https://doi.org/10.5194/hess-2019-329
Preprint. Discussion started: 26 July 2019

Hydrology and Earth System Sciences Discussions
Open Access

Manuscript title

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

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Abstract

On a global scale, coffee has become one of the most sensitive commercial crops that will be affected by climate change. The majority of Arabica coffee (*Coffea arabica*) grows in traditionally shaded agroforestry systems and accounts for ~70% of the coffee production worldwide. Nevertheless, the interaction between plant and soil water sources in these coffee plantations remains poorly understood. To investigate the functional response of dominant shade trees species and coffee (*C. arabica* var. *typica*) plants to different soil water availability conditions, we conducted a study during a normal and more pronounced dry season (2014 and 2017, respectively) and the 2017 wet season in a traditional agroecosystem in central Veracruz, Mexico. For the different periods, we specifically investigated the variations in water sources and root water uptake via MIXSIAR mixing models using $\delta^{18}O$ and $\delta^{2}H$ stable isotopes of rainfall, plant xylem and soil water, along with micrometeorological and soil moisture measurements. To further increase our mechanistic understanding about root activity, the distribution of belowground biomass and soil macronutrients were also examined and considered in the model. Results showed that, over the course of the two dry seasons investigated, all shade tree species (*Lonchocarpus guatemalensis*,

https://doi.org/10.5194/hess-2019-329
Preprint. Discussion started: 26 July 2019

Inga vera and *Trema micrantha*) relied on water sources from deeper soil layers (>15 to 120 cm depth; 86%), while the use of much shallower water sources (<15 cm depth; 60%) was observed in coffee plants. In addition, in these same periods, coffee water uptake was strongly influenced by antecedent precipitation conditions, whereas trees showed little sensitiveness to short-term wetness status. Our findings also showed that during the wet season coffee plants substantially increased the use of near surface water (+48% from <5 cm depth), while shade trees extended the water acquisition to much shallower soil layers (+32% from <15 cm depth) in comparison to drier periods. Despite the plasticity in soil water uptake observed among canopy trees and coffee plants, a spatial segregation of the main water source prevailed during the dry and wet seasons studied. However, more variability in plant-soil water uptake was observed among species in the rainy season when higher soil moisture conditions were present and water limitation was largely absent.

Key words: Shade trees, *Coffea arabica*; water stable isotopes, roots, nutrients, MixSIAR, Mexico

1. Introduction

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

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

Growing a crop in association with shade trees inevitably leads to some degree of competition for the above-ground (light) and below-ground (water and nutrients) resources (Monteith et al., 1991). In an agroforestry system, the outcome of competition for light is relatively predictable due to the hierarchical structure of the canopy (i.e., shade trees intercept part of the sunlight, thereby reducing the amount available for the understory crop). Conversely, competitive interactions for soil resources can be much more diverse and complex. The central hypothesis of agroforestry underscores that crops and trees are complementary in their use of soil resources (Cannell et al., 1996), however the degree to which this occurs will be largely controlled by the spatial and temporal patterns of resource availability, root distribution and root activity, which in turn depend on factors such as climate, soil conditions, crop and tree species, and plantation age, density and management practices (Beer et al., 1998; Lehmann, 2003; van Noordwijk et al., 2015). In addition, below-ground competitive interactions for water and/or nutrients are much more difficult to elucidate than above-ground relationships. So far, the most common approach is to measure the distribution of root abundance of crops and trees, and examine to what extent they overlap or are separated (e.g., Schaller et al., 2003; van Kanten et al., 2005). An important limitation of this method is, however, that the spatial distribution of roots does not always mirror the actual resource capture along the soil profile (Dawson et al., 2002; Lehmann, 2003). Another approach is to examine the vertical patterns of soil water content (Cannavo et al., 2011; Padovan et al., 2015) or nutrient (Schroth et al., 2000, cited in Lehmann, 2003) depletion. These methods are problematic because they cannot provide information on whether resource depletion is caused by the crop, the trees, or both (Cannavo et al., 2011; Padovan et al., 2015). However, the use of hydrogen (δ^2H) and oxygen (δ^{18}O) water stable isotope techniques in combination with Bayesian mixing models provides a powerful tool for quantifying the proportions of different water sources to plant uptake across different ecosystems and regions (Barbeta et al., 2015; Muñoz-Villers et al., 2018; Penna et al., 2018) and can largely overcome the above-mentioned limitations (Dawson et al., 2002; Lehmann, 2003; van Noordwijk et al., 2015). Although rarely implemented, including nutrient and root distribution data along the soil profile to inform these models could provide more comprehensive insights into depth of plant water uptake.

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

Currently, we lack of information on plant water sources in traditional shade coffee plantations. In these agroforestry systems, the higher density and diversity of shade trees could potentially lead to stronger and more diverse tree-crop interactions (van Noordwijk et al., 2015). On the other hand, the dense tree canopy reduces light availability limiting coffee water use. This could lead to a lower soil water demand and thus increased plant water availability during the dry season.

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

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

1. Does a complementary water use strategy between shade trees and coffee shrubs prevail in a traditional shaded agroforestry system?
2. Does competition exist for water sources among tree and coffee species during more pronounced dry periods?
3. What are the seasonal patterns in plant-water source partitioning?

2. Materials and methods

2.1 Study site

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

The climate is classified as temperate humid with abundant rains during the summer (Garcia, 1988). Two distinct seasons can be distinguished: (1) a wet season (May–October), during which rainfall is associated primarily with cumulus and cumulonimbus clouds formed during convective and orographic uplift of the moist maritime air masses brought in by the easterly trade winds; and (2) a (relatively) dry season (November–April), during which most rainfall falls from stratus clouds associated with the passage of cold fronts (Báez et al., 1997). Mean annual rainfall measured nearby the study site during the period 1971−2000 was 1765 mm, with on average monthly rainfall of 389 mm falling during the dry season and 1376 mm falling during the wet season (SMN, 2018). Mean annual temperature over this period was 19.5 °C, with a minimum and maximum monthly average value of 15.5 and 22.5°C observed in January and May, respectively (SMN, 2018). Annual potential evapotranspiration (ET_0) is about 1120 mm (Holwerda et al., 2013).

