The role of scattered trees in soil water dynamics of pastures and agricultural lands in the Central American Tropics

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Abstract

Trees affect the water cycle, and thus the amount of groundwater and surface water, through their effects upon the local microclimate and edaphic properties; in particular through rainfall interception, evapotranspiration, and infiltration. Empirical data about the effects of scattered trees upon hydrological processes have been largely lacking, especially for tropical regions. Although benefits of scattered trees for poverty alleviation and for ecosystem services like carbon sequestration, soil enrichment, biodiversity conservation, and air and water quality have been acknowledged, a balance is needed between conservation and restoration of scattered trees in agricultural landscapes. The overall aim of this thesis is to contribute to the understanding of the role of low-density stands of trees upon soil water dynamics. The general hypothesis was that trees improve the soil water dynamics of degraded soils significantly by increasing soil water contents, infiltrability, and preferential water flows, but that those benefits are not as pronounced in locations that have soils whose inherently good properties are maintained through appropriate management. I also tested whether trees and grasses in pastoral landscapes draw water from different sources, and whether their proportions of use from each source change seasonally. Furthermore, as an evaluation of an alternative tool for research, I explored a new conceptual model relating the effect of vegetation cover on the spatial variability of line conditioned excess (lc-excess) of water stable isotopes and soil water content (SWC). To make that evaluation, a combination of measurements were taken in two contrasting study locations: an agroforestry coffee farm in Central Costa Rica (assumed to be in good physical condition), and a pasture landscape with scattered trees in Copan, Honduras (assumed to be degraded). Measurements included soil infiltrability, SWC, preferential flow, and water stable isotopes. Results showed that trees induced higher infiltrability and preferential flow in the agroecosystem with soil degradation (the pasture), but did not affect infiltrability in the coffee agroforestry system. In the latter, soil moisture was lower under trees than underneath coffee due to the trees' greater transpiration. During the dry season, preferential flow was greater under coffee shrubs than under neighboring trees. The relationship between soil moisture and spatial variation of lc-excess depended on vegetation type and season. Therefore, the conceptual model gave insights into the dominating processes affected by the vegetation during dry and wet seasons. In the pasture with scattered trees, I found a vertical partitioning of soil water between trees and grasses: (1) in the dry season, trees use groundwater preferentially, while grasses used subsurface water without reaching groundwater; and (2) in the wet season, both trees and grasses use soil surface water. In conclusion, my research showed that when soils are prone to degradation, trees may provide benefits in the form of infiltrability and preferential flow that are commonly neglected in hydrological models used currently for policy decisions. However, such benefits are absent when soils are inherently stable. I also found that when water becomes limiting in the surface soils, trees and grasses partition their water use between the subsoil and groundwater, thereby reducing their competition.

Keywords: water uptake, ecohydrology, tree-grass interactions, agroforestry, pasture

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El rol de los árboles dispersos en las dinámicas de agua en el suelo de pasturas y tierras agrícolas del trópico Centroamericano

Resumen

Los árboles afectan el ciclo hidrológico a través de su efecto en el microclima local y las propiedades edáficas, en particular a través de la intercepción, evapotranspiración, e infiltración, y por tanto, la cantidad de agua subterránea y los cursos de agua superficiales. Datos empiricos sobre los efectos de los árboles dispersos en los procesos hidrológicos han sido escazos hasta muy recientemente. A pesar de que los beneficios de los árboles dispersos en servicios ecosistemicos como secuestro de carbono, mejoramiento del suelo, conservación de la biodiversidad, calidad del aire y agua, asi como alivio a la pobreza son reconocidos, se necesita un balance entre conservación y restauración de árboles dispersos en los paisajes agrícolas. El objetivo general de esta tesis es contribuir a la comprensión del rol de los árboles a bajas densidades en las dinámicas de agua en el suelo. La hipótesis general fue que los árboles pueden afectar positivamente las dinámicas de agua en el suelo incrementando el contenido de agua en el suelo, la infiltrabilidad y el flujo preferencial cuando existen signos de degradación de suelo, pero es menor cuando el tipo de suelo y manejo mantienen sus buenas condiciones físicas inherentes. Además, la exploración de un nuevo modelo conceptual que relaciona el efecto de la vegetación con la variación espacial de lc-excess (línea condicionada en exceso de isotopos estables del agua) y el contenido de agua en el suelo (SWC) puede proveer una herramienta alternativa para la investigación. Esto se realizó a través de una combinación de mediciones tomadas en dos sitios de estudio contrastantes; uno en una finca cafetalera agroforestal en la zona central de Costa Rica (donde se asumen buenas condiciones físicas) y la otra en un paisaje de pastura con árboles dispersos en Copan, Honduras (donde asume condiciones de degradación). Las mediciones incluyeron la infiltrabilidad de agua en el suelo, SWC, flujo preferencial e isotopos estables del agua. Los resultados mostraron que los árboles favorecen la infiltrabilidad y el flujo preferencial en el agroecosistema con degradación de suelo, pero no mostró diferencias en infiltrabildiad en el sistema agroforestal. Se obtuvo menor humedad del suelo bajo los árboles que bajo el café debido a la mayor transpiración de los árboles y el flujo preferencial fue mayor bajo el café que bajo los árboles vecinos durante la estación seca. La relación entre la variación espacial en lc-excess y la humedad del suelo dependió del tipo de vegetación y la estación. Entonces, el modelo conceptual dio mayor entendimiento de los procesos dominantes que son afectados por la vegetación durante las estaciones seca y húmeda.. En la pastura con árboles dispersos se presenta una partición vertical del agua, donde: 1) los árboles en suelos más húmedos en la estación seca usan preferencialmente agua subterránea, y 2) en la estación húmeda, tanto árboles como pastos usan agua de las capas superficiales del suelo.

En conclusión, mi investigación mostró que cuando los suelos son propensos a la degradación, los árboles pueden proveer beneficios en forma de infiltrabilidad y flujo preferencial, lo cual comúnmente no se considera en los modelos hidrológicos usados para las decisiones políticas en la actualidad. Sin embargo, cuando los suelos son inherentemente estables, esos beneficios están ausentes. También encontré que cuando el agua se hace limitante en el suelo superficial, árboles y pastos pueden dividir su uso del agua entre agua del subsuelo y agua subterránea para reducir la competencia.

Palabras clave: extracción, ecohidrologia, interacción arboles-pastos

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Dedication

To mom, a mamá

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Benegas*, L., Ilstedt, U., Roupsard, O., Jones, J., Malmer, A. 2014. Effects of trees on infiltrability and preferential flow in two contrasting agroecosystems in Central America. Agriculture, *Ecosystems & Environment*, 183, 185-196.

II Hasselquist, N., Benegas, L., Roupsard, O., Malmer, A., Ilstedt, U. 20XX. Evaporation drives the contrasting relationships between isotopic enrichment and surface soil moisture: a new conceptual model to assess how canopy cover influences local soil water dynamics. *Manuscript submitted to Hydrological Process, special issue on 'Stable Isotopes in Hydrological Studies in the Tropics'. Submitted in September 2017.*

III Benegas*, L., Bargues-Tobella, A., Hasselquist, N., Malmer, A., Ilstedt, U. 20XX. Trees influences soil water partitioning and groundwater in tropical grasslands. *Manuscript.*

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* Corresponding author

The contribution of Laura Benegas Negri to the papers included in this thesis was as follows:

I Participated in the planning of the work. Conducted field experiments and sampling. Made data analysis. Wrote the manuscript with input from all other authors. Acted as corresponding author.

II Participated in the planning of the work. Conducted field experiments and sampling. Participated in the data analysis. Wrote the first draft of manuscript with input from all other authors. Gave input to later drafts by the first author.

III Participated in the planning of the work. Conducted field experiments and sampling. Participated in the data analysis. Wrote the manuscript with input from all other authors.

List of figures

Abbreviations

ANOVA	Analysis of Variance
CATIE	Tropical Agricultural Research and Higher Education Center
CIFOR	Center for International Forestry Research
CRDS	Cavity Ring-Down Spectrometer
DRSSI	Double Ring Steady State Infiltrability
DWS	Dry Wet Soil
FAO	Food and Agriculture Organization of the United Nations
FWS	Field Weight Soil
GISP	Greenland Ice Sheet Precipitation
GMWL	Global Meteoric Water Line
IAEA	International Atomic Energy Agency
LAI	Leaf Area Index
LMWL	Local Meteoric Water Line
MD	Maximum Depth of blue stains
MESOTERRA	Sustainable Land Management Project
PFF	Preferential Flow Factor
RSSSI	Rainfall Simulation Steady Stated Infiltrability
SLAP	Standard Light Antarctic Precipitation
SOERE	Système d'Observation et d'Expérimentation sur le long terme pour la Recherche en Environnement
SWC	Soil Water Content
TSA	Total Stained Area
UID	Uniform Infiltration Depth
USDA	United States Department of Agriculture
WWS	Wet Weight Soil
WHC	Water Holding Capacity
VSMOW	Vienna Sandard Mean Ocean Water
WWAP	United Nations World Water Assessment Programme

1 Background

Scattered trees are keystone structures for biodiversity in landscapes worldwide (Manning et al., 2006). Although their roles in improving soils' moisture, carbon, and nitrogen contents have been known since the 1990s (Jonsson et al., 1999), little empirical data was available until recently regarding how systems with scattered trees affect hydrological processes (Ilstedt et al., 2016). That lack of data needs to be remedied because reliable access to sufficient water is indispensable to social well-being and inclusive growth. Thus, access to water is the core of sustainable development (WWAP, 2015).

