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Positive Effects of Scattered Trees on Soil Water Dynamics in a Pasture Landscape in the Tropics

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As a result of canopy interception and transpiration, trees are often assumed to have negative effects on the local hydrological budget resulting in reduced soil and groundwater resources. However, it has also been shown that trees can have positive effects through reducing surface run-off and improving soil infiltrability and groundwater recharge, especially in many tropical ecosystems characterized by high rain intensity and degradation-prone soils. In this study, we used isotopic measurements of soil water to better understand the main processes by which trees influence local soil water dynamics within a tropical pasture with scattered tree cover in the Copan River catchment, Honduras. We also determined the stable isotope signature of xylem water in grasses and trees to assess potential competition for water sources during the wet and dry seasons. During the wet season, when soil water availability was not limiting, both grasses and trees primarily utilized soil water near the soil surface (i.e., 0–10 cm). In contrast, during the dry season, we observed niche partitioning for water resources where grasses primarily utilized soil moisture at deeper soil depth (i.e., 90–100 cm) while trees relied heavily on groundwater. Moreover, isotopic data of soil water suggest that trees reduce evaporative water losses from the soil surface, as indicated by the lack of correlation between soil water content and lc-excess (line condition excess) values of surface soil water under trees, and enhance preferential flow as suggested by less negative lc-excess values under trees compared to open areas during the dry season. Taken together, our findings provide further support that trees can have positive effects on the local water balance with implication for landscape management, promoting the inclusion of scattered trees to provide water ecosystem services in silvopastoral systems, adding to other ecosystem services like biodiversity or carbon sequestration.

Keywords: niche partitioning, groundwater recharge, land management, ecosystem, tree-grass coexistence, isosource mixing model

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INTRODUCTION

In tropical Central America, 74% (i.e., 84 million hectares) of the total agricultural land was used for meadows and pastures in 2019 (FAOSTAT, 2019), and this area is expected to increase by 32% by 2030 (Acosta and Díaz, 2014). At the same time, the sustainable use of pastures is at risk due to ongoing degradation (Szott et al., 2000; Muchagata and Brown, 2003), resulting in negative consequences on productivity, erosion, and water resources (Martínez and Zinck, 2004). Trees are commonly integrated into pastoral systems for various reasons including reducing soil degradation, increasing carbon stocks, providing protecting shade, and reducing financial risks due to farmers' income diversification (Erdmann, 2005; Verchot et al., 2007; Wassenaar et al., 2007; Harvey et al., 2014; Mulugeta, 2014). Despite their multiple benefits, trees are commonly assumed to decrease valuable soil and groundwater resources due to their higher interception and transpiration compared to shorter vegetation, leading to increased transport of water back to the atmosphere (Giambelluca, 2002, Calder, 2001; Fisher et al., 2009; Ellison et al., 2012, 2017). However, given the prevalent high rain intensity (Lal, 1990; Labrière et al., 2015) and severe soil degradation in many tropical ecosystems, trees could potentially have positive effects on the local water balance by reducing surface run-off and improving soil water infiltrability and groundwater recharge (Bargués Tobella et al., 2014; Benegas et al., 2014; Ilstedt et al., 2016; Bargués-Tobella et al., 2020). According to the *optimum tree cover theory*, intermediate tree densities on soils prone to degradation may maximize groundwater recharge, as the hydrologic gains attributed to tree cover can be proportionally higher than the additional losses from increased transpiration and interception (Ilstedt et al., 2016). Given the importance of water availability for human health, economy, ecosystem functioning, geophysical processes, and social-ecological system resilience at large (Cazenave et al., 2004; Mooney et al., 2005; Falkenmark et al., 2019), the lack of studies on water dynamics, including water source partitioning, in tropical pastures with open tree cover is alarming.

Water is a key resource in determining the structure and composition of vegetation in savanna-like ecosystems (van Wijk and Rodriguez-Iturbe, 2002). It is commonly thought that the coexistence of tree-grass communities is the result of niche partitioning whereby woody and herbaceous plant species do not compete for the same limiting resource, i.e., soil water (Jeltsch et al., 2000; Ward et al., 2013). One possible explanation for the lack of competition between trees (or shrubs) and grasses may be the result of differences in root morphology (Lehmann et al., 1998; Dulormne et al., 2004). Previous studies in temperate ecosystems have shown that trees tend to be more deep-rooted, accessing deeper water sources compared to grasses, which have more fibrous rooting systems and thus rely on soil moisture near the soil surface (Sala et al., 1989; Weltzin and McPherson, 1997; Sankaran et al., 2004; Nippert and Knapp, 2007; Ward et al., 2013). However, evidence for niche-partitioning in tropical and subtropical ecosystems is mixed, and there is disagreement about the extent to which trees and grasses partition soil moisture in these ecosystems (Verweij et al., 2011; Kambatuku et al., 2013; Kulmatiski and Beard, 2013; Ward et al., 2013). Moreover, seasonality may strongly influence the degree to which soil water is partitioned between trees and grasses. For example, in a savanna ecosystem in South Africa, trees used soil moisture near the soil surface (i.e., 25 cm depth) during the wet season and water from deeper depths in the dry season, whereas grasses accessed soil water from the topsoil layer throughout the year (Priyadarshini et al., 2015). In pastures, determining the sources of water for trees and grasses is highly relevant, as competition for water between trees and grasses can reduce grass growth and production (Dulormne et al., 2004).

The analysis of the hydrogen (δ^2H) and oxygen (δ^{18}O) stable isotope ratios of water is a useful tool to assess where individual plants are accessing water within the soil profile (Ehleringer and Dawson, 1992; Brunel et al., 1995; Querejeta et al., 2007). During plant water uptake and transport within woody tissues, the isotopic signature of plant xylem water is assumed to remain unaltered, thereby reflecting the various zone(s) and depth(s) from which plants extract soil water (White et al., 1985). As a result of evaporative water losses from the soil surface, water in the upper soil layers often becomes enriched in the heavy isotopes (^{2}H and ^{18}O), resulting in a vertical variation of soil water δ^2H and δ^{18}O throughout the soil profile (Barnes and Turner, 1998). Thus, the isotopic signature of potential soil water sources at different depths can be compared to the isotopic signature of plant xylem water to better understand the sources of water used by individual plants (Ehleringer and Dawson, 1992; Jackson et al., 1995; Bonal et al., 2000; Hasselquist et al., 2010; Bargués Tobella et al., 2017).