The investigated shade coffee plantation is a so-called traditional commercial polyculture system (*sensu* Moguel and Toledo, 1999), which was established more than 80 years ago. The tree canopy is diverse and consists predominantly of the species *Inga spp*., *Citrus spp*., *Lonchocarpus guatemalensis*, *Trema micrantha* and *Enterolobium cyclocarpum* (Holwerda et al., 2016). The shade trees were planted at a density of ca. 500 ha−1, and currently form a canopy of about 14 m high. The Arabica coffee plants were of the variety *typica*. *Typica* −a tall cultivar of *Coffea arabica*− was the first coffee variety that arrived from Ethiopia to Mexico (Renard, 2010); it has bronze-tipped young leaves and the berries are large. Plants of *typica* variety are tolerant to conditions of low soil fertility and drought, but vulnerable to most pests and diseases (Escamilla et al., 2005). In the study site, this cultivar was planted approximately 20 years ago at a density of about 1700 shrubs ha−1, currently having an average height of ~ 2 m. In this region, the coffee flowering occurs in March or April, fruit development between May and October, and ripening and harvest between October and February (Villers et al., 2009). The management of the plantation involves weed control practices and selective pruning of mature coffee plants and shade trees at irregular times once every ~ 7 years (cf. Hernández-Martínez et al., 2009). No pruning activities occurred during or in between our study periods. A photograph of the coffee plantation is shown in the Supplementary Material.

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

2.2 Hydrometeorological measurements

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

2.3 Isotope sampling

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

In all seven samplings, xylem samples were obtained from three individuals of each of the three dominant shade tree species (*Lonchocarpus guatemalensis*, *Inga vera* and *Trema micrantha*) by extracting ~5-6 cm cores using a Pressler increment borer inserted at 1.2 m above ground. On each occasion, xylem samples were taken from the same individuals but from various aspects of the trunk. The bark was immediately removed after core extraction to avoid contamination of phloem water. For the coffee plants, samples were obtained from ~6 cm segments of mature branches that were cut near the main stem of several shrubs each time. All coffee plants were sampled randomly. During the 2014 and 2017 dry seasons, sampling of coffee shrubs involved 5-6 individuals each time. Since only one sampling occasion was performed during the 2017 wet season, a larger number of individuals (10) was sampled to reduce the uncertainties associated with different sampling sizes between wet and dry seasons respectively. For each tree, we measured diameter at breast height (DBH) and height, and for the coffee plants the diameter of the main stem was measured below its bifurcation in small branches (Table 1).

Bulk soil samples were collected at three locations and at 5, 15, 30, 60, 90 and 120 cm depth each, using a hand auger. Auger sampling points were located so that each of the sampled shade trees and coffee plants had a total of three soil sampling points within their 3 m radius.

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

To establish the local meteoric water line and compare soil water sources with recent rainfall, bulk samples of rainfall were collected weekly at a nearby (~ 5 km) meteorological station over the course of four years (December 2013 to December 2017) as part of a long-term isotope sampling of precipitation (cf. Muñoz-Villers et al., 2018).

2.4 Isotope collection and analysis

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

Xylem and soil samples were extracted using cryogenic vacuum distillation (temperature: 100 ± 1.1°C, vacuum: 3 ± 1.5 Pa and time: 60-70 min) following the method of West et al. (2006). The δ^2H and δ^{18}O isotopic compositions of extracted water samples were then determined using an isotope-ratio mass spectrometer (Thermo Delta Plus XL, Thermo Fisher Scientific, USA). The analytical precision of the instrument was ± 0.60‰ (1 SD) for δ^2H and ± 0.12‰ (1 SD) for δ^{18}O. Samples of precipitation were analyzed for δ^2H and δ^{18}O using a laser water isotope analyzer (L2140-i) from Picarro Inc. (Santa Clara, CA, USA) in high precision and without Micro-Combustion Module mode. The analytical precision was ± 0.65‰ (1 SD) and ± 0.20‰ (1 SD) for δ^2H and δ^{18}O, respectively.

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

2.5 Soil sampling and laboratory determinations

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

To examine pH and N, P and K macronutrient concentrations along the soil profile, soil samples were collected at 5, 15, 30, 60, 90 and 120 cm depth from each borehole (n = 3 samples per soil depth) during three sampling campaigns: Apr. 11, 2014 (dry season), Feb. 27, 2017 (dry season) and Aug. 4, 2017 (wet season). Samples were first air-dried and then sieved using 2 mm screens. Soil pH was determined using a glass electrode pH meter in a 1:2 soil: water ratio. Total carbon (C) and total nitrogen (N) were measured using a TruSpec dry combustion CN analyzer (LECO, USA). Extractable phosphorus (P) was determined by the Bray I method (Bray and Kurtz, 1945). Exchangeable K+ was determined by extracting soil with 1 M NH4OAc at pH 7.0, and then analyzed using flame photometry.

2.6 Root biomass

To examine the root biomass distribution along the soil profile in the study plot, 33 soil cores were obtained using 5 cm diameter and 10 cm long samplers. Soil cores were extracted at

https://doi.org/10.5194/hess-2019-329
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5, 20, 40, 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 depth). All cores were processed immediately in the laboratory. Soil samples were first sieved using 2 mm screens to separate the bigger roots. Next, the samples were washed using a fine nylon mesh sieve, and then separated into diameter classes (< 1 mm, 1–2 mm and > 2 mm) and dried at 70 °C for 48 hours. Root biomass (g m−3) was calculated from the dry weight of the roots and the volume of the core sampler for each class and soil depth.

2.7 Plant water uptake sources and temporal patterns

The MixSIAR Bayesian mixing model framework (Moore and Semmens, 2008; Stock et al., 2018) was used to determine the most likely contributions of water sources for the shade tree species and coffee shrubs sampled over the course of the 2014 (Jan. 23, Apr. 11 and 26) and 2017 (Feb. 27, Apr. 5, May. 20) dry seasons and the 2017 wet season (Aug. 4). To assess temporal changes of the different plant water sources, the seven sampling occasions were modeled separately. The mixture data for the model was the mean xylem water isotopic composition of the shade tree species and coffee shrubs, changing accordingly with the sampling date. The relative contribution of three potential xylem end-member water sources was evaluated. These included rainfall as surrogate for near surface water (< 5 cm depth), shallow soil water (average of 5-15 cm depth) and deep soil water (average of 30-120 cm depth). For each sampling date, the mean and standard deviation of the isotopic signatures of the water sources were introduced into the model as follows: rain water isotope data from a month prior to the xylem sampling and soil water isotope data from the two different grouped soil depths, all corresponding to the date of xylem tissue collection.

Further, we also considered the use of additional data such as soil macronutrients (N, P, K) and root biomass information to constrain model estimates by specifying an ‘informative’ prior distribution of the soil source proportions (Stock et al., 2018). These data were grouped into two classes based on the depth of the soil samplings and corresponding largely with the grouping for soil water: shallow (0-20 cm) and deep (40-120 cm). In addition, the nearest corresponding dry or wet season dataset of soil macronutrients were used according to the date of sampling. The effect of using these priors (i.e. a weight proportion before considering the isotope data) on the water sources distribution was then examined by comparing these with the results of ‘non-informative’ (i.e. all the combinations of proportions of water sources were equally likely) simulations. The results of each of these model runs were accepted based on the examination of Markov Chain Monte Carlo convergence using the Gelman-Rubin and Geweke diagnostic tests (Gelman et al., 2014).