Two-thirds of the world's population (4 billion people) experience severe water scarcity for at least one month out of every year (Mekonnen and Hoekstra, 2016). Tropical Central America has moderate to severe water scarcity for five to six months each year; therefore, it is crucial that this region use water more efficiently, regulate water consumption within each river basin, and share limited freshwater resources judiciously among the competing demands of biodiversity and human welfare (Mekonnen and Hoekstra, 2016). A better understanding of the relationship between freshwater resources and forests could improve the technical basis for sharing those resources, and perhaps also increase the amount of freshwater available within a given region.

Discussion of the relationship between freshwater resources and forests began in the mid-1800s, when French engineers Belgrand and Valles argued that forests reduce the flow of streams (Andreassian, 2003). Most foresters of that time held the opposite view: that forest sustain water flows. In the 1980s, reviews of catchment studies showed that with certain recognized exceptions, runoff from forested areas (coniferous and deciduous) is generally lower than from areas with shorter vegetation (shrubs and grass) (Bosch and Hewlett, 1982). These authors concluded tree-cutting increases water yields in high-rainfall areas as well as in dry areas; the increases are greater in high-rainfall areas, but persist longer in dry areas because their vegetation recovers more slowly.

Another side of this debate was referred to in the 1900s as the “sponge theory”, which asserts that forests absorb large quantities of water during the wet season, and gradually release it during the rest of the year (Smiet, 1987; Myers, 1983). This view was common among tree-planting organizations, as well as being generally adopted by the public. Opposite and contemporary to the “sponge theory” was the “infiltration theory”, which stated that base flow is governed predominantly by geological substrates, and not necessarily by the presence or absence of a forest cover (Roessel, 1938, as translated by Bruijnzeel, 2004).

An intermediate position adopted by some researchers during those early years was that the main benefit of forests is the prevention of soil erosion and floods, rather than increased dry-season flows (Bruijnzeel, 2004). It is now known that in areas with dry seasons, forests also restore or maintain soil quality, especially by increasing infiltration (Brown et al., 2005). To explain that important effect, Bruijnzeel (1989) proposed the “infiltration-evapotranspiration-trade-off hypothesis”, which stated that dry-season flows can increase after afforestation if the increase in infiltration exceeds the increases in evapotranspiration. Conversely, dry-season flows will decrease if the increase in evapotranspiration is larger than increase in infiltration.

In a later work, Bruijnzeel (2004) added that inclusion of trees within reforestation and soil-conservation activities could reduce peak flows and stormflows associated with soil degradation. Most of the factors considered to be important by the infiltration-evapotranspiration-trade-off hypothesis are related to soil conditions, which are likely to be site-specific (Calder et al., 2004).

Bruijnzeel’s hypothesis was commonly rejected for lack of sufficient supporting evidence. Indeed, some studies questioned the hypothesis (Roa-García et al., 2011; Jobbagy and Jackson, 2004; Ellison et al., 2012). However, Ilstedt et al.’s (2007) literature review and meta-analysis provided indirect support by showing that infiltrability increased after tropical afforestation and tree planting for agroforestry. Moreover, a number of recent case studies from different locations provide more-direct support (Qazi et al., 2017; Krishnaswamy et al., 2013), and further indirect support (Zhou et al., 2010; Lin, 2010).

An example of the evidence for interactions that take place in tree-based land usage (according to Bruijnzeel’s hypothesis) is found in Dulorme et al. (2004), who report that the reduced soil water content (SWC) below the trees-plus-grass portion of a silvopastoral system reflects a large uptake of water from matric reserves during the dry season. As a result, the SWC of the trees-plus-grass portion of the system is similar to that of the open-grasses portion.

In summary, evidence provided in studies published to date presents conflicting views of the effects of trees upon soil-water dynamics, mainly because those effects depend upon combinations of factors that include the presence of short or tall vegetation (van Dijk & Keenan, 2007; FAO & CIFOR, 2005). More importantly, the relationship between trees and water yield is determined mainly by (among other things) leaf-area index, transpiration rates of trees and understory vegetation, sapwood area, soil and litter, infiltration, evaporation, and tree interception (Eamus et al., 2005).

The roles of vegetation in determining (1) the infiltration properties of soils, (2) surface-runoff generation, (3) groundwater recharge, (4) flow regulation, and (5) continuous supply of organic material to avoid soil degradation have been key research topics, and should continue to be so (Calder et al., 2004). More work needs to be done, especially on the roles of trees in degraded landscapes and in different combinations of rainfall regimes, soils, and tree species (Malmer et al., 2010; Aranda et al., 2012).

To date, most research into the effect of reforestation upon stream flows has been done on afforestation experiments and on plantations of fast-growing species (Jackson et al., 2005). As noted at the beginning of this section, little empirical data was available until recently on how systems with scattered trees affect hydrological processes (Ilstedt et al., 2016). However, the information thus far available indicates that scattered trees contribute substantially to poverty alleviation and to ecosystem services like carbon sequestration, soil enrichment, biodiversity conservation, and air and water quality. For that reason, restoration and conservation should be balanced to ensure protection and perpetuation of scattered trees in agricultural landscapes (Fischer et al., 2010).

In 2010, agroforestry systems that contained at least 10% trees were used on more than one billion hectares (43%) of the world’s agricultural land. Those systems provided subsistence to more than 900 million people (Zomer et al., 2016). The same authors, in their data on global agricultural areas that contain trees, showed that humid regions that include most of the tropics are the regions with the highest percentage of tree cover. In that same region, countries that are expected to lag behind in development during this century are projected to have the greatest population growths, too, as the world’s total human population climbs to its predicted level of 11 billion. Thus, this region will be under great pressure to increase food production in coming decades (Laurance et al., 2014). That need will present a strong challenge for the management of trees in agricultural landscapes-including systems of scattered trees-not only for human wellbeing, but also for carbon sequestration and provision of habitat and connectivity for biodiversity (Manning et al., 2009).

To face these challenges, researchers must provide additional, fundamental data that elucidate the roles played in soil water dynamics by a range of systems that contain scattered trees. Traditionally, forest and water relationships have been studied using the paired-catchment approach. However, due to the long-term commitments and substantial funding that that approach requires, few such studies have been done in the tropics. Moreover, use of the paired-catchment approach is challenging in dryer conditions. Therefore, new, alternative approaches that can complement traditional methods are urgently needed. A promising alternative method used in this thesis, to provide fundamental data on relationships between water and scattered-tree agricultural systems in the tropics, is isotope hydrology.

2 Introduction

2.1 Tree-mediated hydrologic cycle

The nine major physical processes in the global water cycle (evaporation, condensation, precipitation, interception, transpiration infiltration, percolation, runoff, and storage) form a continuum of water movement (Figure 1). This cycle includes the passage of water from the atmosphere, through the bodies of water on the surface of earth, then through the soil and rock layers underground, to return later to the atmosphere (Oki and Kanae, 2006; Liu and Zeng, 2004).

Compared to agricultural crops and pasture systems, trees have a greater potential to influence the water cycle due to their larger leaf area and extensive root systems (Farley et al., 2005). More specifically, the role of trees in the water cycle is to modify the micro-climate, intercept precipitation, evaporate moisture from vegetative surfaces, transpire soil moisture, capture fog water, and maintain soil infiltration. Indeed, trees may also sustain the precipitation pump throughout continents (Makarieva and Gorshkov, 2007). All of these tree-mediated processes influence the amount of water available from groundwater, surface watercourses, and water bodies (Hamilton, 2008). Moreover, soil–atmosphere water transfer in forest ecosystems is mediated mainly through vegetation (Unsworth et al., 2004). It is well established that changes in tree coverage affect evapotranspiration, which is the most-studied relation between trees and the water cycle (Keppeler and Ziemer, 1990; Bond et al., 2008; Law et al., 2001; Moore et al., 2004). Water moving from the subsurface through plants to the atmosphere via transpiration is no longer available to contribute locally to downstream flow; at the same time, shade provided by vegetation reduces soil evaporation (Ponette-González et al., 2015). Tree cover also affects rainfall interception and-in some situations-fog capture (Pypker et al., 2005; Holwerda et al., 2010), and therefore affects streamflow (Jones and Grant, 1996; Thomas and Megahan, 1998). Water stored in the near subsurface is available to deep-rooted vegetation, and can be transpired. Therefore, enhancing infiltration of water to be transpired by trees may reduce the total volume of water available downstream (Ponette-González et al., 2015). However, the same trees can improve infiltration capacities and readily conduct water vertically for groundwater recharge, by maintaining well-connected macropores (Eldridge and Freudenberger, 2005).

