm 37\%$  and  $69 \pm 41\%$ , respectively), while shallower soil water  
487 was the main source for *T. micrantha* ( $91 \pm 23\%$ ), having significant differences with the other tree  
488 species ( $p < 0.001$ ). Coffee consistently showed the use of near surface water sources ( $98 \pm 5\%$ ; Fig.

489 7d and Supplementary Materials), which was significantly different from all shade tree species ( $p <$   
490 0.001).

491

### 492 ***3.6 Fractionation effects on coffee water sources***

493 To evaluate the effects of xylem deuterium fractionation on our results for coffee water source  
494 uptake, we compared the relative contribution of each soil water source obtained via the single-  
495 isotope ( $\delta^2\text{H}$ ) mixing model with those obtained via the informative two-isotope mixing model. In  
496 general, we observed that the  $\delta^2\text{H}$  model consistently estimated a lower contribution of the shallow  
497 soil water source and a higher contribution of the near surface soil water source (Supplementary  
498 Materials). On average, the reduction in the shallow soil water source ( $-25.7 \pm 29.0\%$ ) coincided very  
499 well with the increase in the near surface soil water source ( $+28.1 \pm 30.6\%$ ). These differences were  
500 most pronounced for the 2017 dry season samplings ( $p > 0.05$ ; Supplementary Materials), during  
501 which the differences in  $\delta^2\text{H}$  between coffee xylem water and soil water were greatest. However,  
502 there were no significant differences between the relative contributions of the intermediate and deep  
503 soil water sources estimated by the two models ( $p > 0.05$ ). In summary, the results of the  $\delta^2\text{H}$  mixing  
504 model suggested an even more pronounced soil water partitioning between coffee and shade tree  
505 species than those obtained with the informative two-isotope mixing model.

506

## 507 ***4. Discussion***

### 508 ***4.1 Methodological aspects***

509 To our knowledge, the ecohydrological study presented here is one of the first that  
510 incorporates biophysical properties as prior information alongside plant water source information  
511 from stable isotope ( $\delta^{18}\text{O}$  and  $\delta^2\text{H}$ ) data into a MixSIAR Bayesian mixing model framework, as a way  
512 to improve our understanding of the processes that lead to differences in the depth of plant water  
513 uptake. Even though our findings did not change significantly by including or excluding the prior  
514 information such as soil macronutrients and root data, exploring plant water source partitioning using  
515 these two model approaches provided more confidence in our results. Therefore, we call for more  
516 studies that combine soil nutrient and root biomass distribution with plant water source information  
517 from  $\delta^{18}\text{O}$  and  $\delta^2\text{H}$  data, to explore the additional value of these biophysical parameters elucidating  
518 plant-soil interactions in different regions and environments.

519 In recent years, some plant, soil and/or deep subsurface water source studies that have used  
520 stable isotopes have identified isotope variation that could be the result of isotope fractionation  
521 processes caused by water molecules interacting with clay surfaces, partially filled pore spaces or  
522 even salts (Chen et al., 2016; Gaj and McDonnell, 2019; Lin et; al., 2017Oerter et al., 2014; Oshun



523 et al., 2015). Our soils were rich in clay content and according to some studies this type of soil  
524 structure can impart isotope fractionation (Lin et al., 2017; Meißner et al., 2014; Oerter et al., 2014;  
525 Orłowski et al., 2016a). Thus far, however, these isotope effects have been more evident in clay-rich  
526 soils having high cation exchange capacities (CEC ~ 30 to 70 cmol<sub>c</sub> kg<sup>-1</sup>; Oerter et al., 2014;  
527 Orłowski et al., 2016b) in combination with low soil water contents (SWC < 20% Meißner et al.,  
528 2014; Orłowski et al., 2016b). In this respect, the soils in our study area are characterized by low CEC  
529 (< 21 cmol<sub>c</sub> kg<sup>-1</sup>; Table 4). This reflects relatively little interaction between cations adsorbed and  
530 clay mineral particles, which indirectly suggests minimal impacts of interlayer water bound in the  
531 soil structure (cf. Vidal and Dubacq, 2009). In addition, our soil samples were collected at relatively  
532 high SWC across the different sampling periods (~ 30% to 60%; Figure 1). As such, we have assumed  
533 that the probability of fractionation due to soil properties that may impact water extraction efficiency,  
534 was very small or completely absent and therefore, the extracted soil water was the same the plants  
535 had access to.

536         With regard to our plant samples, we specifically observed enrichment in the deuterium  
537 composition of the xylem water in the coffee plants in comparison to bulk soil water. It is not  
538 surprising that fractionation was evident for δ<sup>2</sup>H and not δ<sup>18</sup>O, given the higher fractionation factor  
539 of <sup>2</sup>H relative to <sup>18</sup>O (Rundel et al., 2012). Some possible explanations for this xylem water  
540 enrichment could be related to bark evaporation (Ellsworth and Sternberg, 2015) and/or xylem-  
541 phloem water exchange (Cernusak et al., 2005), since we did not remove the bark and cambium from  
542 our coffee branch samples. On the other hand, like many other crops, coffee plants associate  
543 symbiotically with arbuscular mycorrhizal fungi (López-Andrade et al., 2009; Perea-Rojas et al.,  
544 2019). Studies in our coffee growing region of Veracruz have documented the presence of  
545 mycorrhizal structures in coffee roots (Arias et al., 2012; Muleta et al., 2008), which can promote  
546 increases in plant water and nutrient uptake (Augé, 2004; Scheneiger and Jakobsen, 2000). Although  
547 no research has been carried out yet to test the influence of mycorrhizal fungi on isotope fractionation  
548 during coffee root water uptake, this effect could have been present and being also responsible for the  
549 isotopic mismatch between the coffee xylem water and soil water sources, as it has been reported  
550 elsewhere (Poca et al., 2019).

551         We did evaluate the effects of these isotope enrichments in the coffee xylem water on the  
552 relative contributions of the coffee water sources using a single-isotope (δ<sup>2</sup>H) mixing model.  
553 Consistently, the model results estimated a higher near surface water and a lower shallow soil water  
554 source contribution in comparison to the dual isotope informative prior mixing model. In contrast,  
555 the estimated proportions of the intermediate and deep soil water sources were similar between  
556 models. Thus, the effect of fractionation was translated into a more pronounced spatial separation

557 between the main soil water sources of the coffee plants and shade trees, but our overall results were  
558 not different.