Lastly, the relative contributions of the water sources were compared among shade trees and coffee shrubs across all sampling dates using factorial ANOVA and Tukey’s HSD post-hoc

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tests. The analyses were carried out in R Statistical Software version 3.2.4 (R Core Development Team, 2016).

3. Results

3.1 Hydrometeorological conditions

Precipitation (*P*) was 1650 mm in the first study year (Nov. 2013 – Oct. 2014) and 1423 mm in the second study year (Nov. 2016 – Oct. 2017). During the 2013-2014 dry season (Nov – Apr.), rainfall was 323 mm, and mean daily values of temperature (*T*) and vapor pressure deficit (VPD) were 17.6 ± 3.0°C and 0.65 ± 0.39 kPa, respectively. The lowest monthly amounts of *P* and the highest values of *T* and VPD were observed in April at the end of the dry season (Fig. 2a,b). During the 2016-2017 dry season, rainfall was 235 mm, with lowest monthly values registered in January and February at the middle of the season (Fig. 2b). Mean daily *T* was 18.3 ± 2.6°C, with highest values observed at the end of the dry period. Overall, high VPD values prevailed over the course of this dry season (0.78 ± 0.46 kPa on average), although maximum values were particularly observed in February and May.

Compared to long-term (1971−2000) climatic records of the region, rainfall in the first year of study was very close to the mean annual precipitation of 1765 mm (SMN, 2018). In contrast, the second year was drier (~ 300 mm less); the difference was particularly observed during the dry season, which had about 40% lower precipitation than the average value of 389 mm. Also, higher mean monthly temperatures (+ 0.54°C) prevailed across the 2017 dry season in comparison with the 1971−2000 period.

Rainfall during the 2017 wet season (May – Oct.) was lower in comparison to 2014 (1188 mm vs. 1326 mm, respectively) (Fig. 2b). Further, the mean air temperature and vapor pressure deficit were slightly higher in the 2017 wet season than in the 2014 wet season (20.7 ± 1.6 °C and 0.67 ± 0.25 kPa vs. 20.1 ± 1.5 °C and 0.60 ± 0.21 kPa, respectively) (Fig. 2a).

3.2 Soil moisture and antecedent precipitation during sampling campaigns

During the 2014 dry season campaign (Jan. – Apr.), mean soil water content (SWC) was on average 39.8 ± 6.7% in the shallower layers (5-15 cm depth) and 46.0 ± 5.2% in the deeper layers (30-120 cm depth) (Fig. 2b). In comparison, SWC in the 2017 dry season campaign (Feb. – May.) was lower in the shallower layers (32.5 ± 5.8%), meanwhile water content in the deeper layers was similar (48.9 ± 2.9%) with respect to the 2014 dry period. In 2014, lowest SWC values were observed at the end of the dry season (April), whereas the greatest soil moisture depletion in 2017 was registered at the middle of the dry season (February) (Fig. 2b).

During the wet season sampling in August 2017, higher SWC values in the shallower (35.0 ± 3.7%) and deeper (48.9 ± 7.2%) soil layers were generally observed in comparison to the 2017 dry period (Fig. 2b). For the different samplings, antecedent wetness conditions were, respectively, 4, 30 and 13 mm for Jan. 23, Apr. 11 and 26, 2014 and 1, 12, 9 and 43 mm for Feb. 27, Apr. 5, May. 20 and Aug. 4, 2017.

3.3 Stable isotope composition of waters

Over the study periods, a greater range of variation was found in the rainfall isotope composition of the 2013-2014-year (from –126.7 to 14.4‰ δ^2H; from –17.7 to 0.01‰ δ^{18}O) in comparison to the 2016-2017-year (from –113.3 to 15.5‰ δ^2H; from –15.9 to 0.01‰ δ^{18}O) ($p >$ 0.05)(Fig. 3). Overall, mean dry season rainfall was significantly more enriched than the mean wet season rainfall in δ^2H and δ^{18}O ($p \leq 0.001$) (Table 2 and 3). In the second study year, the isotopic compositions of the dry and wet season rainfall were both on average more depleted than the first study year; thus the local meteoric water line of 2016-2017 had a slightly steeper slope in comparison to the one for 2013-2014 (Fig. 3). Nevertheless, the range of variation of deuterium excess values was similar between years (9–29‰ for the first year vs. 9–31‰ for the second year; Fig. 3), and deuterium excess values of rainfall between the dry and wet seasons were not statistically different ($p \geq 0.05$).

For all sampling dates, hydrogen and oxygen isotope composition of bulk soil water showed a consistent pattern of increasing isotope depletion with depth (Supplementary Materials), in which shallower (5-15 cm) soil water was significantly more enriched than deeper (30-120 cm) soil water ($p \leq 0.001$) (Table 2 and 3; Fig. 3). In correspondence, lower values of deuterium excess generally characterized the shallower soil water pool.

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

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

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Across all sampling periods, xylem water of coffee shrubs was more enriched than that of shade trees ($p \leq 0.001$) (Table 2 and 3), and values of δ^2H and $\delta^{18}O$ plant xylem (–40.8 ± 15.0‰ and –4.6 ± 1.6‰, respectively) were on average more positive in comparison to bulk soil water (–46.7 ± 16.4‰ and –6.0 ± 2.3‰, respectively)($p > 0.05$)(Fig. 3).

In the 2014 dry season, xylem water isotope values of shade trees ranged from –65.5 to –32.1‰ for δ^2H and from –7.6 to –3.6‰ for $\delta^{18}O$, meanwhile a larger variation was observed in the xylem water of coffee shrubs (from –46.5 to –9.6 ‰ δ^2H and from –6.3 to –0.6‰ $\delta^{18}O$) ($p \leq 0.001$) (Fig. 3a). Among tree species, *Lonchocarpus guatemalensis* showed the most depleted xylem water isotope signature (–58.1 ± 4.8‰ δ^2H and –6.8 ± 0.5‰ $\delta^{18}O$), whereas *Inga vera* reported the most enriched values with a greater range of variation (–51.0 ± 10.2‰ δ^2H and –5.3 ± 1.1‰ $\delta^{18}O$). Intermediate δ^2H and $\delta^{18}O$ values were observed in *Trema micrantha* (–57.1 ± 5.4‰ and –6.6 ± 0.6‰, respectively) (Fig. 4a). Statistical tests showed that *Inga vera* was significantly different from *L. guatemalensis* and *T. micrantha* in $\delta^{18}O$ ($p < 0.05$).