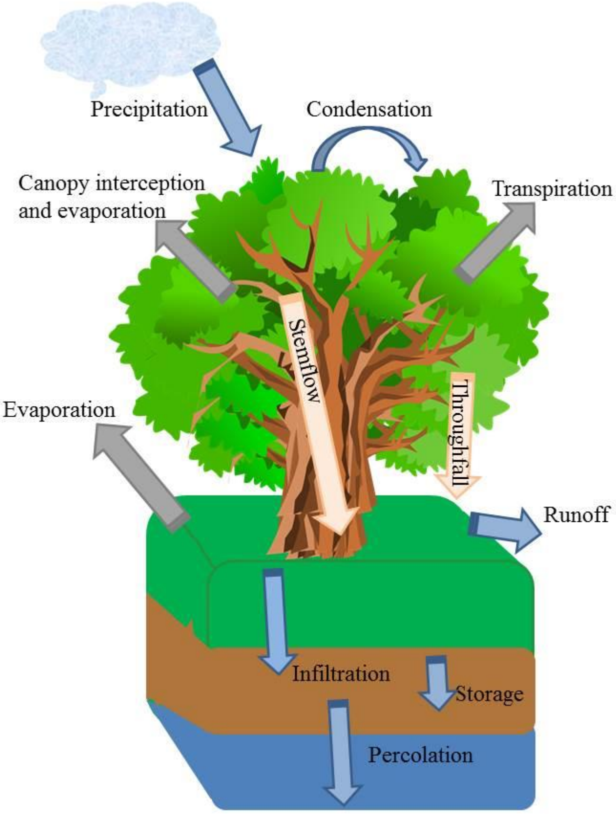

Figure 1. Water cycle mediated by trees

One of the key determinants of vegetation structure is the distribution of soil water or the soil water dynamic (Figure 2) over time (Huxman et al., 2005, Darrouzet-Nardi et al., 2006). Soil water dynamics are affected by several factors, including topography, soil texture, presence of vegetation, water movement processes, depth to water table, and meteorological conditions (Gomez-Plaza et al., 2001). The environmental variable of soil moisture integrates all effects of climate, soil, and vegetation on the dynamics of water-limited ecosystems (D'Odorico et al, 2007).

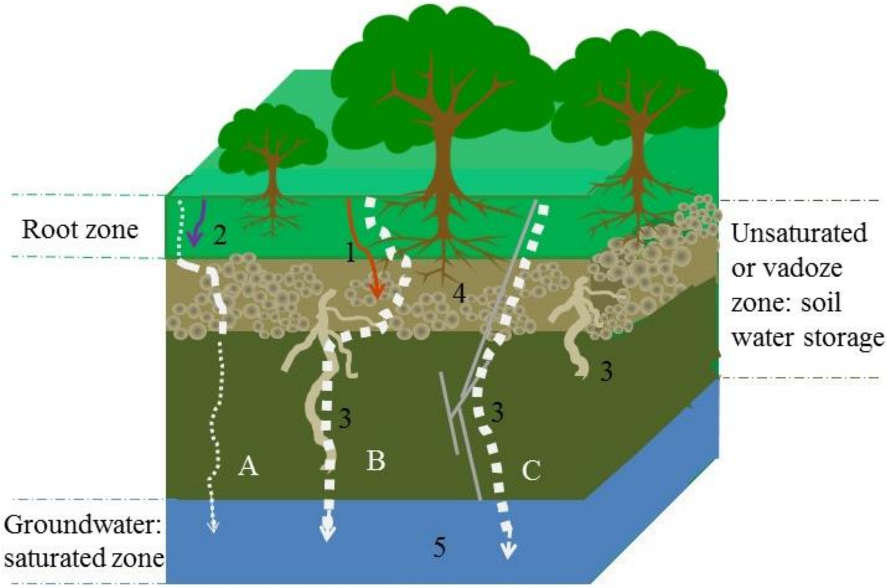

Figure 2. Schematic of main soil water dynamic processes and features: Infiltrability at the soil surface (1) is enhanced by the tree-root system. Matrix flow (2) occurs in small pores. Preferential flow (3) in macro pores (4) is enhanced by root decay, soil fractures, litter deposition, soil fauna, and soil organic matter associated with trees. Letters A, B, and C denote routes along which water may travel downward from the surface to the saturated zone. Route A is the slowest because all water transport through the micropore zone occurs via matrix flow. In contrast, water travels through that zone along tree-enhanced macroporosity in route B, and through tree-induced soil fractures in route C. The faster routes provided by trees decrease exposure of water to evaporation.

Trees could increase the temporal heterogeneity of soil moisture content, given that their canopy may intercept all moisture during short rainfall events, but permit all or part of the rain to fall through during longer rains (James et al., 2003). Trees also increase transpiration and surface shade (van Dijk & Keenan, 2007). In Kenya, soil moisture was lower in plots containing trees than in control plots (crops only), especially at the end of the dry season (Odhiambo et al., 2001). However, the influence of vegetation upon soil moisture content in a Kenyan savanna and in a Ugandan agroforestry system varies: soil surface moisture under trees may be greater than, equal to, or less than in open grasslands depending upon the date and depth (Belsky et al., 1993; Siriri et al., 2013). Trees-specifically sweetgum sprouts (*Liquidambar sty- raciflua L.*)-increased surface soil moisture soon after rainfall. However, soil moisture also increased under the bunch grass underneath both sweetgum sprouts (*Liquidambar sty- raciflua L.*), and a bunch grass and broomsedge grass (*Andropogon virginicus* L.) in the Upper Coastal Plain of Alabama, USA (Mitchell et al., 1993). The sites studied in those works on vegetation and soil moisture are relatively mesic, although plants could probably affect water resources in cases where the resource is scarce (James et al., 2003).

Higher soil moisture can also be found at the base of trees and shrubs due to the contribution of stemflow, which funnels rain water down to the soil surface (Pressland, 1976; Martinez-Meza and Whitford, 1996; Whitford et al., 1997; Siles et al., 2010; Jackson and Wallace (1999). Enhanced subcanopy soil-moisture storage and rainfall efficiency (rainfall/storage ratio) is attributed to trees in grassland ecosystem (Joffre and Rambal, 1988), as are enhanced moisture retention (Saha et al., 2004) and groundwater recharge (Ilstedt et al., 2016). However, water availability can be higher below tree canopies than outside canopies, usually during drying periods. Availabilities are similar after rainfall periods (Ko and Reich, 1993, Mordelet et al., 1993).

In addition to funnelling water into the soil, trees reduce radiant energy via shading (Belsky et al., 1993; Brenner, 1996). In these ways, trees induce microclimatic modifications that have the potential to improve the water-use ratio of understory crops (Bayala and Wallace, 2015). This process can lower soil temperatures, thereby reducing evaporative demand and water stress on understory plants. For instance, a shade cover greater than 30% under agroforestry systems reduced overall evaporative demand from soil evaporation and coffee transpiration in Southern Mexico (Lin, 2010).

In Central Malawi, soil water increased under the influence of tree canopies, and the difference between soil water contents under tree canopies and in open areas was higher at the end of the growing season (Rhoades 1996, 1995). Rhoades attributed this result to the chemical and physical nature of leaves, bark, branches, and roots, which modify (1) decomposition and nutrient availability; and (2) the taxonomic makeup of fauna involved in litter breakdown. The development of a litter layer and (depending upon soil type) the improvement of soil structure cause more rainfall to either infiltrate into the soil, where it is stored for transpiration at a later stage, or percolate deeply enough to recharge the groundwater (Bruijnzeel, 2004; Ilstedt et al., 2007).

Soil macropores are created by living or decayed tree roots and microbial biomass, as well as by nematodes, earthworms, and other soil biota (Rhoades, 1996; Coleman et al., 1991). Macropore systems function as channels for transport of water through the soil (Beven and Germann, 1982). These channels are opened as roots exert compressive forces upon the soil through which they grow, after which root exudates cement the sides of the channels to help prevent them from collapsing. (Angers & Caron, 1998; Johnson and Lehmann, 2006).

Root-induced channels can become preferential flow pathways, associated with tree canopies, that cause water to spread relatively homogeneously within the subsoil (Young et al., 1984; Martinez-Meza and Whitford, 1996; Ghestem et al., 2011; van Noordwijk et al., 1991). Some channels extend upward to points on the surface that receive stemflow, thereby forming a continuous vertical porous zone that contains live and decayed roots (Mitchell et al., 1995; Devitt & Smith, 2002). For example, in an Australian case reported by Yunusa et al. (2002) the total number of large pores after further decomposition of roots was 25% higher in tree-belt subsoil than in cropping subsoil, and the hydraulic conductivity was 27% higher. Furthermore, Noguchi et al. (1997) found relatively high conductivities (ranging from 146.52 to 168.84 mm h^{-1}) in a tropical rain forest in Malaysia.

Various studies have shown how amounts of water reaching the soil and infiltrating into it vary with distance from nearby trees. For instance, soil within 0.3 m of the bases of trees in an agroforestry system in Kenya wetted faster than soil that was either in line with the trees (distance=1.5 m) or out in the open (distance=2.5 m) (Jackson and Wallace, 1999). Similarly, soil infiltrability in agroforestry parklands of Burkina Faso was higher under trees than in open areas (Bargues-Tobella et al., 2014; Sanou et al, 2010), and was higher under trees than on grassy slopes or in cultivated tracts in an area with fine-textured soil in Australia (Eldridge and Freudenberger, 2005).