559

#### 560 **4.2 Complementary water use strategy between shade trees and coffee shrubs**

561 Our findings showed that all shade tree species (*L. guatemalensis*, *I. vera* and *T. micrantha*)  
562 relied mainly on water sources from deep soil layers (> 15 to 120 cm depth), while the use of much  
563 shallower water sources (< 15 cm) was observed in the coffee (*C. arabica* var. *typica*) over the course  
564 of the near normal and the more pronounced dry seasons studied. These findings suggest a spatial and  
565 temporal partitioning of soil water sources between shade trees and coffee plants during drier periods  
566 and water-resource complementary in this coexistence species environment.

567 Although comparisons of our findings with other traditional shade Arabica coffee plantations  
568 are difficult because studies are essentially lacking in this type of agroecosystems, there are a handful  
569 of other investigations carried out in shade coffee monospecific plantations in the humid tropics in  
570 which complementary rather than competitive water use strategies prevailed. For example, Cannavo  
571 et al. (2011) compared the water use and soil water availability of an unshaded coffee vs. a shaded  
572 monoculture (*Inga densiflora*) coffee plantation in Costa Rica, both of 7-8 years old, using soil  
573 moisture measurements and water balance calculations. Their results showed that soil water content  
574 in the deeper soil layers (> 120 cm depth) was lower in the shaded coffee than in the sun-grown coffee  
575 system, while water content in the shallower layers was similar. This suggested that associated shade  
576 trees preferentially used water from deeper soil horizons providing some evidence of  
577 complementarity water use between coffee plants and native *Inga* trees during the dry season.  
578 However, the authors acknowledged that they were unable to separate roots of coffee from those of  
579 trees in the soil profiles, so they could not be certain whether trees were the only individuals extracting  
580 water from deeper sources. In this respect, our study showed that there was always a mixture in water  
581 uptake from different sources (soil group depths), but a separation between the main sources of water  
582 for shade trees and coffee shrubs clearly prevailed.

583 Other investigations in Costa Rica have examined the belowground resource competition of  
584 Arabica coffee in association with fast-growing timber species using data of plant growth, root  
585 distribution and density, and soil moisture and nutrients patterns. For example, the study of Schaller  
586 et al. (2003) carried out in a commercial (*Eucalyptus deplupta*) shade coffee plantation where soils  
587 are highly fertilized, showed that coffee had a relatively even root distribution along the first 40 cm  
588 of soil depth with a higher root density in the proximity of the coffee rows. Conversely, the root  
589 system of *E. deplupta* was much shallower having most roots concentrated in the upper 10 cm of soil.  
590 In this case, the tree root density was found highest in the alleys between the coffee rows. The authors

591 explained that the apparent complementary resource exploitation of this tree-crop system was mainly  
592 attributed to high availability of soil resources and the high competitiveness of the coffee limiting the  
593 expansion of tree roots (cf. Lehmann, 2003). Although in our study we did not determine the depth  
594 distribution of coffee and tree roots, our findings showed that all shade tree species were tapping  
595 water from deeper soil layers than coffee, suggesting that trees are deep rooted and being able to  
596 explore larger soil volumes causing little competition with coffee.

597 In Nicaragua, Padovan et al. (2015) compared the root distribution, soil moisture,  
598 transpiration and leaf water potential patterns in a sun-grown coffee system and an agroforestry of  
599 coffee planted with two timber trees (deciduous *Tabebuia rosea* and evergreen *Simarouba glauca*).  
600 Their findings showed that coffee roots were more abundant than tree roots and mainly concentrated  
601 in the shallower soil layers (0–80 cm depth). Most roots of both tree species were observed in deeper  
602 layers (>100 cm) suggesting a clear niche differentiation with coffee. During the 3-year study period,  
603 volumetric water content along a 2 m soil profile was higher in the sun-grown coffee than in the  
604 shaded coffee, which was explained by greater soil water uptake from trees below the crop rooting  
605 zone (Padovan et al., 2015). Moreover, coffee shrubs in the shaded plantation were more water  
606 stressed (i.e. lowest midday leaf water potentials) during the pronounced dry season studied (Padovan  
607 et al., 2018). Their results suggest that despite the clear hydrological niche segregation, competition  
608 between coffee and shade trees may occur if the dry season is long and severe enough.

609 Our findings also showed that during the wet season coffee plants substantially increased the  
610 use of near surface water (+56%) in comparison to the dry season, while all shade trees also extended  
611 their water acquisition to much shallower soil water pools (+19%). This is largely explained by the  
612 increases in soil moisture in the first 30 cm depth due to frequent rainfall inputs that characterize the  
613 wet season in our study area. This also suggests that coffee had a higher root activity in the top soil  
614 layers during the wet season in comparison to the dry season, as has been documented in other studies  
615 (Huxley et al., 1974). Regarding the shade trees, we observed that *T. micrantha* showed the greatest  
616 response to wetter conditions by drawing most water from the first 15 cm of soil (92%), whereas this  
617 was much less evident in *L. guatemalensis* (21%) and *I. vera* (27%). Although we did not determine  
618 the vertical distribution of roots for each of the shade tree species studied, these findings suggest that  
619 *T. micrantha* has a shallower rooting system than the other tree species. The fact that the *T. micrantha*  
620 trees were more recently planted (i.e. younger with less developed root system) than the *L.*  
621 *guatemalensis* and *I. vera* trees supports this idea. On other hand, the high temperature and rainfall  
622 that characterize the wet season at our study site may favor rapid mineralization of nutrients and their  
623 subsequent leaching to deeper soil layers (i.e. potassium, calcium and magnesium; Table 4). Hence,  
624 for the larger trees studied (*L. guatemalensis*), the availability of water and nutrients at deeper depths

625 could have been an important resource for plant growth in this period, partly explaining the lower  
626 activity of their shallower roots. Despite the changes and the higher variability in depth of water  
627 uptake observed among canopy trees and coffee shrubs, a complementary use of soil water prevailed  
628 during the wet season. Future work should be focused on the distribution and dynamics of tree and  
629 crop roots and their seasonal variation in relation to the availability of nutrients and water in the soil.  
630 Also, it would be desirable to relate these dynamics to crop and shade tree phenology to elucidate  
631 temporal synergistic or competitive water requirements.