In the 2017 dry season, the isotopic composition of shade trees varied from –56.7 to –34.5‰ for δ^2H and from –6.0 to –3.2‰ for $\delta^{18}O$; corresponding values for coffee shrubs varied from –39.6 to –7.8 ‰ for δ^2H and from –4.4 to –1.1‰ for $\delta^{18}O$ ($p \leq 0.001$) (Fig. 3b). *L. guatemalensis* showed the most enriched isotope value (–41.3 ± 5.7‰ δ^2H and –4.6 ± 0.5‰ $\delta^{18}O$), and *I. vera* reported the most depleted values (–48.5 ± 5.1‰ δ^2H and –4.8 ± 0.8‰ $\delta^{18}O$), with differences being suggested for δ^2H ($p < 0.05$). Intermediate δ^2H and $\delta^{18}O$ values were observed in the xylem water of *T. micrantha* (–45.9 ± 3.6‰ and –3.9 ± 0.6‰, respectively), showing differences in $\delta^{18}O$ with the other two species ($p < 0.05$).

Overall, more enriched isotope values of plant xylem water were observed in the 2017 dry season in comparison to those in 2014 ($p \leq 0.001$) (Fig. 3a,b; Fig. 4). Also, lower deuterium excess values were obtained in shade trees and coffee shrubs in 2017 as sign of a more evaporative signature (Table 2 and 3; Fig. 3). Plots of δ^2H xylem water against height for the individual shade trees and coffee shrubs sampled in both dry seasons are shown in Figure 4, in which a similar δ^2H pattern was displayed between trees and coffee shrubs in the 2014 and 2017 years.

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

3.4 Root biomass and macronutrients along soils profile

Overall, most roots were concentrated in the first 5 cm of soil with a sharp decline in biomass at 20 cm depth (Fig. 5a). Fine roots (< 1mm) followed by bigger roots (> 2 mm) dominated the shallower soil layers (< 20 cm), meanwhile roots in general were scarce at deeper depths (> 60 cm). Soil acidity was higher at the near surface layers decreasing gradually as soil depth increased (Table 4). Organic matter (OM) was also greatest between 5 and 15 cm depth, however values decreased rapidly below ~30 to 60 cm depth. Highest concentrations of nitrogen were found in the first 15 cm, although values remain relatively high and constant at deeper layers (Fig. 5b). Phosphorus showed its highest concentration at the topsoil with values decreasing sharply below 30 cm depth. In contrast, lowest concentrations of potassium were found at the near surface layers (< 15 cm depth) while maximum values were observed at 120 cm depth.

3.5 Plant water sources

In general, there was a good agreement between the MixSIAR Bayesian mixing model results using a non-informative and an informative prior distribution (on average 5% difference across all xylem water contributing sources; $p > 0.05$). This indicates that the independent distribution (soil macronutrients and root data) set a *priori* to optimize model source proportion estimates (informative approach) was not influential enough to significantly modify the results obtained using the isotope signatures of the xylem end-member water sources alone (non-informative approach). Having this agreement between models, we present the results of the water source contribution based on the informative prior distribution. Results of the non-informative approach have been provided in the Supplementary Materials.

The model results showed that the deep soil water pool was the main source for the shade trees over the course of the 2014 dry season (Fig. 6 and Supplementary Materials). Across this period, *L. guatemalensis* and *T. micrantha* showed on average higher proportion of deep soil water uptake (91± 12% and 88 ±10%, respectively) in comparison with *I. vera* (74± 14%) ($p > 0.05$). For the coffee plants, the analysis showed that water uptake was mainly sustained by shallow soil water sources (65 ± 23%) (Fig. 6), having significant differences with *L. guatemalensis* ($p < 0.001$), *T. micrantha* ($p < 0.001$) and *I. vera* ($p < 0.05$) tree species across the 2014 dry period studied.

During the 2017 dry season, all shade tree species were tapping high proportions of deep soil water (86 ± 13% for *L. guatemalensis*; 85 ± 19% for *T. micrantha* and 92 ± 12% for *I. vera*; Fig. 7a,b,c and Supplementary Materials). Among samplings, differences were only suggested between *L. guatemalensis and I. vera* at the end of the dry period (Apr. 5) ($p < 0.05$). Coffee water sources were mainly obtained from shallow soil layers (54± 29%) (Fig. 7a,b,c), although in 2017 the contribution of this water source was slightly smaller (9%) in comparison to 2014

(Supplementary Materials), statistical differences were not suggested between dry periods ($p > 0.05$).

Across the individual samplings throughout the two dry seasons, we observed that antecedent precipitation had a stronger effect in the water uptake sources of coffee plants than trees (Fig. 8). For example, when dry antecedent wetness prevailed ($API_{15} < 5$ mm; Fig. 2b) coffee water sources were mainly composed by deep (46 ± 23%) and shallow (38 ± 35%) soil water, meanwhile when wetter antecedent conditions were present ($API_{15} > 10$ mm) the shallower soil water layer (63 ± 22%) was the main contributing source. On the contrary, tree water uptake was essentially sustained by deep soil sources (91± 13% and 80 ± 15%, respectively) at low and relatively high antecedent wetness conditions (Fig. 8). For all species investigated, the relationships between API and the contribution of deep soil water sources were not found statistically significant ($p > 0.05$).

In the 2017 wet season, sources of tree water uptake differed significantly among species (Fig. 7d and Supplementary Materials). During this period, *L. guatemalensis* and *I. vera* still showed the greatest use of deep soil water (64 ± 37% and 70 ± 36%, respectively) ($p > 0.05$), meanwhile shallow soil water was the main source for *T. micrantha* (72 ± 39%; Fig. 7d), having differences with the other two tree species ($p < 0.001$). Coffee consistently showed the use of near surface water sources (69 ± 22%) (Fig. 7d and Supplementary Materials), being significantly different in relation to all shade tree species ($p < 0.001$).

4. Discussion

4.1 Complementary water use strategy between shade trees and coffee shrubs

Our ecohydrological research consistently showed that all shade tree species (*L. guatemalensis*, *I. vera* and *T. micrantha*) relied mainly on water sources from deep soil layers (> 15 to 120 cm depth), while the use of much shallower water sources (< 15 cm) was observed in the coffee (*C. arabica* var. *typica*) over the course of the normal and more pronounced dry seasons studied. These findings suggest a spatial and temporal partitioning of belowground water resources between trees and coffee plants during drier periods and water-resource complementary in the mixed species plantings. Although comparisons with other traditional shade coffee plantations are difficult because studies are essentially lacking in this type of agroecosystems, there are a handful of other investigations carried out in shade coffee monospecific plantations in the humid tropics in which complementary rather than competitive water use strategies prevailed. For example, Cannavo et al. (2011) compared the water use and soil water availability of an unshaded coffee vs. a shaded monoculture (*Inga densiflora*) coffee plantation in Costa Rica, both of 7-8 years old, using soil moisture measurements and water balance calculations. Their results showed that soil water content in the deeper soil layers (> 120 cm depth) was lower in the shaded coffee than in the full sun coffee system, while water content in the shallower layers was similar. This suggested that associated shade trees preferentially used water from deeper soil horizons providing some evidence of complementarity water use between coffee plants and native *Inga* trees during the dry season. However, the authors acknowledged that they were unable to separate roots from coffee than those of trees in the soil profiles, so they could not be certain whether trees were the only individuals extracting water from deeper sources. In this respect, our study showed that there was always a mixture in water uptake from different sources (soil depths), but a separation between the main sources of water for shade trees and coffee shrubs clearly prevailed.