In contrast, trees can also reduce soil moisture and groundwater recharge. For example, the (usually) deep roots of trees in seasonally dry climates may be able to access soil water-and even groundwater-during dry periods (e.g. Nepstad et al., 1994; Dye and Versfeld, 2007). Because water transpired through leaves comes from the roots, plants with deep roots may be able to maintain a more constant rate of transpiration, thus increasing evaporative losses from an ecosystem. Transpiration rates will be higher for fast-growing species and dense forests, and during early stages of tree growth (van Dijk and Keenan, 2007; Meinzer et al., 2005; Giertz et al. (2005).

Box 1. The approach of “trees outside the forest”

To designate systems that contain trees at densities lower than those of forests, Foresta et al., (2013) proposed the term “trees outside forest”. Foresta et al. used that term for “all lands predominantly under an agricultural use with trees and/or shrubs whatever their spatial pattern (in line, in stands, scattered)”. As reference values for tree densities, the authors define thresholds like area ≥ 0.05 ha; canopy cover ≥ 5% if trees are present, or ≥ 10% for combined trees, bushes and shrubs; width ≥ 3 m; and length ≥ 25 m. Previous to Foresta et al., (2013), the term “scattered trees outside the forest (STOF)” was proposed by Manning et al. (2006), who considered these systems collectively as ‘‘scattered-tree ecosystems’’. The key defining feature of STOFs is their dispersed pattern of trees. This definition, which was intended to be broader than that of ‘‘savanna: mixed tree–grass systems characterized by a discontinuous tree canopy in a continuous grass layer” (Scholes & Archer, 1997; House et al., 2003; Bray, 1960), includes natural, cultural, and recently modified ecosystems, as well as disturbed and undisturbed ones. Other synonyms for scattered trees (depending upon the region and nature of the surrounding ecosystem) include isolated trees (Dunn, 2000), remnant trees (Guevara et al., 1986; Harvey and Haber, 1998), pasture trees (Otero-Arnaiz et al., 1999), and paddock trees (Gibbons and Boak, 2002). According to the earlier definition, STOFs are associated primarily with annual/permanent crops and pastures, and secondarily with non-cultivated/non-managed lands (e.g. parts of savanna land, mountainous regions, and peatlands).

Agroforestry systems-in which trees are present within stands of cover crops-are examples of “trees outside forests”, a category that also includes modalities such as silvopastoral systems and dryland parklands. (See Box 1 for a discussion of the concept “trees outside forests”.) Agroforestry is an agricultural production system with several proven benefits, both for farmers and for society at large (Jose, 2009). Among those benefits are (1) poverty alleviation, and (2) ecosystem services like carbon sequestration, soil enrichment, biodiversity conservation, and improved air and water quality.

Under agroforestry systems, trees affect water resources by reducing the soil’s bulk density and improving its structure. Alegre and Cassel (1996) attribute those effects to root growth and biological activity in the root zone (Alegre and Cassel, 1996). Increased infiltration through the root system leads to higher water content after the principal recharge event, thereby potentially reducing runoff and soil loss (Anderson et al., 2009). Results from a Costa Rican study support that assertion: runoff was indeed lower under a coffee agroforestry system than in a coffee monoculture, and water infiltration was higher (Cannavo et al., 2011).

2.2 Vertical water partitioning under agroecosystems with scattered trees

Interactions between trees and understory plants can be either positive (i.e. facilitative or complementarity) or negative (i.e. competitive) (Jose et al., 2004). Examples of positive interactions in agroforestry practices include establishment of live fence and fodder banks in treeless croplands (Takimoto et al., 2009). Those practices have the important additional benefit of increasing carbon sequestration. Another facilitative interaction is the interception and recapture, by deep-rooted trees, of nutrients that leach downward beyond the reach of shallow-rooted crops (Mugendi et al., 2003). Deep roots of trees may also help improve the physical properties of soils, and increase the supply of hydraulically lifted water (Fernandez et al., 2008). In contrast, negative interactions occur when trees and understory vegetation compete for light, nutrients, and water (Kho, 2000), and when allelopathic effects (Mallik, 2008) exist within the same pool of understory plants.

In his influential model, Walter (1971) hypothesized that trees have roots in both the topsoil and subsoil, while grasses have roots only in the topsoil. This difference between rooting systems results in a stable equilibrium if the grasses' water-use efficiency is greater than the trees'. In such a case, grasses are superior competitors for water stored in the top layers of the soil, due to their high root density and more-pronounced growth response to water. Meanwhile, only trees have access to water stored in deeper soil layers (Schwinning and Kelly, 2013). The resulting stable equilibrium between trees and grasses is explained by the niche theory, or niche partitioning hypothesis, which posits that woody species use mostly deep-soil water, and grasses use soil water mainly from the upper soil profile (Sala et al., 1989). A common assumption in agroforestry, based upon that hypothesis, is that root systems of different plant-life forms (trees, herbaceous crops, or grasses) occupy different soil strata, and use the soil resources complementarily (Schroth, 1999; Fernandez et al., 2008). However, exceptional cases exist in which this hypothesis does not apply. For instance, in some semi-arid tropical ecosystems the detrimental effects of competition for water and light exceed the beneficial effects of trees upon site fertility (Ong et al., 1991; Corlett et al., 1992; Mobbs et al., 1998). That same phenomenon is known to reduce crop yields in some agroforestry systems in the humid tropics (Sanchez, 1995; Van Noordwijk et al., 1998; Mobbs et al., 1998).

It is possible for positive and negative interactions between trees and understory species to proceed simultaneously (Holmgren et al., 1997). The set of positive and negative interactions present within an agroforestry system shifts with time due to the usual changes in the environment and in the growth requirements of plants (Holmgren et al., 1997; Kikvidze et al., 2006; Priyadarshini, et al., 2015). The relationship between stress and plant interactions has been also conceptualized as the ‘stress-gradient hypothesis. This hyphotesis states that net competitive effects are more important, or at least more intense (Brooker et al. 2005), in relatively benign, low-stress environments, whereas facilitative effects are more important in relatively harsh, high-stress environments (Bertness & Callaway 1994). For instance, in an agroforestry system of broad-leaved savanna in South Africa, Priyadarshini et al. (2015) found that water sources tapped by trees and understory species can overlap, as when both trees and grasses use water from the topsoil after rainfall. The same authors reported that partitioning of water use resumes after the topsoil dries out. (I.e., all tree species revert to using groundwater or subsoil water). Overall, evidence available at this time indicates that the degrees and specifics of water partitioning vary greatly among ecosystems. A sample of the literature (Table 1) on studies from tropical and sub-tropical regions shows no evidence of niche partitioning between trees and grasses in most cases. However, some studies report both competition and water-source partitioning. The latter phenomenon implies that some species access resources unavailable to others, or that species use the same resource in different places or at different times (Vandermeer, 1989).

Table 1. *Summary of representative reports on vertical partitionings of soil water in agroforestry systems.*

Tree species	*Grass species*	Evidence of competition (-), niche partitioning (+) or no evidence (0)	Country	Landscape	Annual rainfall (mm)	Soil type	Reference
Cussonia barteri, *Crossopteryx febrifuga*, and *BrideIia ferruginea*	*Hyparrhenia* sp. and *Andropogon* sp	-	Republic of Guinea, West Africa	Humid savanna	1210	Tropical ferrugineous	Le Roux et al. (1995)
Bridelia ferruginea, *Crossopteryx febrifuga* and *Cussonia barteri*;	P*yparrhenia* spp. and *Andropogon* spp.	0	Côte d'Ivoire	Humid savanna	1200	Sandy-textured tropical ferrugineous, with gravel and stones frequent below 30 cm	Mordelet et al. (1997)
Prosopis glandulosa, *Zanthoxylum fagara*, *Celtis palida*, *Ziziphus obtusifolia*, *Porlieria angustifolia*, *Schaefferia cuneifolia*	*C4 grasses*	0	USA	Subtropical savanna parkland	720	Typic and Pachic Argiustolls	Midwood et al. (1998)

Tree species	*Grass species*	Evidence of competition (-), niche partitioning (+) or no evidence (0)	Country	Landscape	Annual rainfall (mm)	Soil type	Reference
Terminalia sericea, Sclerocarya birrea and Dichrostachys cinerea	*Hyperthelia dissoluta* and *Setaria sphacelata.*	0	South Africa	Mesic savanna	736	Granite-derived, nutrient-poor, well-drained, coarse-grained, and moderately deep (between 1 m and 1,5 m),	Verweij et al. (2011)
Byrsonima crassa, Eriotheca pubescens, Hymenaea stigonocarpha, Miconia ferruginata, Qualea grandiflora Roupala montana, Schefflera macropata, Symplocos rhamnifolia	*Echinolaena inflexa, Rhynchospora consanguinea, Aristida gibbosa, Schizachirium sanguineum, Axonopus aureus, Panicum campestre, Erichrysis cayensis*	+	Brazil	Neotropical savanna, closed	1450	Deep, well-drained oxisols	Rossatto et al. (2013)

2.3 Water stable isotopes as an alternative method for measuring influence of trees upon soil water dynamics

Trees are involved in five key processes that determine soil water dynamics: infiltration, percolation, storage, and water use (i.e. transpiration/evaporation). It is common for quantitative studies of those processes to employ traditional field methods, such as the application of a constant head by using the single- or double-ring pressure infiltrometer (Reynolds and Elrick, 1990; Bagarello et al., 2009); the tension infiltrometer (Rienzner and Gandolfi, 2014); or the disc infiltrometer (Warrick, 1992). Other commonly-used methods and apparatuses include rainfall simulators (Tricker, 1979); lysimeters (Geyh 2000); sap-flow measurements and thermometric techniques (Granier, 1987); time-domain reflectometry (for soil humidity) (Ledieu et al., 1968); and micro-meteorological techniques (Bowen ratio and eddy-covariance) (Barr et al.,1994).