632

### 633 ***4.3 The role of antecedent wetness in coffee water uptake***

634 Despite the relatively small sample size, our study showed that antecedent wetness strongly  
635 influenced the water uptake patterns of coffee plants (cf. Huxley et al., 1974). We found that under  
636 relatively wet antecedent conditions prevailing after small rainfall events during the dry season, coffee  
637 substantially increased the use of near surface soil water sources, possibly as an opportunistic strategy  
638 to overcome the soil water deficits in this period and taking advantage of their much shallower rooting  
639 system compared to trees. Conversely, tree water uptake was mainly sourced by deeper soil water  
640 layers showing less sensitiveness to higher antecedent wetness. In this respect there are no  
641 comparative studies in shade coffee agroecosystems evaluating the functional response of plant water  
642 uptake over a range of antecedent wetness. Nevertheless, plant and soil water interactions under dry  
643 and relatively wet conditions have been examined in other types of agroforestry systems. For  
644 example, in the study of Gao et al. (2018) carried out in a semiarid region in China, the authors  
645 evaluated the seasonal variations in water use of jujube (*Ziziphus jujuba*) trees planted with annual  
646 (*Brassica napus*) and perennial (*Hemerocallis fulva*) crops. Using stable isotope techniques and  
647 Bayesian mixing modelling, their results showed that jujube trees generally tapped water (> 58%)  
648 from deep soil layers (60-200 cm depth) at low antecedent wetness, while *B. napus* and *H. fulva* crops  
649 primarily extracted water (> 65%) from intermediate (20-60 cm) and shallow (0-20 cm) soil layers.  
650 This exhibits a complementary water use strategy between trees and crops. However, at higher  
651 antecedent wetness both the jujube trees and crops extracted most water from the first 0-60 cm of soil  
652 depth (> 65%). This indicated that both species exhibited an opportunistic strategy for accessing  
653 resources at shallower soil depths. In this case, contrary to our findings, tree roots rather than crop  
654 roots showed the stronger capacity to switch rapidly from deep to shallow sources in response to  
655 increased soil water availability.

656

### 657 ***4.4 Implications and future directions***

658           The consistent complementarity in plant water use strategies observed under different  
659 hydrometeorological conditions in the coffee plantation studied provides support to the central tenet  
660 of agroforestry systems (Cannel et al., 1996). Based on our findings, *L. guatemalensis*, *I. vera* and *T.*  
661 *micrantha* provide good choices for coffee shade trees due to their complementarity in soil water use.  
662 Since these tree species obtained their water from deeper soil layers than the coffee, this could mean  
663 that they utilize nutrients leaching beyond the reach of the coffee plants, and so contribute to improved  
664 nutrient cycling and increased overall productivity of the system (van Noordwijk et al., 2015).

665           Nevertheless, the current outcome may change given the new coffee management practices  
666 that consist on replacing traditional coffee varieties (e.g. *C. arabica* var. *typica*) with others (*C.*  
667 *arabica* var. *costa rica*; *C. canephora*) that may exhibit deeper roots systems and perhaps different  
668 water (and nutrient) uptake strategies, in response to prevalent diseases such as leaf rust or root  
669 nematodes. Therefore, future research should be focused on evaluating the water source partitioning  
670 of traditional vs. new coffee disease-resistant varieties and their relation to shade tree water use. In  
671 this respect, there are further questions with regard to strategic use of shade tree species, whereby  
672 fast-growing species might be more (commercially) productive but also more competitive. Some  
673 evidence from elsewhere has shown that such management practices do not necessarily increase  
674 competition and may even enhance the water use efficiency as part of drought-avoidance  
675 mechanisms. For example, in southeast China, Wu et al. (2016) used  $\delta^2\text{H}$  and  $\delta^{18}\text{O}$  stable isotope  
676 methods to examine the seasonal water use of a fast-growing rubber tree species (*Hevea brasiliensis*)  
677 planted with Arabica coffee. Their findings showed that rubber trees were mostly accessing water  
678 from intermediate (15-50 cm depth) and deep soil layers (50-110 cm), meanwhile coffee was mostly  
679 tapping water from the topsoil (< 15 cm). Additionally, rubber trees showed strong root plasticity in  
680 soil water uptake avoiding competition with coffee during the rainy and relatively dry seasons.  
681 However, more research is needed since these results depend largely on tree-crop specie combinations  
682 and local climatic and soil conditions.

683           In addition to effects of changing management practices, climate warming may induce  
684 changes in plant transpiration throughout the year (e.g. Karmalkar et al., 2011). In our study, we used  
685 a water stable isotope approach along with root and soil macronutrients data to estimate the relatively  
686 contribution of the plant water sources. However, for a more complete assessment of the plant and  
687 soil interactions, seasonal plant water fluxes need to be quantified. Our results so far have made the  
688 first steps towards serving coffee producers to make better decisions on sustainable coffee and water  
689 management, as well as providing new insights into water resources in general, which are urgently  
690 required for implementing efficient and equitable management programs in humid tropical  
691 environments (Hamel et al., 2018). However, future work should be focused on water use of

692 individual trees and coffee shrubs using ecophysiological and hydrological techniques in order to  
693 know how much water is used from the different soil water pools.

694

## 695 **5. Conclusions**

696 This study provides the first baseline information on plant water sources for a traditional  
697 shade coffee plantation in the humid tropics. Our results showed that coffee water uptake was mainly  
698 sustained from shallow soil sources (< 15 cm depth) while all shade trees relied on water sources  
699 from deeper soil layers (>15 to 120 cm depth). This complementary strategy in soil water use between  
700 crops and trees was consistent over the course of the near normal and the more pronounced dry  
701 seasons investigated. Across these same periods, we observed that antecedent precipitation had a  
702 strong influence in coffee plants increasing their water uptake to near surface soil water sources as an  
703 opportunistic strategy to overcome the reduced water availability. In the wet season, coffee plants  
704 substantially increased the use of near surface water (< 5 cm depth), whereas shade trees expanded  
705 their water acquisition to the first 15 cm of soil depth. Overall, a greater soil water partitioning  
706 prevailed among tree and coffee species when higher soil moisture conditions were present.  
707 Nevertheless, despite such variability in plant-soil water interactions across seasons, a clear spatial  
708 segregation of the main water source prevailed between shade trees and coffee plants during the rainy  
709 and dry periods investigated.