The isotopic signature of soil water can also be used to examine how plants influence local soil water dynamics. We recently developed a conceptual model that describes how the isotopic signature of soil water and variation in soil water content (SWC) can be used to better understand the relative influence of canopy cover on local soil water (Hasselquist et al., 2018). The model uses the relationship between soil moisture and lc-excess (line condition excess, Landwehr and Coplen, 2006) of surface soil water to tease apart different processes by which trees can influence local soil water dynamics through transpiration, canopy interception, and evaporation. Additionally, the isotopic signature of mobile soil water at deeper soil depths can be useful to differentiate between preferential and matrix flow (Brooks et al., 2010; Zhao et al., 2013; Evaristo et al., 2015; Bargués-Tobella et al., 2020). Under preferential flow, water moves quickly through the soil profile through macropores, thereby by-passing much of the soil matrix, and as a result, is subject to less evaporative water losses. Thereby, under preferential flow, the isotopic signature of deep soil water is more similar to the isotopic composition of recent precipitation (i.e., less negative lc-excess values). In contrast, more negative lc-excess values of deeper soil water would suggest matrix flow as a result of previously evaporated water slowly percolating downward through the soil profile (Hasselquist et al., 2018).

In this study, we measured soil moisture and the isotopic composition of soil and xylem water to assess how trees influence local water dynamics and the potential competition between grasses and trees for soil water within a pasture landscape in the Copan River catchment, Honduras. Measurements were made in both the wet and dry seasons to see how seasonality affects the role trees play in the local soil water dynamics. More specifically, we hypothesized that (1) grasses utilize soil water near the soil surface regardless of season, (2) trees use surface soil water during the wet season but shift to deeper water sources as the upper soil layers dry out during the dry season, and (3) soil water content is higher under trees compared to adjacent open areas (covered

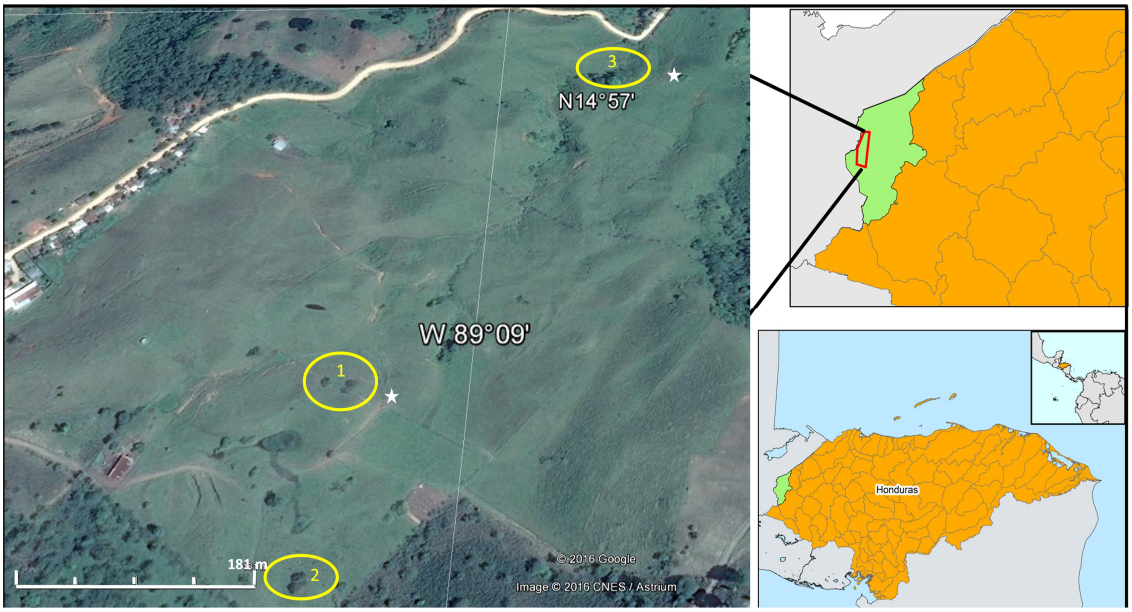

FIGURE 1 | Field site location in pasture landscapes in the Copan River catchment, Honduras. Yellow circles show the three sites: (1) El Malcote (Byrsonima crassifolia (L.) Kunth), (2) Sesesmiles (Ficus colubrinae Standl.), and (3) El Zapote (Lonchocarpus hedyosmus Mig.); white stars show the location of the two wells.

by grasses) because of reduced soil evaporation and greater soil infiltrability and preferential flow under trees.

MATERIALS AND METHODS

We selected a study area in the Copan River catchment, a 620 km^2 catchment located near the border between Honduras and Guatemala (14°94′N, 89°15′W) (**Figure 1**). Pastures are the predominant land use within the catchment, covering 30% of its area (CATIE-MESOTERRA, 2009). The soils are classified as Typic Argiustolls, according to the USDA Soil Taxonomy 1999. The textural class of the topsoil is sandy clay loam and sandy loam, and at deeper depths (> 1 m) it varies between loam, clay loam and sandy loam. The climate is described as tropical savanna according to the Köppen-Geiger classification system (Peel et al., 2007). Average annual precipitation is 1,772 mm based on data collected during the past 32 years (Victor López, personal communication), with a pronounced dry season between November and April (**Figure 2**).