All of these methods have their specific advantages, as well as their characteristic problems and sources of uncertainties. The problems include difficulties in making measurements in certain conditions of surface topography; the need to carry a substantial water supply or to disturb soil at the site; realistic simulation of rainfall and drainage; and uncertainties as to whether measurements made at specific points are representative of the region of interest. In addition, it is often difficult to determine the underlying processes responsible for measured results.

The use of water stable isotopes has emerged recently as a valuable complement to these traditional field methods (Volkmann and Weiler, 2014). The use of water-molecule isotopes in hydrological processes is based on the premise that one can trace a water molecule through the hydrological cycle (McGuire and MacDonnell, 2008). Tracing of water stable isotopes has several applications, such as obtaining hydrologic information about specific sources of groundwater recharge, and relating the movement of soil water to plant water sources, and to the rate of soil evaporation (Geyh 2000; McGuire and McDonnell 2008). Because water stable isotopic composition may reflect precipitation events and seasonal precipitation variations, the isotopic compositions of precipitation and soil water provide information about mixing and residence times of water along a soil profile (Gazis and Feng, 2004). Thus, a study of the seasonal variations in isotopic compositions of precipitation and soil water can reveal (for example) seasonal infiltration patterns, flow velocity, and the mechanism of soil water flow (Gazis and Feng, 2004; Gehrels et al., 1998).

One advantage of isotopic technics is that water stable isotopes behave conservatively, meaning that oxygen and hydrogen isotopes do not react with catchment materials, and therefore retain their distinctive fingerprints until they either mix with waters of different compositions (Kendall and Cadwell, 1998) or are exposed to evaporation. Other advantages of isotopic techniques include relatively easy processing of sample water in the field and laboratory, and (recently) the development of inexpensive instrumentation, based upon laser spectroscopy, that is capable of high temporal and spatial resolution (Sanchez-Murillo and Birkel, 2016; Gupta et al., 2009; Good et al., 2014; Unkovich et al., 2013). In practice, isotopic analysis may be used either in place of traditional field methods; or in conjunction with them to improve their performance and aid in interpreting their results.

2.3.1 Use of water stable isotopes to disentangle the trees' influence upon soil water dynamics

To use water stable isotopes in studying a region's soil water movements that are related to soil evaporation and plant water sources, researchers must understand (1) the region's baseline hydrology; (2) isotopic variations in water sources, precipitation, and water vapour over vegetation systems (Gat 1996; Ingraham 1998; Bariac et al., 1989; Brunel et al., 1991; Harwood et al., 1998); and (3) changes in isotope values along the soil-plant-atmosphere continuum (Dawson et al., 2002). The water stable isotopes method determines the abundance of stable isotopes in a water sample from the isotopic ratios $^{18}O/^{16}O$ and $^{2}H/H$. The isotopic ratios are calculated as δ values in parts per thousand, using a standardized equation which relates the ratio of heavy to light isotopes in the sample to the ratio in the reference standard (Vienna Sandard Mean Ocean Water-VSMOW) (Buttle and McDonnell, 2004).

Several hydrologic processes and plant functions are reflected in the distribution of stable isotopes of water within the soil-plant-atmosphere continuum (Burgess et al., 2000). The validity of using of isotopic tracers to measure transpiration (Kendall and Doctor, 2003) and other interactions between hydrogeological and ecological processes (Koeniger et al., 2010) is a consequence of the above-mentioned conservative behaviour of water stable isotopes. During water mixing process, the stable isotopes of water in the conducting tissue of plants can be the sum of stable isotopes from the various soil water reservoirs from which the plants may be extracting (Brunel et al., 1991). Water uptake by roots does not lead to fractionation (assuming an isotopic steady state over annual timescales), so the isotopic composition of transpired water is operationally defined as being equal to that of the plant's xylem water (Allison et al., 1984; Yakir and Wang, 1996; Welp et al., 2008; Simonin et al., 2013).

After water uptake by plants via transpiration, tissues undergoing water loss (i.e. leaves or non-suberized stems), are expected to show evaporative enrichment in the heavier isotopes of hydrogen and oxygen. The magnitude of this enrichment of leaf water will depend upon humidity gradients, transpiration rate, and the isotopic composition of atmospheric water (Dongmann et al., 1974; Zundel et al., 1978; Leaney et al., 1985; Ehleringer and Dawson, 1992). However, as long as sap water has not been in transpiring tissues, the isotopic composition should reflect the sources from which water has been taken up. All of these characteristics of oxygen and hydrogen isotopes within the soil-water-atmosphere continuum provide useful clues for disentangling vegetation-mediated soil water dynamics.

2.4 Line conditioned excess as an indicator of soil water dynamics

A useful indicator for integrating isotopic measurements with soil water dynamics is the line conditioned excess (Lc-excess) (Landwehr and Coplen 2006). Values of this indicator reflect source-water differences, as well as the full complexity of physical processes that produce surface waters. The Lc-excess can help to distinguish water samples that have undergone evaporation under non-equilibrium conditions (Dansgaard, 1964) from those that have maintained the isotopic characteristics of regional precipitation (Evaristo et al., 2016). The concept and construction of Lc-excess differs from the method of deuterium excess (d-excess) (Landwehr and Coplen 2006). D-excess measures the relative proportions of ^{18}O and ^{2}H contained in water, as an index of deviation from the global meteoric water line (GMWL: $\delta D=8\delta^{18}O+10$) in a graph of δ^{2}H versus δ^{18}O (Froelich, 2002). It is often considered to be an indicator of evaporation conditions. Because it is affected by multiple vapour sources (initial oceanic vapour and evapotranspiration from different continental water sources, mostly recycled air moisture), it is more complicated to interpret than the lc-excess (Landwehr and Coplen 2006; Gat et Matsui, 1991; Lai and Ehleringer, 2010; Aemisegger et al., 2014; Delattre et al., 2015).

When the researchers' goal is to account for the residual water in the soil after the trees' effects on soil water dynamics, the Lc-excess index is more suitable than the d-excess because Lc-excess refers to the isotopic enrichment of the water that remains after evaporation. (I.e., the remaining water that is not evaporated is often enriched in ^{18}O). In contrast, d-excess refers to the water vapor that is lost during evaporation, which is often depleted in isotopes relative to the Local Meteoric Water Line (LMWL). That is, its composition on a plot of δ^{2}H versus δ^{18}O will be above the LMWL. As a result of the conservation of mass, if the remaining water becomes enriched in ^{2}H (i.e., plots below the LMWL), then the water vapor must become depleted in ^{2}H relative to the LMWL (i.e., plots above the LMWL).

The difference between d-excess and Lc-excess is shown in Figure 3. The blue point on the LWML represents the isotopic signature of one rain event (i.e., precipitation). Assuming that this is the only water that enters the system, the red point represents the isotopic signature of the water that remains after evaporation. (Note that it plots below the LMWL). Using the red and blue points, we can construct the dotted evaporation line. Thus, the grey point to the left side of the isotopic signature of the rain event (i.e., the blue point) represents the isotopic signature of depleted water vapor derived from evaporation. The difference between the δ^{2}H values of the grey and red points (assuming the same ^{18}O values for both) reflects the d-excess.

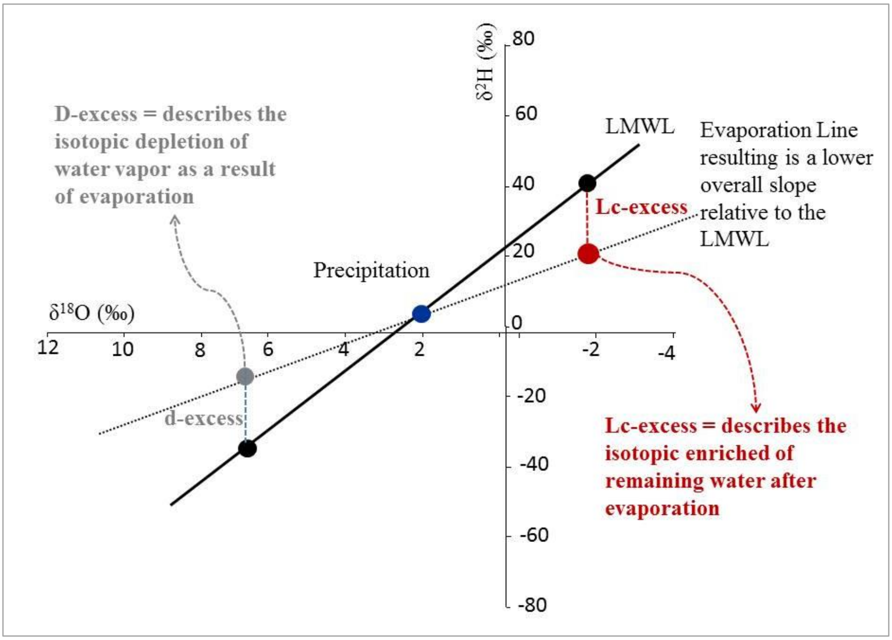

Figure 3. Comparison between d-excess and Lc-excess as a function of the variation of the slope of the Local Meteoric Water Line (LMWL). The red and grey points are on the evaporation line. Points on the LMWL to the left of the isotopic signature of the rain event (blue dot) represent the depleted water vapour derived from evaporation (i.e., the grey point). The differences between the δ^{2}H values of the grey and red points (assuming the same ^{18}O values for both) reflect the d-excess

and Lc-excess, respectively. Higher values of d-excess represent greater evaporation of water into the atmosphere. Adapted from Clark and Fitz (1997).