710

711 **Author contributions.** LEMV designed the experiment. LEMV, MSAB and FH collected the field  
712 data. MSAB performed all the Bayesian mixing model analysis. JG contributed in the data analysis.  
713 LEMV prepared the first draft of the manuscript. FH, MSAB and JG edited and commented on the  
714 manuscript several times, and TED carried out the final revision. Later, all the co-authors  
715 contributed with revisions.

716

717 **Competing interests.** The authors declare that they have no conflict of interest.

718

## 719 **Acknowledgments**

720 We would like to thank Raul Monge and Daniel Tejada for their permission to conduct this  
721 research in “La Orduña” coffee plantation. We also thank Melissa López-Portillo for performing the  
722 cryogenic extractions and Stefania Mambelli and Wembo Yang for analyzing the water isotope  
723 samples at UC-Berkeley, USA. Angel Zaragoza, Erika Mendoza, Alitzel Guzmán and Carlos Alcocer  
724 are thanked for their assistance in the sampling campaigns. The Instituto de Ecología, A.C. (INECOL)  
725 is thanked for the laboratory facilities to carry out the root separation and oven-dry weights. We also

726 thanked Adriana Hernández and Esperanza Huerta for helping in the root separation process. This  
727 research was supported by the PAPIIT-UNAM (No. IB100313 and IB100113) grants, respectively to  
728 LE Muñoz-Villers and F Holwerda, and by the INFRA-CONACyT-México (No. 187646) grant to F  
729 Holwerda. Additional support was provided by the NSF-USA (No. 1313804) and by the Scottish  
730 Funding Council via the University of Aberdeen (SP10192). Data analysis and partial writing of the  
731 manuscript was performed during LEMV sabbatical leave (March-July 2018) hosted by Josie Geris  
732 at the University of Aberdeen, UK, and granted by the *Programa de Apoyos para la Superación de*  
733 *Personal Académico* (PASPA) of the UNAM. Lastly, we appreciate the valuable comments of  
734 reviewers Adriá Barbeta, Matthias Beyer and Daniele Penna and Editor Matthias Sprenger that helped  
735 to improve an earlier version of the manuscript.

736

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**Table 1.** Characteristics of the shade trees and coffee plants sampled for water isotope analysis during 2014 and 2017. Numbers between parentheses are the standard deviation.

Family	Species	Canopy layer	2014		2017		<i>n</i>
			DBH cm	Height m	DBH cm	Height M	
Fabaceae	<i>Lonchocarpus guatemalensis</i>	Overstory	101.5 (12.6)	20.3 (1.3)	119.8 (12.1)	21.0 (1.2)	3
Fabaceae	<i>Inga vera</i>	Overstory	39.3 (15.7)	10.7 (4.8)	48.1 (13.3)	9.6 (1.2)	3
Cannabaceae	<i>Trema micrantha</i>	Overstory	13.16 (6.8)	8.15 (3.1)	23.3 (7.2)	15.2 (2.2)	3
Rubiaceae	<i>Coffea arabica</i> var. <i>typica</i>	Understory	12.7 (2.1)	2.83 (0.7)	n.a.	n.a.	5* 6** 10***

\* Number of individuals sampled each time in the 2014 dry season

\*\* Number of individuals sampled each time in the 2017 dry season

\*\*\* Number of individuals sampled in the 2017 wet season

**Table 2.** Mean  $\pm$  (SD) H and O stable isotope composition of 2013-2014 precipitation, tree xylem water and bulk soil water of the 2014 dry season sampling, and corresponding *d*-excess values (‰)

Precipitation <i>n</i> = 41						Bulk soil water <i>n</i> = 54												Shade trees xylem water <i>n</i> = 27			Coffee shrubs xylem water <i>n</i> = 14		
Dry season			Wet season			0-5 cm depth			>5-15 cm depth			>15-30 cm depth			>30-120 cm depth								
$\delta^2$ H	$\delta^{18}$ O	<i>d</i> - exce ss	$\delta^2$ H	$\delta^{18}$ O	<i>d</i> - exce ss	$\delta^2$ H	$\delta^{18}$ O	<i>d</i> - exce ss	$\delta^2$ H	$\delta^{18}$ O	<i>d</i> - exce ss	$\delta^2$ H	$\delta^{18}$ O	<i>d</i> - exce ss	$\delta^2$ H	$\delta^{18}$ O	<i>d</i> - exce ss	$\delta^2$ H	$\delta^{18}$ O	<i>d</i> - exce ss	$\delta^2$ H	$\delta^{18}$ O	<i>d</i> - exce ss
1. 6 $\pm$ 8. 5	- 1.9 $\pm$ 1.4	17.0 $\pm$ 5.1	- 42. 4 $\pm$ 36. 1	- 7.2 $\pm$ 4.3	14.9 $\pm$ 2.8	- 20. 5 $\pm$ 7.8	- 2.4 $\pm$ 1.0	-1.5 $\pm$ 4.1	- 30. 8 $\pm$ 9.4	- 3.7 $\pm$ 1.1	-1.2 $\pm$ 6.3	- 54. 7 $\pm$ 10. 3	- 7.0 $\pm$ 0.9	1.2 $\pm$ 6.6	- 66. 8 $\pm$ 8.6	- 8.7 $\pm$ 1.3	3.0 $\pm$ 4.7	- 55. 4 $\pm$ 7.6	- 6.2 $\pm$ 1.0	-5.8 $\pm$ 4.1	- 25. 5 $\pm$ 10. 8	- 3.4 $\pm$ 1.8	1.7 $\pm$ 5.0