Other investigations in Costa Rica have examined the belowground resource competition of Arabica coffee in association with fast-growing timber species using data of plant growth, root distribution and density, and soil moisture and nutrients patterns. For example, the study of Schaller et al. (2003) carried out in a commercial (*Eucalyptus deplupta*) shade coffee plantation where soils are highly fertilized, showed that coffee had a relatively even root distribution along the first 40 cm of soil depth with a higher root density in the proximity of the coffee rows. Conversely, the root system of *E. deplupta* was much shallower having most roots concentrated in the upper 10 cm of soil. In this case, the tree root density was found highest in the alleys between the coffee rows. The authors explained that the apparent complementary resource exploitation of this tree-crop system was mainly attributed to high soil resources availability and the high competitiveness of the coffee limiting the expansion of tree roots (cf. Lehmann, 2003). Although in our study we did not determine the depth distribution of coffee and tree roots, our findings showed that all shade tree species were tapping water from deeper soil layers than coffee, suggesting that trees are deep rooted and being able to explore larger soil volumes causing little competition with coffee.

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

Our findings also showed that during the wet season coffee plants substantially increased the use of near surface water (~70%) in comparison to the dry season, while all shade trees also extended their water acquisition to much shallower soil water pools. This is largely explained by the increases in soil moisture in the first 30 cm depth due to frequent rainfall inputs that characterize the wet season in our study area. This suggests that coffee had a higher root activity in surface soil layers during the wet season in comparison to the dry season, as has been documented in other studies (Huxley et al., 1974). Regarding the shade tree species, we observed that *T. micrantha* showed the greatest response to the wet season conditions by drawing most water from the first 15 cm of soil (72%), whereas this was much less evident in *L. guatemalensis* (30%) and *I. vera* (29%). Although we did not determine the vertical distribution of roots for each of the shade tree species studied, these findings suggest that *T. micrantha* has a shallower rooting system than the other tree species. The fact that the *T. micrantha* trees were more recently planted (i.e. younger with less developed root system) than the *L. guatemalensis* and *I. vera* trees supports this idea. On other hand, the high temperature and rainfall that characterize the wet season at our study site may favor rapid mineralization of nutrients and their subsequent leaching to deeper soil layers (i.e. potassium; Table 4). Hence, for the larger trees studied (*L. guatemalensis*), the water and nutrients available at deeper depths could have been an important resource for plant growth in this period, partly explaining the lower activity of their shallow roots. Despite the changes and the higher variability in depth of water uptake observed among canopy trees and coffee shrubs, a complementary use of soil water prevailed during the wet season. Future work should be focused on the distribution and dynamics of tree and crop roots and their seasonal variation in relation to the availability of nutrients and water in the soil. Also, it would be desirable to relate these dynamics to crop and shade tree phenology to elucidate temporal synergistic or competitive water requirements.

4.2 The role of antecedent wetness in coffee water uptake

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

4.3 Implications and future directions

The consistent complementarity in plant water use strategies observed under different hydrometeorological conditions in the coffee plantation studied provides support to the central tenet of agroforestry systems (Cannel et al., 1996). Since the trees obtained their water from deeper soil layers than the coffee, this could mean that they utilize nutrients leaching beyond the reach of the coffee plants, and so contribute to improved nutrient cycling and increased overall productivity of the system (van Noordwijk et al., 2015).

Nevertheless, the current outcome may change given the new coffee management practices that consist on replacing traditional coffee varieties (e.g. *C. arabica* var. *typica*) with others (*C. arabica* var. *costa rica; C. canephora*) that may exhibit deeper roots systems and perhaps different water (and nutrient) uptake strategies, in response to prevalent diseases such as leaf rust or root nematodes. Therefore, future research should be focused on evaluating the water source partitioning of traditional vs. new coffee varieties and their relation to shade tree water use. In this respect, there are further questions with regard to strategic use of shade tree species, whereby fast-growing species might be more (commercially) productive but also more competitive. Some evidence from elsewhere has shown that such management practices do not necessarily increase competition and may even enhance the water use efficiency as part of drought-avoidance mechanisms. For example, in southeast China, Wu et al. (2016) used $\delta^{2}H$ and $\delta^{18}O$ stable isotope methods to examine the

https://doi.org/10.5194/hess-2019-329
Preprint. Discussion started: 26 July 2019

seasonal water use of a fast-growing rubber tree species (*Hevea brasilensis*) planted with Arabica coffee. Their findings showed that rubber trees were mostly accessing water from intermediate (15-50 cm depth) and deep soil layers (50-110 cm), meanwhile coffee was mostly tapping water from the topsoil (< 15 cm). Additionally, rubber trees showed strong root plasticity in soil water uptake avoiding competition with coffee during the rainy and relatively dry seasons. However, more research is needed since these results depend largely on tree-crop specie combinations and local climatic and soil conditions.

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

Finally, in our methodology we used prior information alongside the stable water isotope approach to better understand plant water uptake dynamics. Even though our results did not change significantly by including or excluding the root and nutrient data, exploring plant water source partitioning using these two approaches provided more confidence in our results. We would recommend that other authors also consider using nutrient and root data in combination with plant xylem water end members to better understand water uptake patterns, especially to explore the additional value of this information in different environments.

5. Conclusions

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

Author contributions. LEMV designed the experiment. LEMV, MSAB and FH collected the field data. MSAB performed the Bayesian mixing model analysis. JG contributed in the data analysis. LEMV prepared the first draft of the manuscript. FH, MSAB and JG edited and commented on the manuscript several times. TED carried out the final revision.

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

Acknowledgments

We would like to thank Raul Monge and Daniel Tejeda for their permission to conduct this research in “La Orduña” coffee plantation. We also thank Melissa López-Portillo for performing the cryogenic extractions and Stefania Mambelli and Wembo Yang for analyzing the water isotope samples at UC-Berkeley, USA. Angel Zaragoza, Erika Mendoza, Alitzel Guzmán and Carlos Alcocer are thanked for their assistance in the sampling campaigns. The Instituto de Ecología, A.C. (INECOL) is thanked for the laboratory facilities to carry out the root separation and oven-dry weights. We also thanked Adriana Hernández and Esperanza Huerta for helping in the root separation process. This research was supported by the PAPIIT-UNAM (No. IB100313 and IB100113) grants, respectively to LE Muñoz-Villers and F Holwerda, and by the INFRA-CONACyT-México (No. 187646) grant to F Holwerda. Additional support was provided by the NSF-USA (No. 1313804) and by the Scottish Funding Council via the University of Aberdeen (SP10192). Data analysis and partial writing of the manuscript was performed during LEMV sabbatical leave (March-July 2018) hosted by Josie Geris at the University of Aberdeen, UK, and granted by the *Programa de Apoyos para la Superación de Personal Académico* (PASPA) of the UNAM.