Consequently, Lc-excess can be used as a mathematical expression for the offset between the LMWL and the analysed soil water samples. Lc-excess values close to zero indicate little difference between soil water samples and local precipitation, whereas more-negative values indicate a greater degree of evaporation (Landwehr and Coplen 2006).

It is well known that compositions of waters that have undergone non-equilibrium evaporation usually plot below and to the right of the LMWL on a graph of δ^{2}H versus δ^{18}O. The physical significance of that phenomenon is that as evaporation proceeds, the water that is left behind becomes more enriched with the heavier isotopes, resulting in evaporation lines whose slopes are less than eight (Barnes and Allison 1988, Kendall and Caldwell 1998). That enrichment occurs because of the disproportional impact that kinetic fractionation processes have on oxygen isotopes compared to hydrogen isotopes (Kendall and Caldwell 1998). Isotopic enrichment via kinetic fractionation takes place during evaporation after a rain event (Sprenger et al., 2016). Examples of that effect are reported by Goldsmith et al. (2012) and McCutcheon et al. (2017), who found isotopic enrichment of water in shallow soil and depletion at deeper depths in a tropical montane cloud forest and in a semiarid catchment in the USA.

The foregoing gives an indication of how researchers might use isotopic analyses to help identify the dominant processes responsible for variations in soil water under different vegetation covers. Those processes are rainfall interception, evaporation, transpiration and preferential flow. The necessary work entails relating soil water contents need to distribution of water stable isotopes, and to the occurrence of isotopic fractionation within a soil profile.

2.5 New conceptual model for the effects of canopy cover on local soil water dynamics

In this thesis, I used and evaluated a new conceptual model (Figure 4) for understanding mechanisms by which canopy cover affects local soil water dynamics. I sought to know, specifically, whether that model may help researchers understand how trees as a whole affect soil water dynamics (**Papers II and III**).

Elsewhere in this document, I say-for sake of brevity-that I designed my experimental plan to test hypotheses that I based upon predictions inferred from this conceptual model. Actually, the model and plan co-evolved during the course of this my thesis work: hypotheses that I inferred from an early version of the model suggested certain "scoping" experiments, whose results then led to a more-comprehensive and -detailed model, which in turn led to new, empirically testable hypotheses, and so on.

Specific predictions were inferred about spatial and temporal variations of the Lc-excess in soil water. For example, canopy trees can affect surface soil moisture directly by transpiration (black arrow, Figure 4A) or by interception of incoming precipitation (blue arrow and grey arrows, Figure 4A). Presence of canopy trees can also influence surface soil moisture by reducing evaporative losses from the soil surface (red arrow, Figure 4A). These three pathways are associated with different isotopic fractionation processes. I hypothesized that these processes (and thus their associated pathways) could be teased apart by examining the relationship between surface soil water content (SWC) and the isotopic composition of surface soil water (Figure 4B).

Experiments based upon this model should also be capable of identifying whether flow of water downward into the soil is dominated by matrix flow, or by preferential flow, or neither. Isotopically enriched soil water (yellow portion, Figure 4A) deep in the soil profile would indicate matrix flow. In contrast, preferential flow would be indicated if water in a site’s surface soil is enriched (blue portion, Figure 4A), while the site’s subsoil water has essentially the same isotopic composition as the local precipitation. (That is, if the lc-excess is close to zero in the subsoil.)

I explored such predictions empirically by measuring stable isotopes and soil moisture at appropriately chosen times and locations in the soil profiles of two contrasting ecosystems. On the whole, I analysed the resulting data according to the original calculation described in Landwehr and Coplen (2006). However, instead of reporting the Lc-excess as δ^2H_M - δ^2H_p, I reported it as $\delta^2H_p - \delta^2H_M$ (lc-excess, **Paper II**), where ^2H_M = deuterium measured, and $^2H_{p=}$ deuterium predicted. So that higher values of the excess could be interpreted straightforwardly as an effect of increased evaporation.

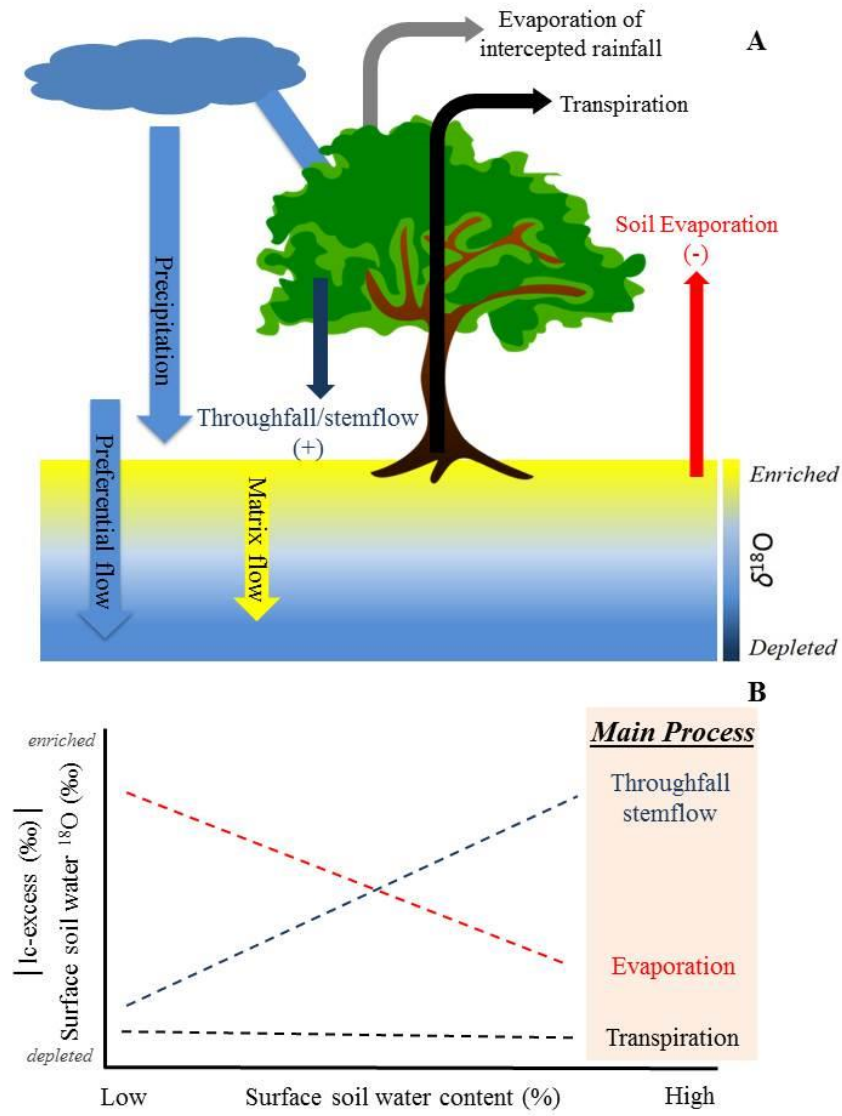

Figure 4. Schematics of the conceptual model of how trees influence local soil water dynamics. In (A), canopy trees affect surface soil moisture either by transpiration (black arrow) or by interception (grey arrow) of incoming precipitation/throughfall (blue arrow). Isotopically enriched soil water (yellow) at deeper soil depths would suggest matrix flow, whereas similar isotopic values between subsoil water and precipitation (blue) would indicate preferential flow. (B) shows the relationship, predicted by the conceptual model, between surface SWC and the isotopic composition of surface soil water.

2.6 Objectives and hypotheses

The main goal of this thesis was to understand better the roles of low-density stands of trees in soil water dynamics. An additional goal was to aid future research by exploring a new conceptual model relating the effects of vegetation to the spatial variability of lc-excess and soil water content (Figure 3). To those ends, I studied the relationships, in two agroforestry systems, between soil water content, infiltrability, preferential flow pattern, and presence of trees. The two systems were (1) a degraded pasture in Copan, Honduras, with less-resilient soils and only scattered clumps of trees (Figure 4); and (2) an agroforestry coffee farm in Central Costa Rica, with porous, resilient, well-maintained volcanic soils and a dense cover of trees and coffee plants (Figure 5). I assumed that such in contrasting landscapes, the effects of trees upon on soil water dynamics would be significantly different.

The specific objectives of this thesis were (i) to relate water infiltrability and preferential flow (in both systems) to distance from trees, and compare infiltrability to rainfall intensities; (ii) to identify which processes (transpiration, soil evaporation, and interception) dominate the variations in soil water, and to identify the influence of three vegetation types (tree, coffee and grasses) upon these processes, by testing a new conceptual model relating spatial variation of soil water content to its lc-excess values; and (iii) to determine the type of interaction between trees and grasses with respect to vertical water uptake (i.e. the presence of niche partitioning or not), and consequently, how trees influence the way grasses partition vertical water uptake.