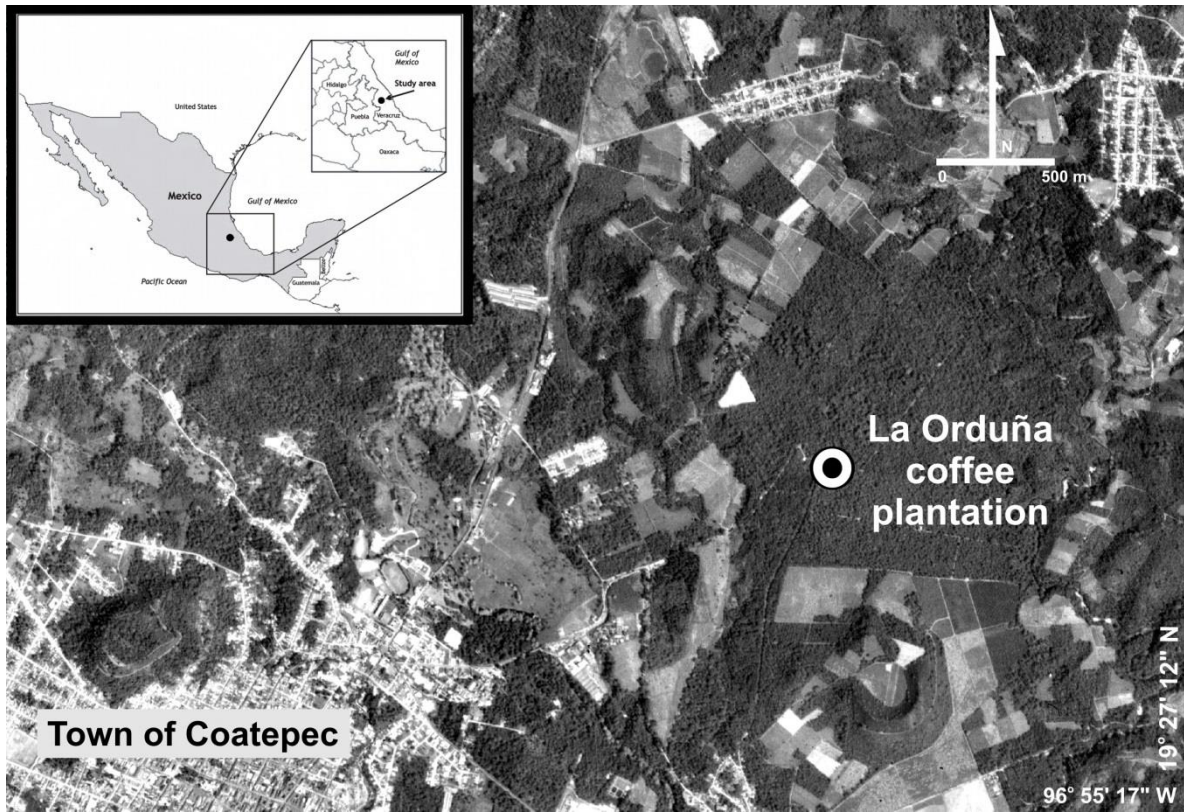
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**Table 3.** Mean  $\pm$  (SD) H and O stable isotope composition of 2016-2017 precipitation, tree xylem water and bulk soil water of 2017 dry season sampling, and corresponding *d*-excess values (‰)

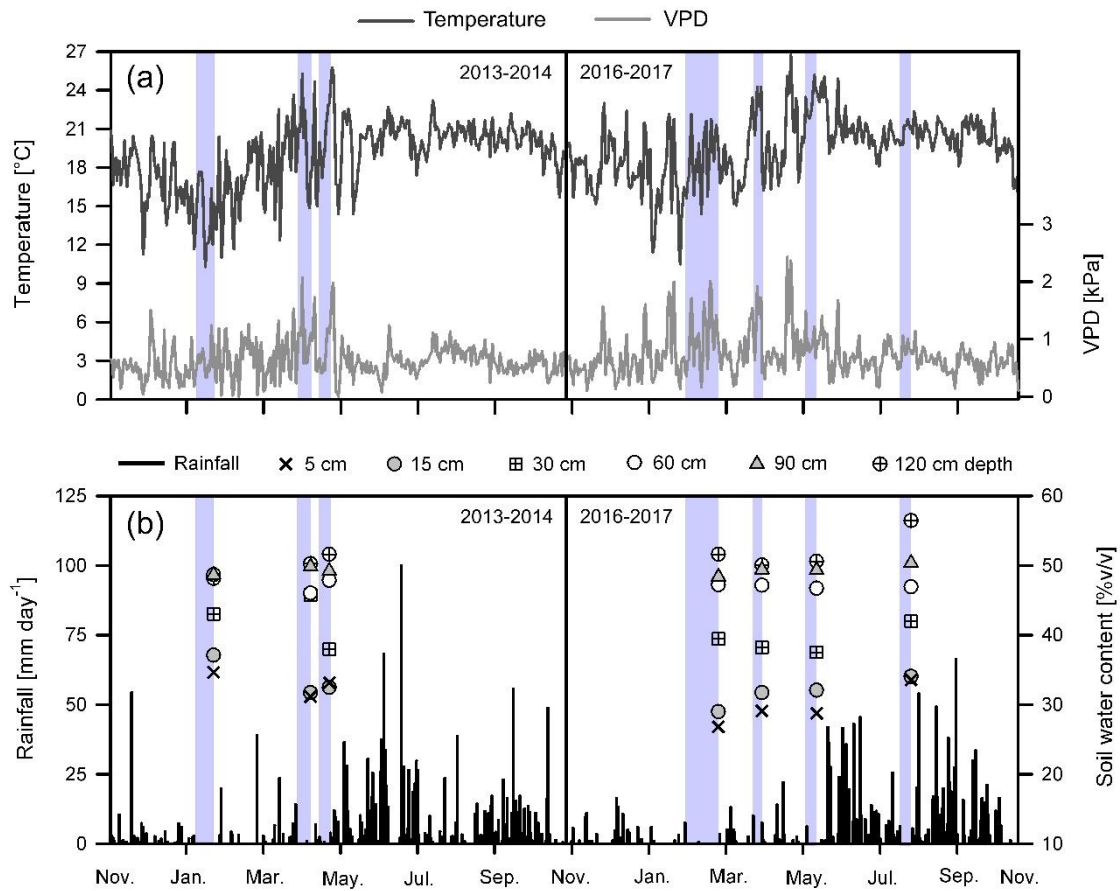
Precipitation <i>n</i> = 39						Bulk soil water <i>n</i> = 54												Shade trees xylem water <i>n</i> = 24			Coffee shrubs xylem water <i>n</i> = 18		
Dry season			Wet season			0-5 cm depth			>5-15 cm depth			>15-30 cm depth			>30-120 cm depth								
$\delta^2$ H	$\delta^{18}$ O	<i>d</i> - exce ss	$\delta^2$ H	$\delta^{18}$ O	<i>d</i> - exce ss	$\delta^2$ H	$\delta^{18}$ O	<i>d</i> - exce ss	$\delta^2$ H	$\delta^{18}$ O	<i>d</i> - exce ss	$\delta^2$ H	$\delta^{18}$ O	<i>d</i> - exce ss	$\delta^2$ H	$\delta^{18}$ O	<i>d</i> - exce ss	$\delta^2$ H	$\delta^{18}$ O	<i>d</i> - exce ss	$\delta^2$ H	$\delta^{18}$ O	<i>d</i> - exce ss
- 2.9 $\pm$ 16. 0	- 3.0 $\pm$ 1.8	21.5 $\pm$ 4.3	- 47. 8 $\pm$ 34. 4	- 7.9 $\pm$ 4.1	15.2 $\pm$ 3.3	- 24. 3 $\pm$ 3.9	- 2.2 $\pm$ 0.5	-6.9 $\pm$ 6.6	- 32. 1 $\pm$ 5.3	- 3.6 $\pm$ 0.5	-3.4 $\pm$ 4.1	- 41. 9 $\pm$ 5.7	- 5.7 $\pm$ 0.6	3.4 $\pm$ 4.8	- 47. 3 $\pm$ 3.8	- 6.5 $\pm$ 0.5	5.0 $\pm$ 3.2	- 44. 9 $\pm$ 5.6	- 4.4 $\pm$ 0.7	-9.7 $\pm$ 5.4	- 21. 3 $\pm$ 7.2	- 2.8 $\pm$ 1.0	1.3 $\pm$ 6.2