Within the Copan River catchment, we selected three sites: El Malcote, Sesesmiles and El Zapote (**Figure 1**). In all cases, these sites were characterized by an agroforestry system that has been under cattle pasture for the past 20 years, with a ground cover of native and introduced grass species, including *Cynodon dactylon* (L.) Pers., *Cynodon plectostachyus* (K.Schum.) Pilg., *Panicum maximum* Jacq., and *Brachiaria brizantha* (A.Rich.) Stapf. Within the landscape, there are scattered clumps of native tree species with three trees per clump on average as well as living fences of introduced tree species (e.g., *Gliricidia sepium* (Jacq.) Walp.) to mark farm boundaries. We selected three sites that represented one of the three dominant tree species each, sampled as follows: site 1, El Malcote (*Byrsonima crassifolia* (L.) Kunth); site 2, Sesesmiles *(Ficus colubrinae* Standl.); and site 3, El Zapote (*Lonchocarpus hedyosmus* Mig.). Average tree density in the pasture landscape ranged between 5 and 7 trees ha^{-1}, based on Google Earth images acquired in 2007. Although we identified representative grass species in the sites, but besides they were well mixed spatially, their differences were not statistically significative, thus, we pooled all species under the category of "grasses." The root system of Cynodon dactylon mostly develops within 0–25 cm depth but can go as deep as 70–80 cm in sandy soils, with underground biomass mostly rhizomatous. Creeping solons of 0.5–1.5 m length, but can reach 20 m, spread rapidly with numerous culms (8–40) (Heuzé et al., 2015). While *Brachiaria brizantha* have deep roots (down to 2 m) and short rhizomes (Heuzé et al., 2016). And the roots of Panicum maximum are fibrous, long and and occasionally have rhizomes, which confer some drought tolerance; the roots are fibrous, long and gnarled and occasionally have rhizomes, which confer some drought tolerance (Peters et al., 2010).

The mean animal load was 1.8 AU ha^{-1} (Animal Unit equivalent to 400 kg live weight per ha) n Sesesmiles, where the reference for sustainable livestock management is between 1 and 1.3 AU ha-^{1} (Cristobal Villanueva, personal communication). At El Malcote and El Zapote we estimated that the animal load could be even greater. At all three sites, there were visible signs of soil degradation due to cattle trampling and overgrazing.

Vegetation Sampling for Isotopic Analysis

In each site, we collected three samples from three trees located within a clump, which were of the same species in each site, together with three samples of grasses located underneath the

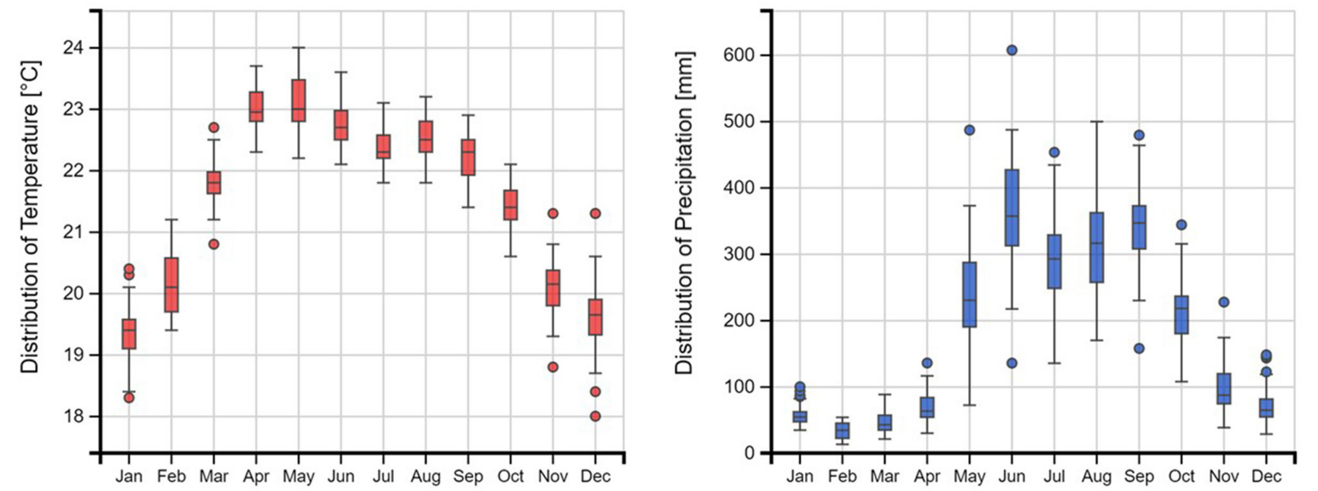

FIGURE 2 | Mean monthly rainfall (on the right) and temperature (on the left) distribution (average 1990-2019), in the Copan River catchment, Honduras (Zepner et al., 2020).

trees and another three samples of grasses in the adjacent open area at a distance from the center of the clump equivalent to one length of the tallest tree (ca. 20 m). Samples were collected in both the dry (January 2013) and wet (June 2013) seasons.

We randomly selected three trees per clump. For each selected tree, twig samples were collected from three locations in the tree crown at random cardinal directions. We cut suberized twigs, ∼10 mm in diameter and 50–80 mm long, from individual trees. Twigs were collected at 150 cm height or from the lower branches in taller trees at three different locations within each tree canopy to minimize any bias based on location within the canopy.

Grass samples were collected also following random cardinal directions both below the tree canopy and in the open areas. We collected culms, the non-photosynthetic part of the stem near the junction with roots, from individual grasses.

Both collected twigs and culms were immediately placed in a capped vial, wrapped in parafilm and stored in a refrigerator (4°C) until water extraction for stable isotope analyses.

Soil Sampling for Soil Water and Isotopic Analyses

At the same time and location where grass samples were collected, we also collected soil samples using a soil core (8 cm diameter) to a depth of 100 cm. From individual soil cores, two samples were taken for water extraction and isotopic analyses; one corresponding to topsoil (0–10 cm depth), and the other to subsurface soil (90–100 cm depth). Freshly collected soil samples were placed in capped glass vials, wrapped in parafilm and refrigerated at 4°C until water extraction for isotopic analyses.

Rain and Groundwater Sampling

Rain water samples were collected during the rainy season of 2013 (from 64 events in total) in two open areas within the catchment using plastic funnels (25 cm in diameter) connected to opaque collection bottles. Water was collected from the collection bottles immediately after each rain event and placed in 20 ml bottles, sealed with parafilm, and stored in a refrigerator (4°C) until isotopic analysis.

Two wells of 3 m depth were installed to collect shallow groundwater samples; one well was located next to sites 1 and 2, whereas the second well was located closer to site 3 (**Figure 1**). Groundwater samples were collected using a stick fastened to a plastic bottle (20 ml) when water was available in the well, which was usually after heavy rain events.