The general hypothesis was that trees in degraded landscapes affect soil water dynamics positively by increasing soil water contents, infiltrability, and preferential water flows. I also hypothesized that those effects would be smaller in systems where the soil's inherent physical condition is good, and is maintained by appropriate management practices. The last can also be considered as the "stress gradient hyphotesis" (Maestre et al., 2009). Derived from these central hypotheses, the following sub-hypotheses were tested in the two study locations:

1. Trees improve infiltrability significantly in the degraded Honduran agrosilvopastoral system, but less so in the well-maintained Costa Rican coffee agroforestry system. (**Paper I**).

2. In the Costa Rican coffee agroforestry system, soil moisture will be lower near shade trees than near coffee shrubs because trees have lower throughfall and stemflow, plus higher transpiration. In the Honduran agrosilvopastoral system, the soil water content will be higher under trees than in the open because trees increase soil infiltration and preferential flow, while also reducing evaporation.
3. Preferential-flow capacity will be higher near trees due to greater macroporosity (**Paper I**). However, because the actual preferential flow is also affected by the influence of trees on soil water content (**Paper II and III**), preferential flow will be greater under coffee shrubs than under neighbouring canopy trees. An additional basis for this hypothesis is that the greater canopy interception and throughfall under coffee shrubs lead to higher soil moisture, which helps to initiate preferential flow (**Paper II**). In contrast, the scattered trees in the Honduran pasture may lead to both higher macroporosity and improved soil water contents. Thus, actual preferential flow at the Honduran site will be higher under nearby trees (**Paper III**).
4. Because the relationship between the spatial variation of soil water content and its corresponding isotopic signature (lc-excess) is affected by the system's dominant hydrological processes, the presence of trees influences the magnitude and direction of this relationship (**Paper II and III**).
5. Because trees and grasses in the Honduran agrosilvopastoral system compete for water during the dry season, but use complementary sources (and have a facilitation relationship) in the wet season, soil water will partition vertically between trees and grasses (**Paper III**).

By testing hypothesis 5 in this thesis, I hoped to contribute to verifying one of the most important premises supporting agroforestry and scattered-trees systems, which is that trees and grasses use complementary sources of water when its availability in the surface soil is limited.

3 Materials and Methods

3.1 Study locations

The two study locations in this thesis were used together in **Paper I** (Turrialba, Aquiares, Costa Rica; and Copan, Honduras), and separately in **Paper II** (Turrialba, Aquiares, Costa Rica) and **Paper III** (Copan, Honduras). The primary aim of using these two study sites was not to make comparisons, but to test the thesis hypotheses on contrasting systems, both of which have land uses that are common in the tropics, and in which trees can have a role in hydrological ecosystem services. The Costa Rican site represents humid tropics with stable, highly-permeable volcanic soils, while the Honduran site represents seasonally dry tropics with soils that are less resistant to degradation and less resilient in the face of climate change.

3.1.1 Turrialba, Aquiares, Costa Rica

The Aquiares, Turrialba, Costa Rica coffee agroforest farm (Figure 5) is part of a long-term experiment of the Coffee-Flux observatory (SOERE F-ORE-T), which is managed by researchers from CIRAD, France who are based in the Tropical Agricultural Research and Higher Education Center (CATIE) in Costa Rica. The research described in this thesis was conducted in the Mejias Creek microcatchment (−83˚44’ W and 9˚56’ N) (Figure 7 a), in which elevation ranges from 1020 to 1280 m.a.s.l, with a mean slope of 20%. Annual precipitation is 3014 mm (Gomez-Delgado et al, 2011), with the lowest rainfall occurring between December and March. Soils are Eutrandepts Andisols (USDA, 1999): coarse-textured layers, very stable, with high biological activity and high contents of organic matter and allophane (Kinoshita et al., 2016; Tobón et al., 2010). Mean monthly net radiation ranged in 2009 from 5.7

to 13.0 MJ m^{-2} d^{-1}, air temperature from 17.0 to 20.8 °C, relative humidity from 83 to 91%, wind speed at 2 m high from 0.4 to 1.6 ms^{-1} and Penman-Monteith reference evapotranspiration (Allen et al., 1998) from 1.7 to 3.8 mmd^{-1}.(Gomez-Delgado et al., 2011).

Figure 5. View of the coffee agroforestry system in the Aquiares, Turrialba, Costa Rica. Location (a) is an example of trees surrounded by an irregularly distributed coffee stands, and (b) is an example of gaps possible to find below trees, in this case, the picture shows angle with a closer

look than picture (a). This thesis compared soil water dynamics of areas covered only by tree canopy to those of areas covered only by coffee.

3.1.2 Copan River catchment, Honduras

This site, located in the lower subcatchment of the Copan River, was part of the Mesoamerican Sustainable Land Management Project (MESOTERRA), which was a research and development project run by CATIE (CATIE-MESOTERRA, 2009; Pezo et al., 2010). The Copan River catchment extends from 14˚43’ to 14˚58’N, and from 88˚53’to 89˚14’ W (Figure 7 b). Annual precipitation at this site is 1772 mm, with a pronounced dry season from December to May. Soils are of the Typic Argiustolls class (USDA, 1999). I studied three farms located in three communities (El Malcote, Sesesmiles, and El Zapote) of the subcatchment. All of the farmlands that I studied therein have been used as cattle pastures for the last twenty years. The mixture of native grass and introduced species that covers them contains scattered, naturally-distributed trees (Figure 6).

Figure 6. Views of the pasture landscape in Copan, Honduras: a) General landscape; b) and c), examples of the arrangement of clumps of trees. In this thesis, soil water dynamics in the open pasture were compared to those below clumps of trees.

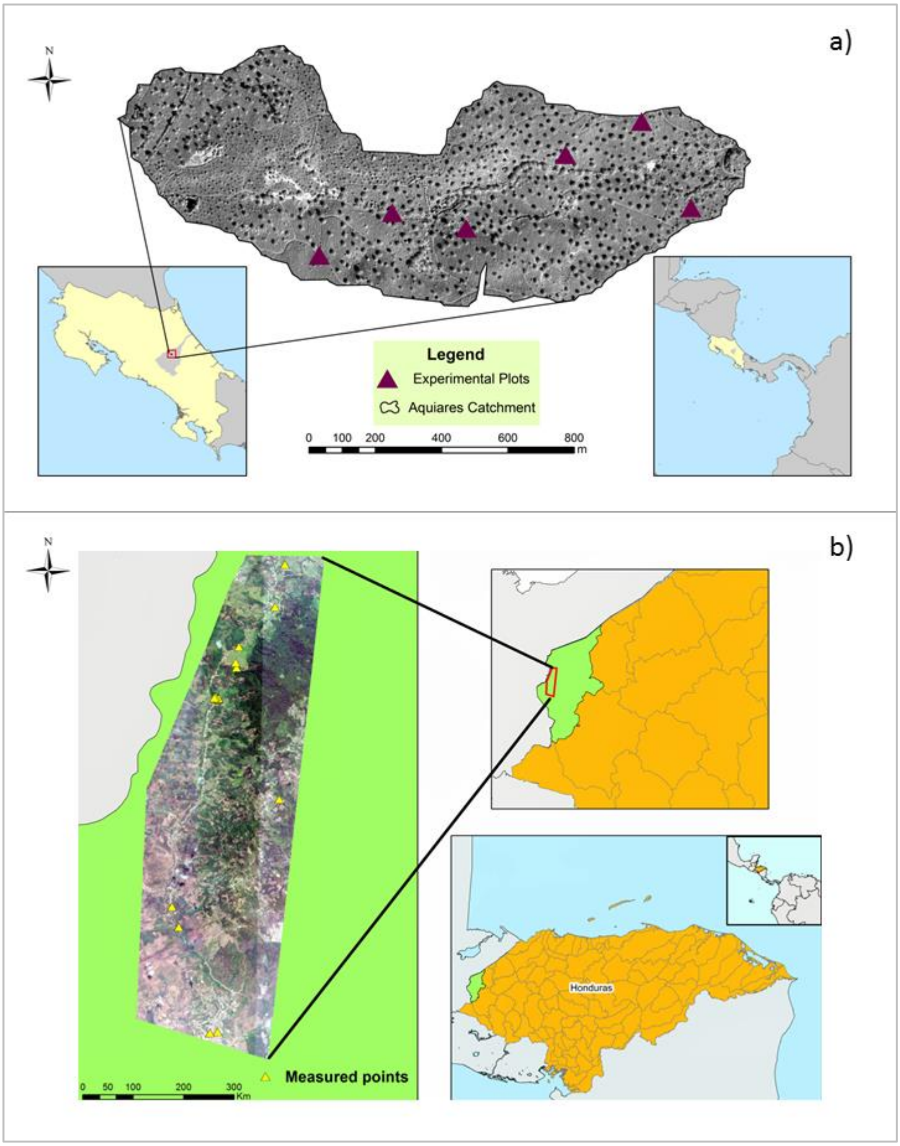

Figure 7. Location of the study sites: a) Coffee agroforest in Turrialba, Aquiares, Costa Rica, and b) Pasture landscapes in Copan, Honduras.