**Table 4.** Soil characteristics (average values) determined at the different depths

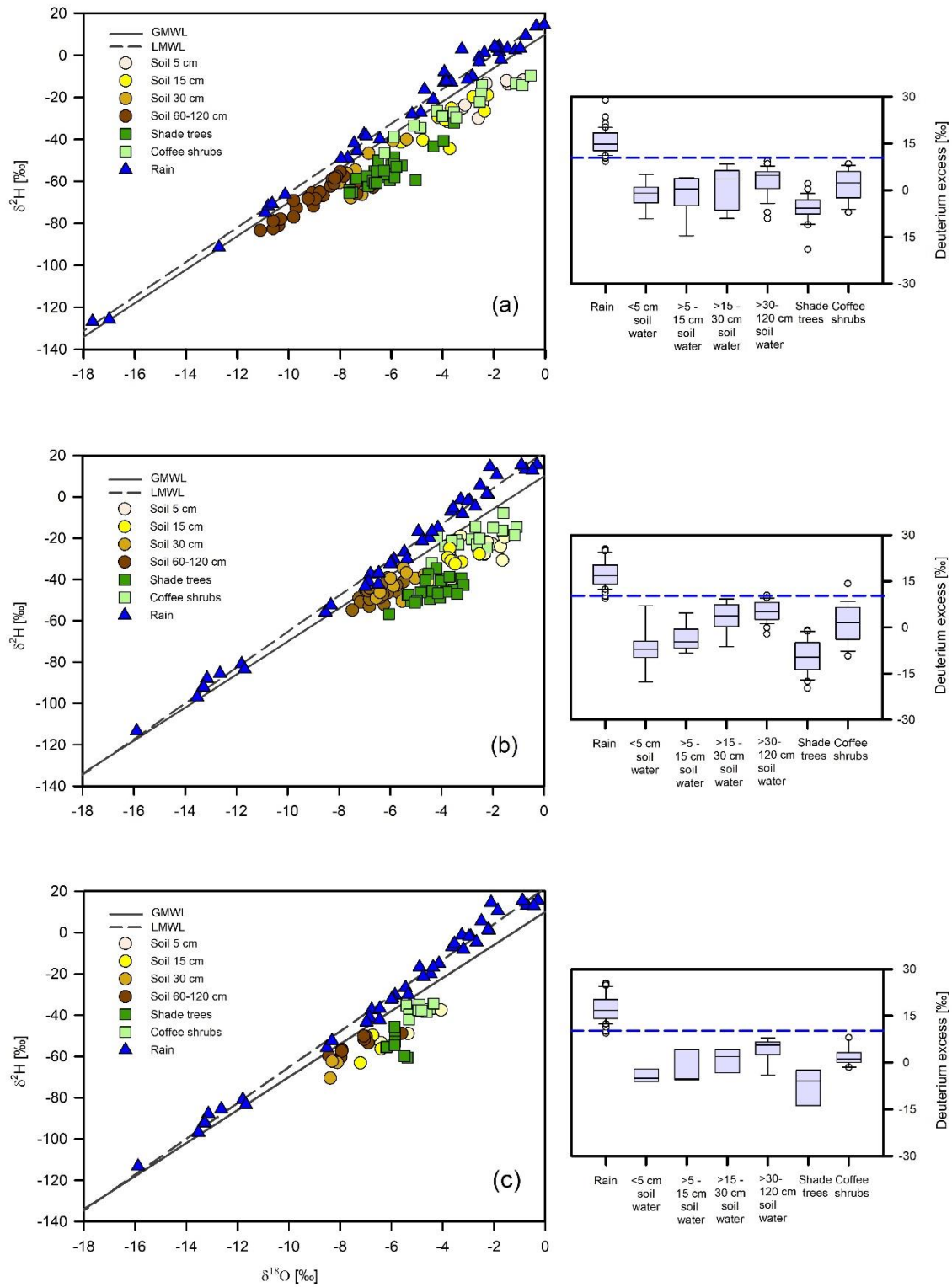
Soil depth	pH (H <sub>2</sub> O)	P	Na	K	Ca	Mg	CEC	BS	OM	C	N	Clay	Loam	Sand
(cm)		(mg kg <sup>-1</sup> )	(cmol <sub>c</sub> kg <sup>-1</sup> )					(%)						
5	4.07	33.33	1.47	0.60	3.86	0.87	16.10	0.42	5.18	3.01	0.38	60.83	25.1	13.9
15	4.12	4.60	1.08	0.47	0.95	0.12	13.27	0.20	2.89	1.90	0.30	63.8	24.3	11.9
30	4.34	n.d.	2.22	0.77	1.92	0.54	14.65	0.37	1.55	1.31	0.23	70.9	18.6	10.5
60	4.95	n.d.	2.36	0.93	3.81	1.21	20.35	0.41	1.02	0.69	0.22	66.9	16.3	16.8
90	5.10	n.d.	2.75	1.11	3.78	1.27	18.85	0.47	0.48	0.50	0.20	66.1	14.9	19.1
120	5.16	n.d.	3.00	1.45	3.76	1.20	17.60	0.53	0.41	0.51	0.20	65.1	14.0	20.9



**Figure 1.** Study site location in the municipality of Coatepec, Veracruz, Mexico. Source: QuickBird Satellite Image (2010). Copyright DigitalGlobe, Inc.