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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		*n*
			DBH cm	Height m	DBH cm	Height m	
Fabaceae	*Lonchocarpus guatemalensis*	Overstory	101.5 (12.6)	20.3 (1.3)	119.8 (12.1)	21.0 (1.2)	3
Fabaceae	*Inga vera*	Overstory	39.3 (15.7)	10.7 (4.8)	48.1 (13.3)	9.6 (1.2)	3
Cannabaceae	*Trema micrantha*	Overstory	13.16 (6.8)	8.15 (3.1)	23.3 (7.2)	15.2 (2.2)	3
Rubiaceae	*Coffea arabica* var. *typica*	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

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Table 2. Mean ± (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 deuterium excess values (‰)

Precipitation *n* = 41						Bulk soil water *n* = 54						Shade trees xylem water *n* = 27			Coffee shrubs xylem water *n* = 14		
Dry season			Wet season			5-15 cm depth			30-120 cm depth								
δ^2H	δ^{18}O	*d*-excess	δ^2H	δ^{18}O	*d*-excess	δ^2H	δ^{18}O	*d*-excess	δ^2H	δ^{18}O	*d*-excess	δ^2H	δ^{18}O	*d*-excess	δ^2H	δ^{18}O	*d*-excess
1.6 ± 8.5	–1.9 ± 1.4	17.0 ± 5.1	–42.4 ± 36.1	–7.2 ± 4.3	14.9 ± 2.8	–25.6 ± 9.9	–3.0 ± 1.2	–1.3 ± 5.2	–63.8 ± 10.4	–8.3 ± 1.4	2.0 ± 5.0	– 55.4 ± 7.6	– 6.2 ± 1.0	–5.8 ± 4.1	– 25.5 ± 10.8	–3.4 ± 1.8	1.7 ± 5.0

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Table 3. Mean ± (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 deuterium excess values (‰)

Precipitation *n* = 39						Bulk soil water *n* = 54						Shade trees xylem water *n* = 24			Coffee shrubs xylem water *n* = 18		
Dry season			Wet season			5-15 cm depth			30-120 cm depth								
δ^{2}H	δ^{18}O	*d*-excess	δ^{2}H	δ^{18}O	*d*-excess	δ^{2}H	δ^{18}O	*d*-excess	δ^{2}H	δ^{18}O	*d*-excess	δ^{2}H	δ^{18}O	*d*-excess	δ^{2}H	δ^{18}O	*d*-excess
–2.9 ± 16.0	–3.0 ± 1.8	21.5± 4.3	–47.8 ± 34.4	–7.9 ± 4.1	15.2 ± 3.3	–28.6 ± 5.9	–3.0 ± 0.9	–4.9 ± 5.4	–45.3 ± 4.7	–6.2 ± 0.6	4.6 ± 3.6	–44.9 ± 5.6	–4.4 ± 0.7	–9.7 ± 5.4	–21.3 ± 7.2	–2.8 ± 1.0	1.3 ± 6.2

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

Soil depth (cm)	pH (H_2O)	OM (%)	C (%)	N (%)	K ($cmol_c\ kg^{-1}$)	P ($mg\ kg^{-1}$)
5	4.07	5.18	2.54	0.38	0.60	33.33
15	4.12	2.89	1.90	0.30	0.47	4.60
30	4.34	1.55	1.31	0.23	0.77	n.d.
60	4.95	1.02	0.69	0.22	0.93	n.d.
90	5.10	0.48	0.50	0.20	1.11	n.d.
120	5.16	0.41	0.51	0.20	1.45	n.d.

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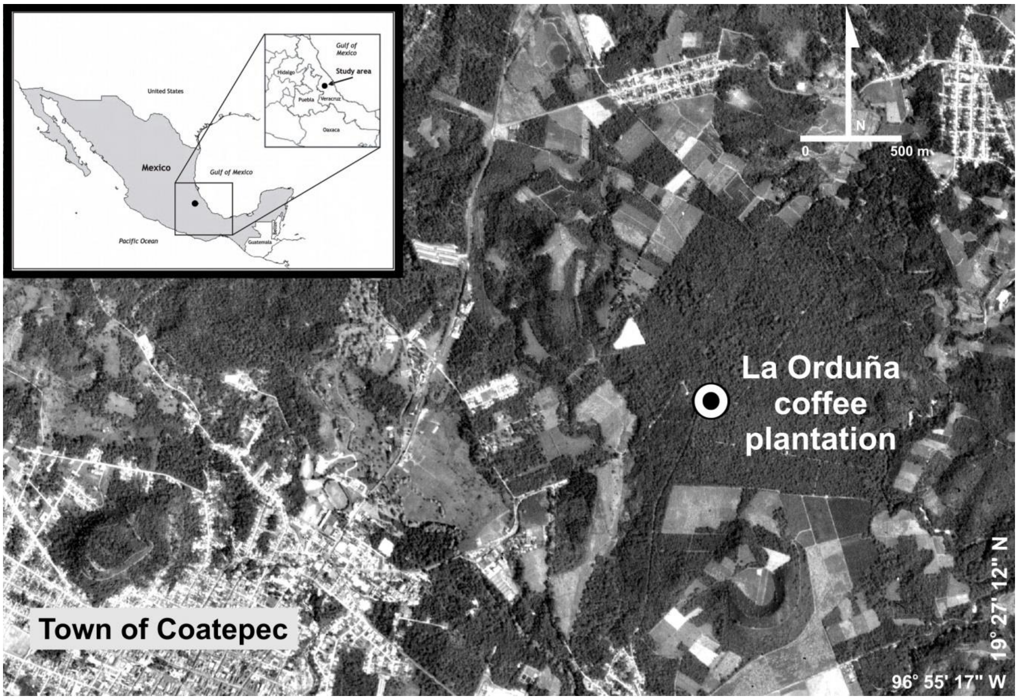

Figure 1. Study site location in the municipality of Coatepec, Veracruz, Mexico. Source: QuickBird Satellite Image (2010). Copyright DigitalGlobe, Inc.