Isotopic Analysis

A cryogenic vacuum distillation line (Ehleringer et al., 2000) was used to extract water from vegetation and soil samples following the procedure described in Bargués Tobella et al. (2017) and Hasselquist et al. (2018).

Gravimetric soil water content (SWC) was calculated as: [(fresh weight—dry weight)/dry weight x 100], where fresh and dry weight correspond to the sample weight before and after thorough water extraction (100 °C, 1.5 h), respectively. The isotopic composition of water extracted from soil and plant material was analyzed using Cavity Ring-Down Spectroscopy (CRDS) on a Picarro L2130-i isotopic water analyzer (Picarro Inc., Sunnyvale, CA, USA, Picarro, 2012) at the SLU Stable Isotope Laboratory (SSIL) at the Department of Forest Ecology and Management, Swedish University of Agricultural Sciences (SLU), Umeå. We use the delta notation (‰) to the Vienna Standard Mean Ocean Water (VSMOW) to express all isotopic values (van Geldern and Barth, 2012). We obtained an analytical precision of 0.05‰ for δ^{18}O and 0.26‰ for δD, based on repeated analysis of control samples.

lc-excess values of soil water were calculated as described by Landwehr and Coplen (2004) to obtain a relative index of evaporation. To do this, we used the measured δ^{18}O signature of soil water (topsoil water and at 100 cm depth) ($\delta^{18}O_M$) and the Local Meteoric Water Line (LMWL) we obtained for

Copan [$\delta D = 8.05\ (\delta^{18}O) + 16.55$]. We then calculated the predicted δD signature (δD_P) of each topsoil water sample as $\delta D_P = 8.05\ \delta^{18}O_M + 16.55$. Finally, we calculated the lc-excess values of our samples by subtracting the predicted δD signature from the measured one (lc-excess = $\delta D_M - \delta D_P$). Values close to zero indicate little difference between the samples and local precipitation, whereas more negative values indicate a greater degree of evaporation (Landwehr and Coplen, 2006). These analyses are based on the conceptual model on how trees can potentially influence soil water dynamics proposed by Hasselquist et al. (2018).

Data Analysis

The proportion of different water sources used by trees and grasses was estimated using the IsoSource mixing model (Phillips and Gregg, 2003, available at http://www.epa.gov/wed/pages/models/stableIsotopes/isosource/isosource.htm). In this model, the mean $\delta^{18}O$ signature of xylem water was compared to that of soil water at two different depth intervals (0–10 cm and 90–100 cm), and to that of shallow groundwater (water table at 3 m depth) to estimate the relative contribution of surface, subsurface and groundwater sources to water uptake by trees and grasses. Using an isotopic mass balance approach, this model provides the distribution and mean contribution from each potential water source. We used a source increment of 1% as suggested by Phillips and Gregg (2003) and a mass balance tolerance of 0.1‰. The mixture was defined for each vegetation type/location (tree, grass underneath tree, grass in open area) according to its mean $\delta^{18}O$ xylem water signature at each site (3 replicates per site). We defined a total of 18 mixtures [3 sites x 3 vegetation types/locations x 2 seasons-dry and wet-].

Although we recognize the advances in the Bayesian mixing models which include posterior parameter estimates and the extent of uncertainty in source contributions to the mixture population (Semmens et al., 2013), we still rely in simplicity of earlier linear mixing models (e.g., IsoSource), which are easier to evaluate, such that if a consumer's isotopic signature is outside the mixing polygon bounding the proposed mixture sources, then mass balance cannot be established and there is no logical solution. Such assumption is not inherent in the Bayesian mixing models, because the source data are distributions not average values, and these models will quantify source contributions even when the solution is very unlikely (Smith et al., 2013). Also recognizing the limitations of IsoSource, Phillips and Gregg (2003) emphasized that the outputs of IsoSource should be characterized in terms of the distribution of the solutions, not just of a single value such as the mean or most likely value. For practicality, we choose the single isotope framework ($\delta^{18}O$), based on previous studies showing no significant differences using only δ2H and only $\delta^{18}O$ by IsoSource model (Wang et al., 2019), and for practicality, we decide to use only d18O.

To test differences in soil moisture we used a general linear model (one way ANOVA) with SWC as response variable and season, soil depth and location (i.e., under trees and open areas) as fixed explanatory variables and site as a blocking factor. However, blocking for site was never significant in this or any other analysis, and we therefore removed it from all statistical analyses. We tested the relation between soil water content at 0–10 cm depth with lc-excess to assess different mechanisms by which trees may influence local soil water dynamics following the model of Hasselquist et al. (2018). This is a conceptual model able to explain that trees can directly affect surface soil moisture by either transpiration and/or interception of incoming precipitation. Surface soil moisture derived by changes in evaporative water losses from the soil surface is also affected by trees. Different isotopic fractionation processes that can be disentangled by examining the relationship between surface soil water content and the isotopic composition of surface soil water. The model also allows to assess different pathways in which water moves throughout the soil profile (i.e., matrix vs. preferential flow).

For this purpose, we used a general linear model (one way ANOVA)with lc-excess as response variable and season and location (under trees vs. open areas) as dependent variables together with the corresponding interactions. To assess the presence of preferential flow, we use a second GLM to check the relationship between lc-excess at 0–10 cm and lc-excess at 90–100 cm (topsoil vs. subsoil water lc-excess), again with season and location as additional dependent variables. To test if the proportion of water used from each of the three considered sources (i.e., 0–10 cm, 90–100 cm and groundwater) varied with season and vegetation type we used three general linear models with the mean percentage of uptake from each source as separate response variables and vegetation type/location (tree, grass under trees and grass in open areas), and season as explanatory fixed variables. All data were tested for normal distribution and homogeneous variance using the Shapiro-Wils test and the