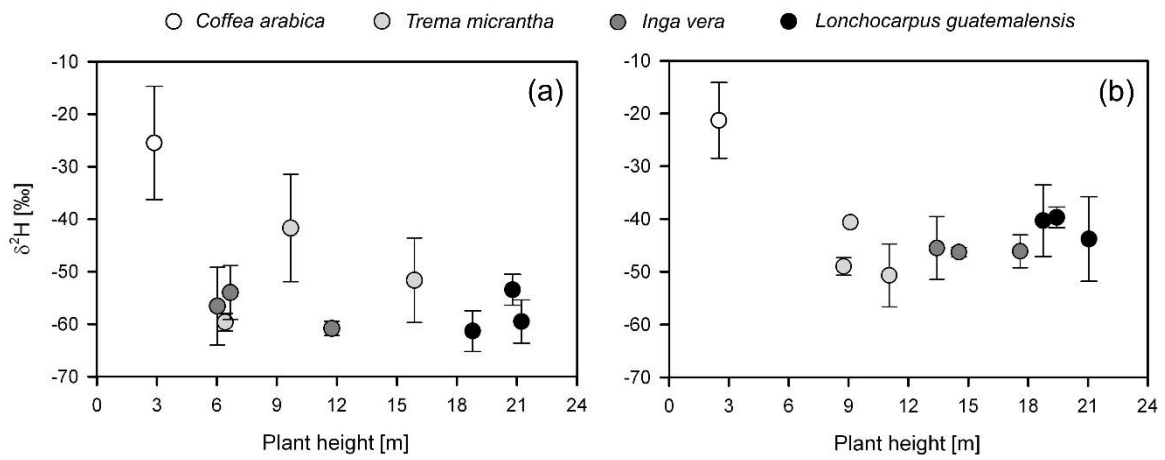
**Figure 2.** (a) Daily mean air temperature and vapor pressure deficit (VPD) and (b) and daily total rainfall ( $P$ ), as measured from November 2013 to October 2014 and from November 2016 to October 2017, and volumetric soil water content (SWC) measured at different depths during the sampling campaigns in the study area; different depths are indicated by the unique symbols shown in the lower panels (the key to the symbols is at top). The blue-colored areas indicate the 6- to 22-day period of minimum rainfall (< 5 mm) preceding the dates of isotope sampling in January (mid dry season) and April (late dry season) of 2014, and in February (mid dry season), April and May (late and end of dry season), and August (mid wet season) of 2017.



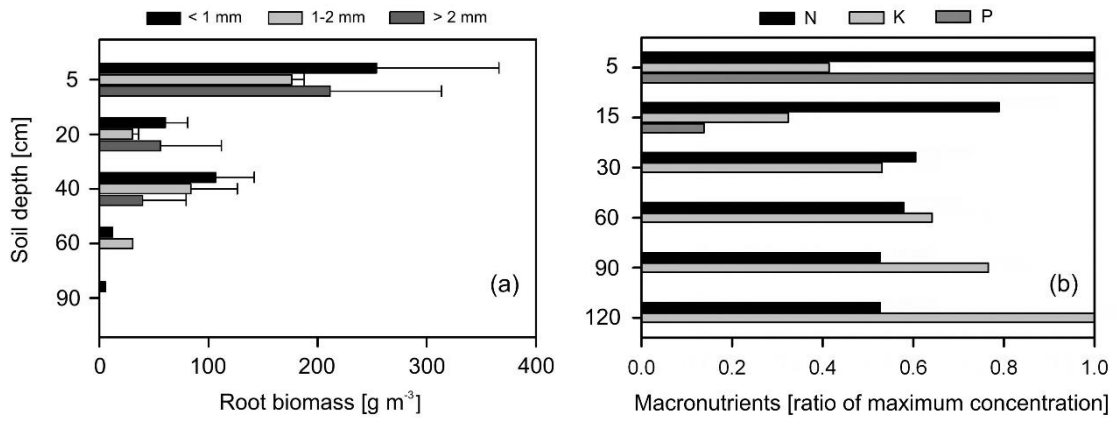
**Figure 3.** (a) Isotope composition of xylem water for shade trees and coffee shrubs, bulk soil at different depths as observed during the three sampling dates (Jan. 23, Apr. 11 and Apr. 26, 2014),

and isotope values of rainfall during the period December 2013 to November 2014. The dashed line represents the 2013–2014 local meteoric water line (LMWL;  $\delta^2\text{H} = 17.82 + 8.26 * \delta^{18}\text{O}$ ), (b) Isotope composition of xylem water for shade trees and coffee shrubs, bulk soil at different depths during the three sampling dates (Feb. 27, Apr. 5 and May. 20, 2017) and isotope values of rainfall during the period December 2016 to November 2017, and (c) Isotope composition of xylem water for shade trees and coffee shrubs, bulk soil at different depths during the middle of the 2017 wet season (Aug. 4) and isotope values of rainfall during the period December 2016 to November 2017. The dashed lines in panels (b) and (c) represent the 2016–2017 local meteoric water line (LMWL;  $\delta^2\text{H} = 21.0 + 8.36 * \delta^{18}\text{O}$ ). The solid line in all panels represents the global meteoric water line (GMWL;  $\delta^2\text{H} = 10 + 8 * \delta^{18}\text{O}$ ). The panels on the right show the deuterium excess values for the plants and soil water sources and rainfall preceding the sampling campaigns. The dashed blue line represents the deuterium excess value of the GMWL.