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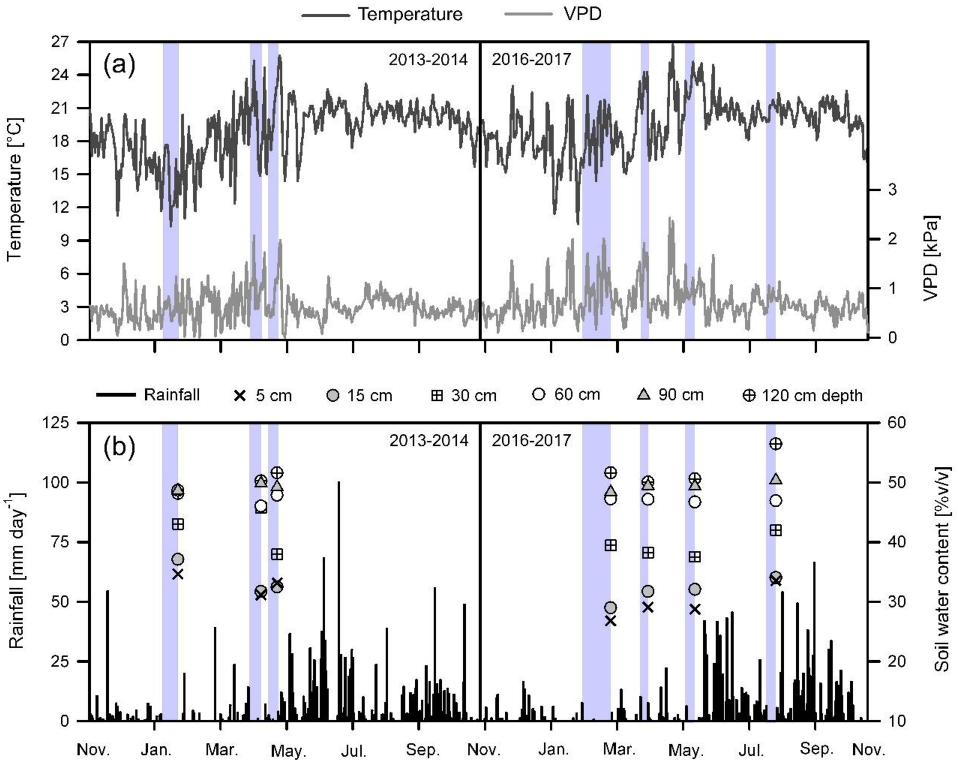

Figure 2. (a) Daily mean air temperature and vapor pressure deficit (VPD) and (b) and daily total rainfall (*P*), as measured from November 2013 to October 2014 and from November 2016 to October 2017, and volumetric soil water content (SWC) measured at different depths during the sampling campaigns in 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.

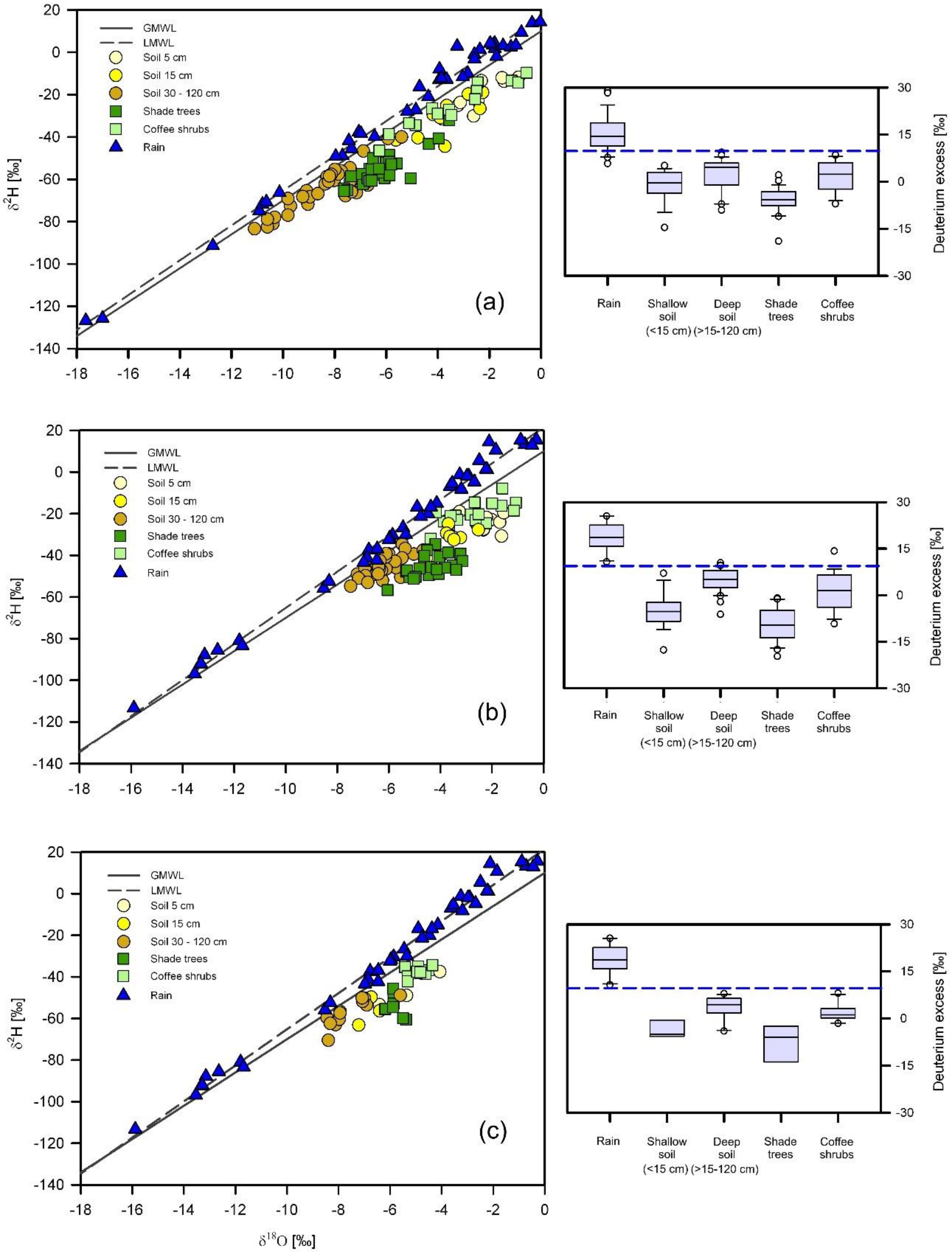

Figure 3. (a) Isotope composition of xylem water for shade trees and coffee shrubs, bulk soil at different depths as observed during the three sampling dates (Jan. 23, Apr. 11 and Apr. 26, 2014),

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; δ^2H = 17.82 + 8.26* δ^{18}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. The dashed line represents the 2016–2017 local meteoric water line (LMWL; δ^2H = 21.0 + 8.36* δ^{18}O), 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 solid line represents the global meteoric water line (GMWL; δ^2H = 10 + 8* δ^{18}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.