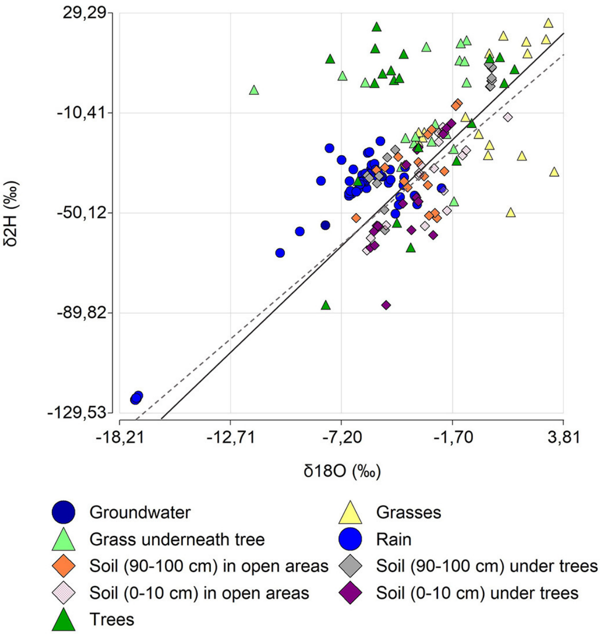

FIGURE 3 | Dual-isotope plot diagram of the study site and sampling process.

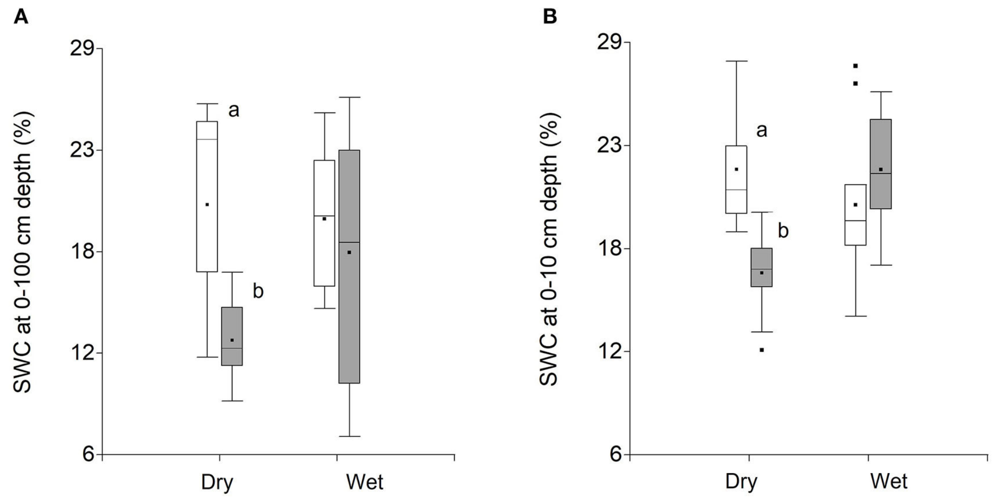

FIGURE 4 | Mean (±SE) soil water content at 0–10 cm **(A)** and 90–100 cm **(B)** under trees (white bars) and in adjacent open areas (gray bars) during the wet and dry season. Bars with different lowercase letters have statistically significant differences ($p < 0.05$).

Levene statistic, respectively. We used InfoStat statistical software (National University of Cordoba- FCA-UNC, Argentina) for the analyses of mean proportional water uptake partitioning, and Minitab 19 (Kowalski and Montgomery, 2010) for the general linear regressions.

RESULTS

Distribution of Water Sources and Vegetation Isotope Signatures

The dual-isotope plot diagram (**Figure 3**) confirms precipitation and groundwater signatures proximity, and the presence of evaporation and mixing processes given that soil water samples deviate from the GMWL, falling below it in most cases. Vegetation samples of trees and grasses underneath trees plotted mostly above the GMWL showing little overlap with soil samples.

Soil Water Content Under Trees and in Open Areas

During the dry season, mean SWC at 0–10 cm and 90–100 cm depth was *ca.* 1.3 times higher ($p < 0.05$) and 1.6 times higher ($p < 0.05$) under trees compared to the adjacent open areas, respectively (**Figures 4A,B**). In this study, open areas represent zones in between trees which are covered by grasses. In contrast, during the wet season, there was little difference in SWC between open areas and areas under trees at both 10 and 100 cm depth (**Figures 4A,B**).

Water Sources Used by Trees and Grasses

During the wet season, both trees and grasses primarily utilized topsoil water, whereas during the dry season, they shifted to deeper water sources. The relative contribution of topsoil water to grasses water uptake was only *ca.* 25% on average during the dry season, a value significantly lower than that for the wet season with 62% on average ($p < 0.001$; **Figure 5**, top panel). In the dry season, grasses obtained 45% of their water from the subsoil, while trees relied mostly on groundwater (79 %) (**Figure 5**). The distribution of the mean fractional contribution of the three considered water sources to the water uptake of each sampled plant is shown in **Figure 6**.

Soil Water Dynamics—Relationships Between Soil Water Content and lc-excess Under Trees and in Open Areas

There was anearly significant positive relationship between SWC and lc-excess of topsoil water for treatment (under trees and open areas, $p < 0.09$), but not for the season ($p > 0.05$). We also tested these relationships separately by treatment and season (**Figure 7**); Results showed no significant relationship between SWC and lc-excess under trees neither during the dry ($p > 0.05$) or wet seasons ($p > 0.05$). In the open areas, there was a significant positive relationship between SWC and lc-excess during the dry season ($p < 0.05$), but not during the wet season ($p > 0.05$).

Preferential Flow—Relationships Between lc-excess Values at Different Soil Depth Under Trees and in Open Areas

In general, lc-excess values of bulk soil water samples did not differ between treatment ($p > 0.05$) or seasons ($p > 0.05$; **Figure 8**). However, the interaction between treatment and soil depth was nearly significant ($p < 0.09$, **Table 1**), indicating more negative lc-excess values near the surface compared with deeper soil depths under trees, with the opposite situation in open areas.