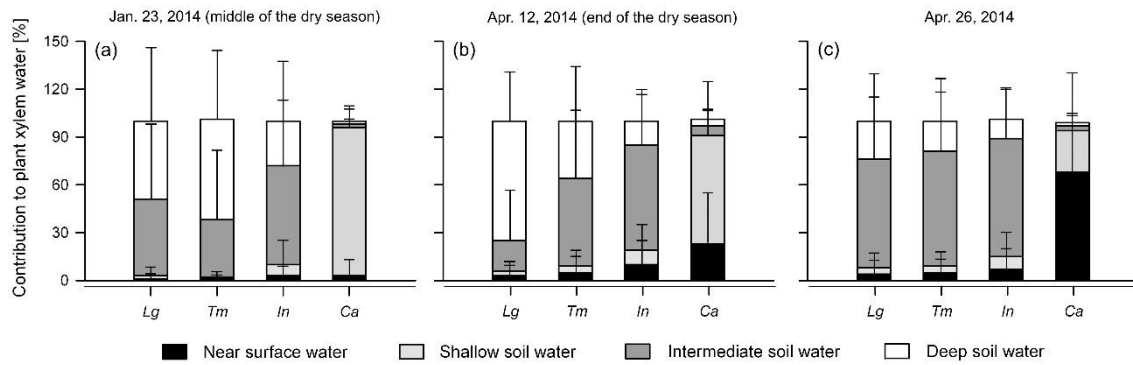




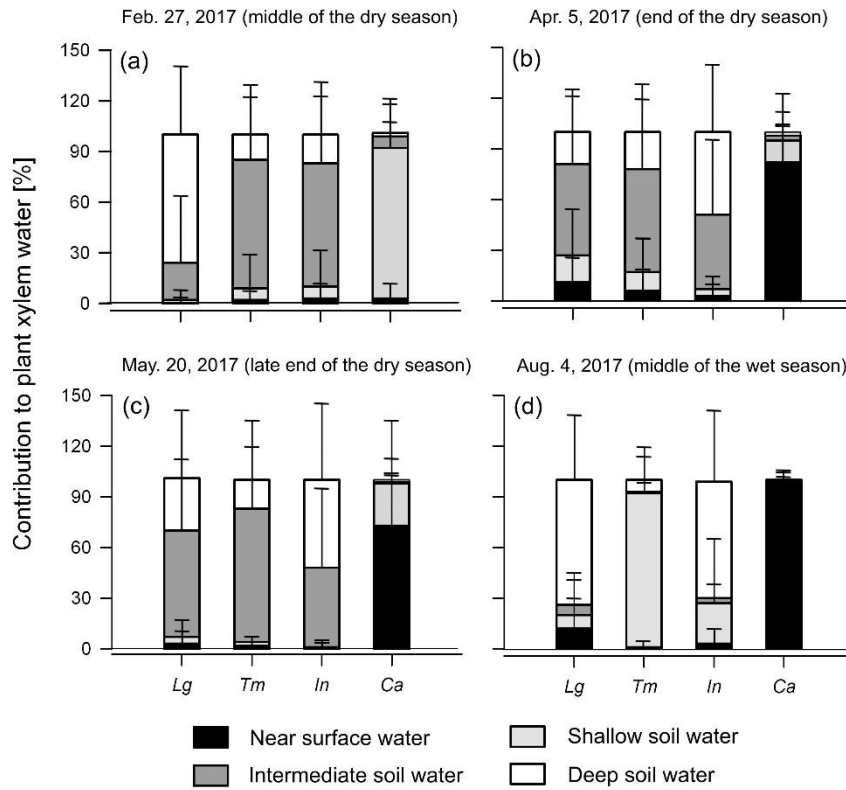
**Figure 4.** Plant height vs  $\delta^2\text{H}$  xylem water for coffee plants and shade tree species corresponding to (a) the 2014 and (b) 2017 dry season samplings.



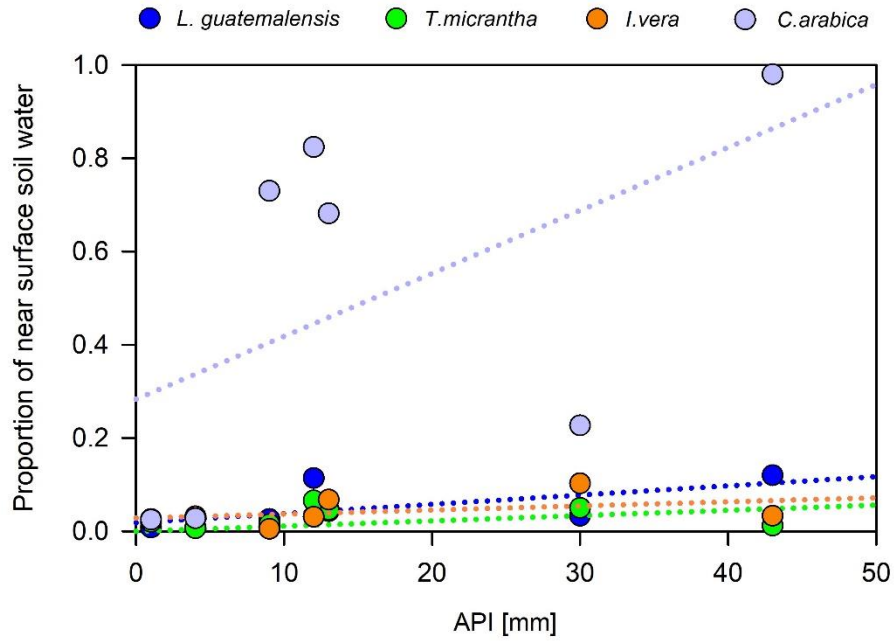
**Figure 5.** (a) Distribution of root biomass for three size classes of roots (different color bars), the error bars in represent one standard deviation of uncertainty and (b) macronutrients distribution along the soil profile, here normalized and expressed as in ratio to their maximum values (absolute values in Table 4).



**Figure 6.** MixSIAR Bayesian mixing model results showing the mean likely contribution of each water source to the xylem water of shade canopy trees and coffee shrubs. (a), (b) and (c) show results for the sampling dates of Jan. 23, Apr. 12 and Apr. 26, 2014 respectively, using the informative prior distribution. *Lg*: *L. guatemalensis*; *Tm*: *T. micrantha*; *In*: *I. vera* and *Ca*: *Coffea arabica*. Error bars represent one standard deviation of uncertainty.



**Figure 7.** MixSIAR Bayesian mixing model results showing the mean likely contribution of each water source to the xylem water of shade canopy trees and coffee shrubs. (a), (b), (c) and (d) show results for the sampling dates of Feb. 27, Apr. 5, May. 20 and Aug. 4, 2017 respectively, using the informative prior distribution. *Lg*: *L. guatemalensis*; *Tm*: *T. micrantha*; *In*: *I. vera* and *Ca*: *Coffea arabica*. Error bars represent one standard deviation of uncertainty.



**Figure 8.** Contribution of deep soil water to plant uptake at different antecedent precipitation conditions across the 2014 and 2017 dry seasons.