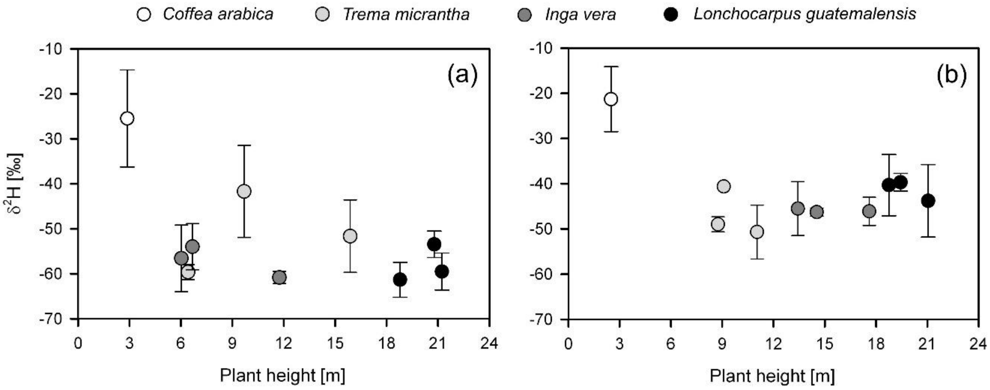

Figure 4. Plant height vs δ^2H xylem water for coffee plants and shade tree species corresponding to (a) the 2014 and (b) 2017 dry season samplings.

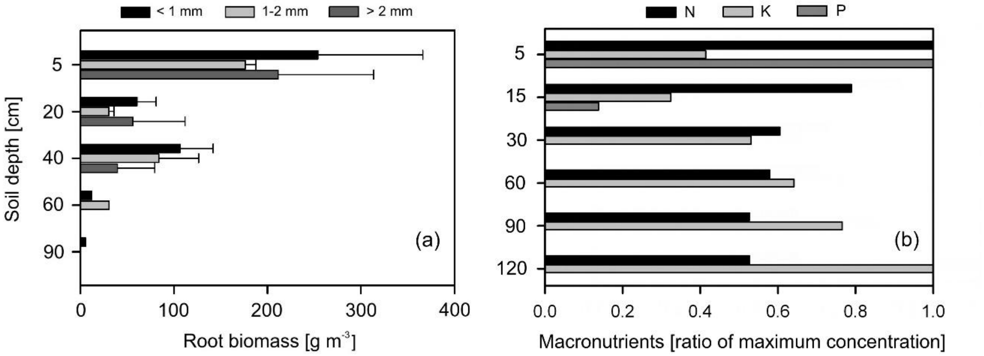

Figure 5. (a) Distribution of root biomass for three size classes of roots (different color bars), and (b) macronutrients distribution along the soil profile, here normalized and expressed as in ratio to their maximum values (absolute values in Table 4).

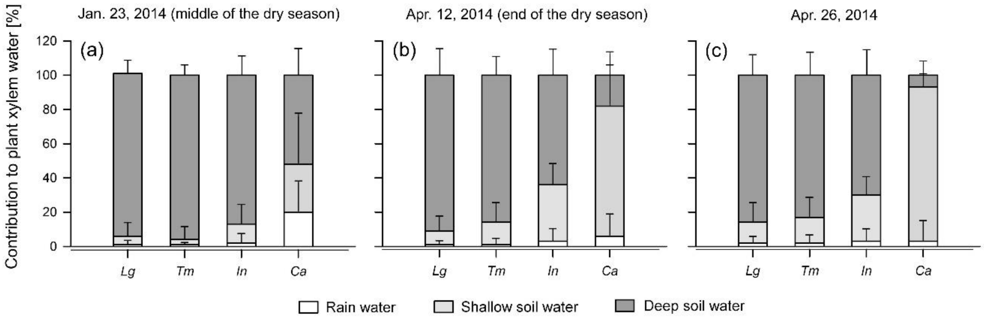

Figure 6. MixSIAR Bayesian mixing model results showing the mean likely contribution of each water source to the xylem water of shade canopy trees and coffee shrubs. (a), (b) and (c) show results for the sampling dates of Jan. 23, Apr. 12 and Apr. 26, 2014 respectively, using the informative prior distribution.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

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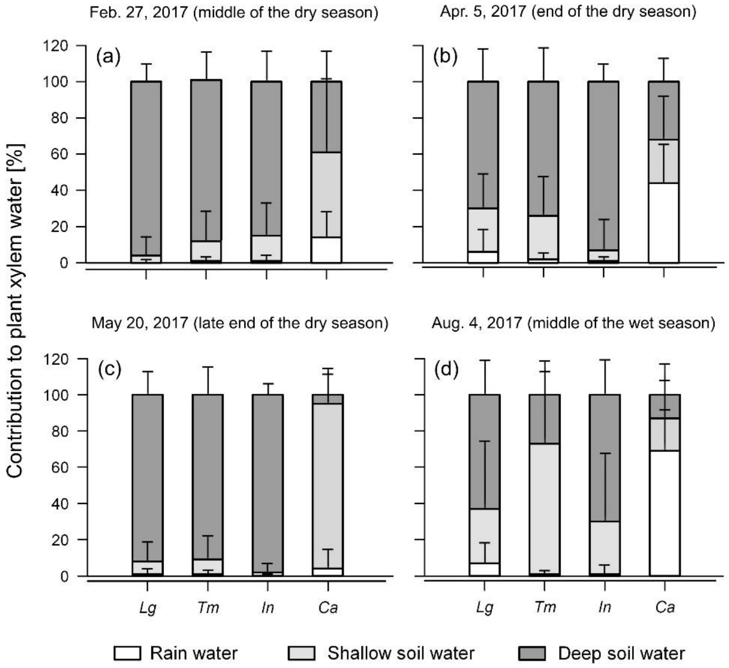

Figure 7. MixSIAR Bayesian mixing model results showing the mean likely contribution of each water source to the xylem water of shade canopy trees and coffee shrubs. (a), (b), (c) and (d) show results for the sampling dates of Feb. 27, Apr. 5, May. 20 and Aug. 4, 2017 respectively, using the informative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

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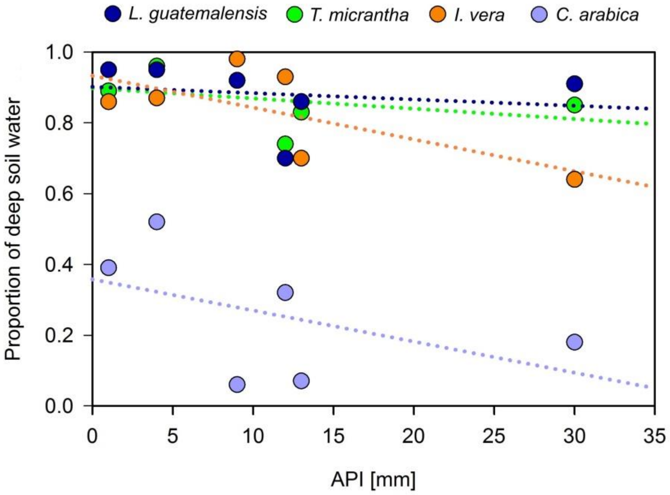

Figure 8. Contribution of deep soil water to plant uptake at different antecedent precipitation conditions across the 2014 and 2017 dry seasons.