DISCUSSION

Forest hydrology models intended for policy decisions on tree-water interactions often only consider evapotranspiration effects of trees. It is also commonly assumed that enhanced

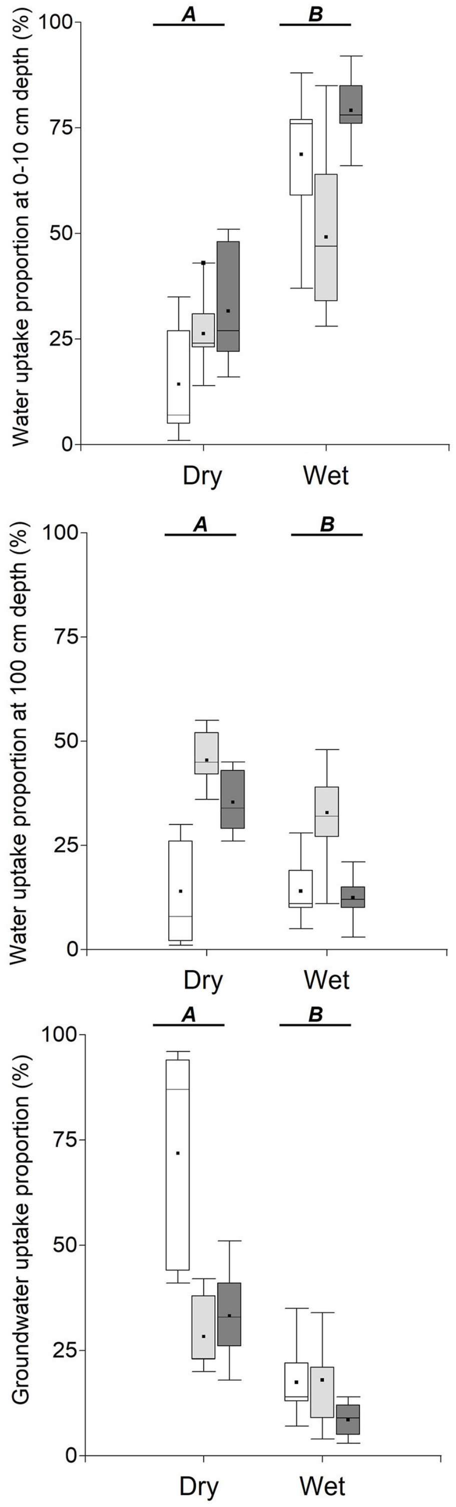

FIGURE 5 | Proportion of water uptake from the three considered water sources (0–10 cm depth, 90–100 cm depth, groundwater) by vegetation type/location in pasture landscapes in Copan, Honduras. White boxplots = trees, light gray=grasses in open areas, and dark gray = grasses underneath trees. Different letters at upper case show statistically significant differences between seasons, and at lower case, statistically significant differences between vegetation types/location ($p < 0.05$).

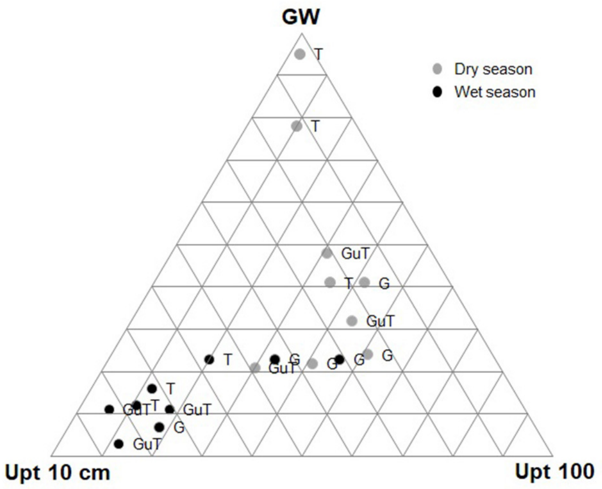

FIGURE 6 | Summary distribution of the mean fractional contribution of each of the three considered water sources (0–10 cm depth, 90–100 cm depth, groundwater) to the water uptake of the 18 plants that were sampled (3 sites × 3 vegetation types/location (trees—T, grasses underneath tree -GuT, and grasses in open areas -G) x 2 seasons) in pasture landscapes in Copan, Honduras.

transpiration by trees can reduce deep soil water drainage and thus groundwater recharge compared to croplands without trees (Jobbagy and Jackson, 2004). However, these generalizations may be biased since studies like ours from degraded seasonally dry tropical areas with an open tree cover are largely absent (Malmer et al., 2010; Ellison et al., 2017). Results from this study show that such assumptions oversimplify the impacts of trees on soil water dynamics in tropical agroforestry pastures with scattered trees. Specifically, we found that during the dry season, soil moisture was higher under tree canopies compared to open areas both at 0–10 and 90–100 cm depth. We also present soil isotopic data that suggests that evaporation of soil water is the main process influencing topsoil moisture, occurring when rainfall is low (dry season), as shown by the positive relationship between SWC and lc-excess of topsoil water in open areas, with greater isotopic enrichment of topsoil water in drier soils.

We used a combination of measurements, including stable isotopes of soil and plant xylem water, together with soil moisture at different depth intervals to gain insight on the main processes influencing soil water dynamics under trees in a tropical agroforestry pasture. Using the framework described in Hasselquist et al. (2018), we investigated potential relationships between soil water content and lc-excess of surface soil water as a way to gain a better understanding of how trees influence local soil water dynamics. Although only nearly significant ($p < 0.09$), we found a positive relationship between SWC and lc-excess of topsoil water in open areas during the dry season, suggesting that variation in surface soil water in open areas was largely driven by evaporation (**Figure 7A**). This relationship was not observed under trees, suggesting that, in this case, evaporative soil water losses were not the main driver influencing topsoil

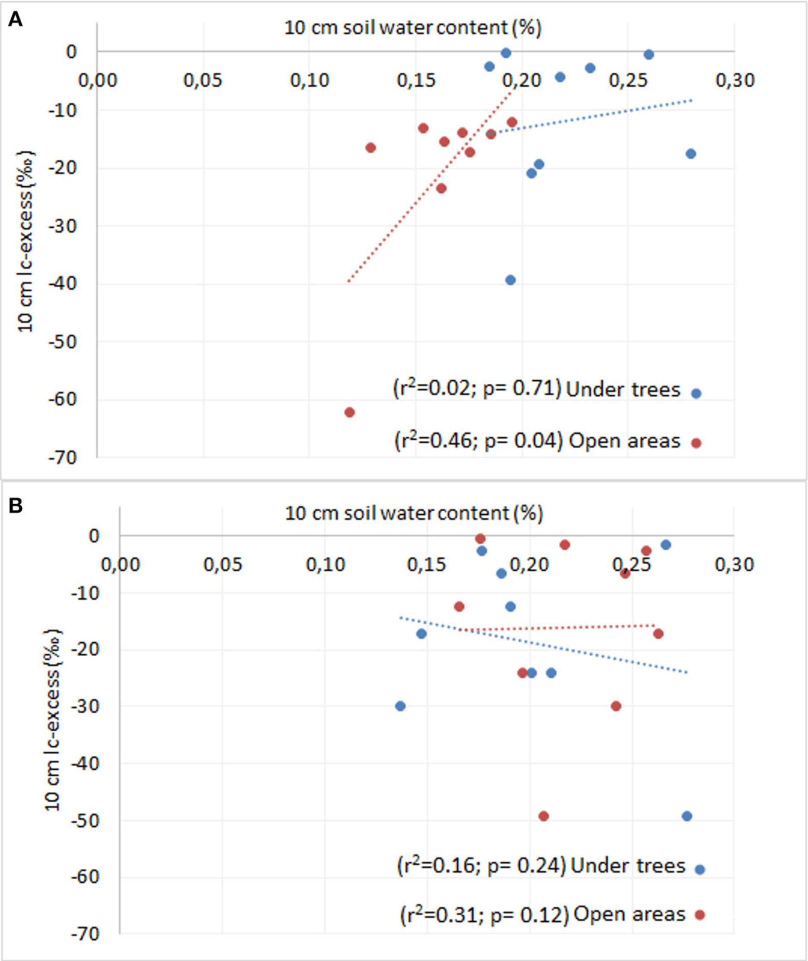

FIGURE 7 | Relationships between lc-excess of soil water and SWC at 0-10 cm depth under trees and open areas (squares) in a pasture landscapes in Copan, Honduras during the dry **(A)** and wet seasons **(B)**.

moisture. This, in turn, may help explain why SWC at 0–10 cm depth was ca. 1.3 times higher under trees compared to open areas during the dry season (**Figure 4A**). Similar results were attributed to shade tree effects by Akpo et al. (2005). It is well known that tree canopies drastically reduce incoming solar radiation in open grassland ecosystems (Belsky et al., 1989; Ko and Reich, 1993; Scholes and Archer, 1997) thereby lowering soil temperatures and consequently evaporative water losses from the soil surface (Jackson and Wallace, 1999; Lin, 2010). Other studies in savanna ecosystems in Africa (Georgiadis, 1989; Weltzin and Coughenour, 1990; Belsky et al., 1993), as well as in Central and South America (Kellman, 1979; Garcia Miragaya et al., 1994) have also reported improved soil water contents beneath isolated trees. During the wet season, although not significant, we found a negative relationship between SWC and lc-excess of surface soil water under trees, which according to the conceptual model described by Hasselquist et al. (2018) would suggest that canopy interception (Allen et al., 2014) plays an important role in the spatial variation of soil water dynamics in this ecosystem and may help explain the lack of differences in SWC under trees compared to open areas during the wet season.

Although not significant, we observed that lc-excess values of soil water were less negative under trees compared with open areas at the subsoil (**Figure 8**), which suggests a significant amount of recent rainwater quickly by-passing the topsoil thereby escaping evaporative water losses at the soil surface. Additionally, these results also suggest that trees lead to less evaporation of topsoil water. This finding supports the idea of enhanced preferential flow under trees compared to open areas, which is consistent with previous dye-tracing studies in the same pasture showing greater levels of macroporosity and occurrence of preferential flow in the vicinity of the trees (Benegas et al., 2014). Similar results have been observed in an agroforestry parkland in semiarid Burkina Faso, where the degree of preferential flow was highest close to trees, and minimal in large open areas (Bargués Tobella et al., 2014; Bargués-Tobella et al., 2020). Preferential flow is more easily initiated when the

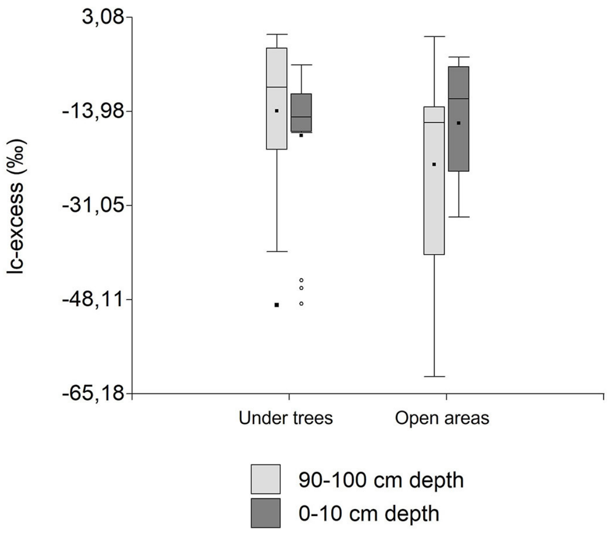

FIGURE 8 | Mean ± SE lc-excess values of bulk soil water collected at different soil depths (0-10 cm vs.90-100 cm) under trees and in adjacent open areas in pasture landscapes in Copan, Honduras.

TABLE 1 | Summary of the general linear model for preferential flow analysis (relationships between lc-excess values at different soil depth under trees and in open areas).

Source of variation	Degree of freedom	Mean Square	*P* value
Model	7	282.18	0.22
Treatment	1	252.91	0.27
Season	1	93.99	0.49
Soil Depth	1	41.74	0.64
Treatment*Season	1	369.61	0.18
Season*Depth	1	106.88	0.47
Treatment*Depth	**1**	**632.01**	**0.08**
Treatment*Season*Depth	1	478.12	0.13
Error	64	200.63	
Total	71		

Bold values represent the nearly significant term in the linear model.

topsoil layer approaches near-saturated conditions (Alaoui et al., 2011) which in turn may explain the less negative lc-excess values of deep soil water under trees compared with open areas (**Figure 8**). Macroporosity and soil water holding capacity are enhanced by biological processes (i.e., bioturbation, release of organic acids, production of root exudates, etc) (Coleman et al., 1991; Rhoades, 1996; Lavelle et al., 2006; Villalobos-Vega et al., 2011; Beven and Germann, 2013), which in turn favors soil infiltration, thereby reducing surface runoff (Weiler and Naef, 2003). Therefore, in some ecosystems it has been shown that trees can enhance groundwater recharge and reduce surface runoff (Sandström, 1998; Bruijnzeel, 2004; van Dijk and Keenan, 2007; Xiong et al., 2008; Niemeyer et al., 2014; Ilstedt et al., 2016).

At the wet season, but in open areas, lc-excess of soil water collected at 100 cm, although no significantly different, was less negative compared to soil water collected at 10 cm depth. This result could imply the presence of preferential flow in open areas in the wet season, when water on the soil surface is more available. Streamflow and groundwater recharge are generated by non-uniform infiltration processes across the landscape, particularly at hillslope scales. Variables such as soil thickness, depth to water table, and rainfall characteristics may influence these processes (Berry et al., 2018).

In this study, we also determined the isotopic signature of plant xylem water to better understand the sources of water used by trees and grasses during the dry and wet season in a tropical agroforestry pasture. During the wet season, both trees and grasses primarily utilized soil water near the soil surface (i.e., 0–10 cm depth; **Figure 5** top panel). However, during the dry season, both grass and trees utilized deeper water sources, with grasses primarily accessing water at deep soil depth (90–100 cm), and trees primarily utilizing groundwater (**Figure 5** lower panel). This finding of different water sources for grasses and trees during the dry season supports Walter's two-layer hypothesis (Walter et al., 1971), which describes the below-ground partitioning of soil resources between woody and herbaceous vegetation. According to this hypothesis, grasses primarily use soil water near the soil surface because of their intense and shallow root system. In contrast, woody savannah trees tend to be deeper rooted, and thus primarily rely on soil moisture at depths below the rooting depths of grasses. Walter's hypothesis generally holds for dry savannahs, which is the ecosystem for which the hypothesis was developed, although it is important to point out that some studies do not support this hypothesis (Le Roux et al., 1995; Mordelet et al., 1997; Kulmatiski et al., 2010; Verweij et al., 2011; February et al., 2013). Our finding of trees utilizing deeper water sources compared to grasses during the dry season suggests niche partitioning when topsoil water availability becomes limiting, which is consistent with Walter's two-layer hypothesis and related studies (Strang, 1969; Sala et al., 1989; Ehleringer et al., 1991; Smit and Rethman, 2000; Miller et al., 2010; Rossatto et al., 2013). This finding is not consistent with previous studies, including tropical systems, that have shown similar water sources for trees and grasses (Le Roux et al., 1995; Seghieri et al., 1995; Mordelet et al., 1997; Le Roux and Bariac, 1998; Ludwig et al., 2003; February and Higgins, 2010; Verweij et al., 2011), thereby suggesting competition for soil water sources between trees and grasses (Walter et al., 1971; Walker et al., 1981; Walker and Noy-Meir, 1982). Even though competition is a likely interaction between trees and grasses, it often occurs only when soil water is not limiting (Maestre et al., 2005; Brooker et al., 2008), which is consistent with the findings from this study, which indicate that trees and grasses were primarily accessing shallow water sources during the wet season.

It is interesting to note that during the dry season, when SWC content near the soil surface was reduced, grasses also shifted to deeper water sources, suggesting a plasticity response in grass roots function in response to resource availability (Sala et al., 1989; Doussan et al., 2003). Among the grass species in this study, *Cynodon spp*. has the deepest root system, which can reach to 2 m depth in ecosystems characterized by drought periods with water limitations (Etemadi et al., 2005). Additionally, *Panicum* *maximum*, the most abundant grass in our system, has been reported to take up water from below 1 meter depth in primary forests and savanna-like abandoned pastures in eastern Amazon (Moreira et al., 2000). *Brachiaria spp* also have a rooting system that can penetrate depths $> 1\,\text{m}$ (Rattan and Stewart, 2013), with certain *Brachiaria* species having greater root biomass at deeper depth (i.e., *B. humidicola* and *B. dictyoneura*) making them better adapted to longer dry periods than other grass species (i.e., *B. brizantha* and *B. decumbens*) (Guenni et al., 2002). These morphological features of the grasses at our study site support our finding that grasses would be able to utilize deeper (i.e., 90–100 cm depth) water sources during the dry season. Moreover, these findings provide a mechanistic understanding of how these grasses can overcome seasonal water limitation, which is crucial for improving the foliage value and carrying capacity in these ecosystems (Sarmiento, 1992).

In conclusion, our results show that the positive coexistence of grasses and trees in the studied pasture landscape is possible through a spatiotemporal partitioning of water resources. During the wet season, when topsoil water is not limiting, both trees and grasses primarily utilized soil water near the soil surface (i.e., 0–10 cm depth). In contrast, during the dry season, both grasses and trees utilized deeper water sources, with grasses primarily accessing soil water at deeper soil depths (i.e., 90–100 cm) while trees relied heavily on groundwater. This finding of niche partitioning during the dry season provides a mechanistic understanding of the coexistence of trees and grass in pasture landscapes with scattered trees. Additionally, our results highlight that trees may have a positive effect on local soil water dynamics through reduced evaporative soil water losses during the dry season and enhanced preferential flow under trees. Nevertheless, we recognize that different species with higher water demands, and relatively greater planting densities may result in different outcomes. In any case, providing further support that trees can positively affect the local water balance, which has important implications for landscape management. Promoting the inclusion of scattered trees in pasture systems to provide water ecosystem services in the silvopastoral systems are adding to other ecosystem services like biodiversity or carbon sequestration.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://doi.org/10.7910/DVN/C0EF3X.

AUTHOR CONTRIBUTIONS

LB, UI, and AM contributed to the conception and design of the work. LB acquired, organized the data base, performed statistical analysis, and wrote the manuscript. AB-T, NH, and UI revised critically the work and contributed with the manuscript drafting. All authors contributed to manuscript revision, read, and approved the submitted version.

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