3.2 Field Measurements

I performed three experiments, only two of which were performed at each site. In the first experiment, which was carried out at both sites, I traced a series of randomly oriented (north, west, south, east) transects that had one tree or a clump of trees at one end, and no other trees upon them. Along the transects, I performed infiltrability tests and assessed soil properties, water holding capacity, preferential flow, and macroporosity (**Paper I**). The second experiment, conducted only in Aquiares, Turrialba, Costa Rica agroforestry site, I compared the local soil water dynamics at five sites under trees and below coffee shrubs, and under two rain intensities that represented precipitation events in the dry and wet seasons (**Paper II**).

The third experiment was conducted only at the three sites in the lower Copan River subcatchment. That experiment had two purposes: (1) to compare the soil moisture underneath trees and under grasses, and (2) to assess the proportions of water sources used by trees and grasses (**Paper III**).

I also studied water sources of trees and coffee shrubs at the Aquiares site, but could not use the results because of problems with isotopic enrichments in the plant tissues.

3.2.1 Infiltrability

I used two complementary methods to measure infiltrability: (1) Double Ring Steady State Infiltrability (DRSSI) for steady-state infiltrability, and (2) Rainfall Simulation Steady State Infiltrability (RSSSI) tests.

The DRSSI method estimates the maximum steady-state infiltrability by using measured data to calculate the cumulative infiltration rate as a function of time. The final DRSSI values were modelled using Philip’s equation (Philip, 1957). For the RSSSI method, I used pre-selected simulated rainfall intensities representative of the maximum that is known to occur at each study site. The surface runoff volume was collected, and infiltrability was determined indirectly by calculating the difference between simulated rainfall and collected runoff water.

According to Hillel (1998), infiltrability is high during early stages of ponded infiltration, when pressure gradients predominate over gravitational forces. The gradients decrease as infiltration progresses, eventually leaving gravity as the only acting force. As a result, the infiltrability decreases to a final, constant rate. That rate, known as the steady-state infiltrability, is sometimes called the infiltration capacity.

Practical equipment and analysis

For the DRSSI tests, I used a metallic double ring with a 25 cm inner ring, 35 cm outer ring, and (as suggested by Reynolds et al., 2002) a 10-cm water head (Figure 8 c).

The rainfall simulator used in RSSSI tests was a modified version of that described by Imeson (1977). The area of its water-emitting surface was 60 cm^2. Water droplets were emitted through nozzles having a diameter of 0.50 mm each. The simulator was mechanically oscillated during the experiments to ensure that the simulated rainfall was distributed evenly within the receiving area. Simulated intensities averaged approximately 70 mm h^{-1}, with a peak of 80 mm h^{-1} (Figure 8 a). Those intensities were selected after consideration of historical rainfall measurements, which showed that the maximum 10-minute intensity at the Aquiares was 106 mm h^{-1}, and that the maximum five-minute intensity at Copan was 82.9 mm h^{-1}. I calculated Infiltrability (usually at intervals of five to ten minutes, depending upon how rapidly the simulated rainfall entered the soil) by subtracting the measured cumulative surface runoff volume from the cumulative simulated rainfall. When that difference no longer changed between measurements, its value was reported as the steady state infiltrability.

At both study sites, I conducted experiments along randomly-oriented transects (north, west, south, east). Each of the six transects in the coffee agroforest originated under the center of a tree canopy. They contained coffee plants elsewhere along their lengths, but no other trees, and were divided into two sections: (1) the section beneath the origin-canopy (under the tree crown), and (2) the section distant from the tree (under coffee plants only).

We performed a total of five DRSSI tests at 1-m intervals (60 in Aquiares; Fig. 1a, **Paper I).** In the Copan pastures, transects contained a clump of trees at the point of origin, and only open pasture elsewhere along their lengths (Fig. 1b, **Paper I**). Each transect was divided into an open-pasture section and the section beneath the canopy of the trees. I did five infiltrability measurements under the canopies of each Copan transect, at 1-m intervals. In addition, I measured infiltrability at three locations in the distant open-pasture sections of each transect. The positions at which infiltration was measured in the open pasture were separated from each other by a distance equal to the height of the tallest tree in the clump.

At each study site, RSSSI experiments were conducted at the origins, midpoints, and endpoints of four selected transects, for a total of 12 RSSSI experiments.

3.2.2 Macroporosity and preferential flow

At the end of each of the twelve RSSSI tests, I measured macropore flow according to the method given by Flury and Wai (2003), in which dye tracers are allowed to infiltrate into the ground so that flow patterns can be made visible and quantifiable (Mooney and Morris, 2008). In this thesis, the purpose of dye-pattern analyses was to detect possible differences in macropore flow between the two sections of selected transects. (I.e., near trees and distant from them). I also measured soil macroporosity and water-holding capacity, in order to relate them to macropore flow.

I defined soil macroporosity as the abundance of pores with a diameter greater than 0.05 mm. Also known as transmission pores, these are routes for rapid drainage after heavy rainfall or irrigation, and are important for soil aeration when the soil is at field capacity (Rowell, 1994). Macroporosity was assessed using the assumption that macropores are drained at water holding capacity (WHC). Under that assumption, the difference between total porosity and WHC provides a measure of macroporosity. WHC was determined by a gravimetric method in which 5 cm-high soil samples were allowed to drain freely, then weighed, and subsequently heated at 100 to 110 °C until they ceased to lose weight. The weight that a sample lost during the time between draining and end of heating was reported as the sample’s measure of macroporosity (Gardner et al., 2000).

Sampling equipment and analysis

For each macropore flow measurement, I prepared 18 l of a solution of 20 g of Brilliant Blue dye per litre of water. That quantity (300 ml) was sufficient to provide 300 ml of simulated precipitation during the corresponding RSSSI test.

The solution was applied after the rainfall simulations reached a steady-state condition. An hour later, I began the excavation of a pit on one side of the runoff area, and continued to remove soil in 10-cm layers until the dye was no longer detectable. As excavation proceeded, care was taken to ensure that the vertical wall nearest the runoff test area remained smooth enough to produce good photographs for documentation of the depth to which dye had penetrated. I placed a graduated frame (Figure 7 b) on the walls as a reference for image analysis of digital photographs, which I took with a 24 mm wide-angle lens (Sony Cyber-shot DSC-WX10). The distance between the wall and the lens of the camera was 50 cm.

To determine the amount of dye within the soil, images were analysed using the ENVI image analysis program, Version 4.7 (ITT Visual Information Solutions—www.ittvis.com). The two colours of interest (soil with and without Brilliant Blue) were separated through a supervised Mahalanobis distance classification (Richards, 1999). According to Perumal and Bhaskaran (2010), the Mahalanobis classification method is more accurate than unsupervised classification methods, and more accurate than other supervised classification methods as well, because of its capabilities to (among other things) filter out shadows and classify the highly-varied clusters.

In each photograph, the area defined by the frames was used as individual region of analysis. To account for the whole region of analysis in each pit, I summed the depths of each frame, in the vertical position, in which dye was found. For comparison, I also calculated (within the soil region of analysis) the ratio of “Brillant Blue”-dyed pixels to undyed pixels. The values reported from this analysis were percentages of blue coverage at each depth and position (horizontal and vertical), from which I calculated a series of indices: the uniform infiltration depth (UID), maximum depth of blue stains (MD), total stained area (TSA), preferential flow fraction (PFF), and the ratio TSA/MD (Table 2, **Paper I).**

To determine the soil’s water holding capacity (WHC), undisturbed soil was sampled horizontally (through the vertical walls of the pits) using a stainless steel cylinder (diameter = 7.5 cm and height = 5 cm). The soil samples were weighed (field weight soil: FWS), then saturated from below by placing a filter tissue at the bottom of the cylinder (held in place with rubber rings) and slowly adding water every hour for 8 h until saturation was achieved, at which point the sample was re-weighed to determine the weight of the saturated soil (wet weight soil: WWS). The sample was drained for 1 h, then re-weighed before and after drying to constant weight at 105°C for 24 h, to obtain the dry weight soil (DWS). The water-holding capacity was calculated as WHC (%) = 100*(WWS – DWS)/DWS (Rowell, 1994).

Figure 8. Main experimental methods to investigate the soil water dynamics: a) Rainfall Simulator; b) Frame of dying soil layer; c) Double ring infiltrometer; and d) Zero-tension wick lysimeter device.

3.2.3 Water dynamics: water in soils

I measured soil water content and soil water movement in the upper 50 cm of soil using the soil coring and thermogravimetric method described in Section 3.2.2. Additionally, I used wick lysimetry to determine the moving water at the depth of 50 cm. Water sampled with wick lysimeters was used for isotopic measurements, which were also made on soil samples after cryogenic soil water extraction.

The wick lysimetry method uses fiberglass wicks to apply capillary suction (Brown et al., 1986; Knutson and Selker, 1994; Steenhuis et al., 1998; Zhu et al., 2002) to collect soil water by gravity (Holder et al., 1991). More specifically, a sort of “water column” is formed by emplacing the wick (hygroscopic rope) vertically in the soil, thereby forcing soil water enter into collectors. In Fig. 8d, for example, the wicks are inside the hose and inside the horizontal pvc tube. In this way, the apparatus maintains the lower soil boundary at a pressure below atmospheric, thereby avoiding the problem of water divergence that is common to zero-tension lysimeters (Abdulkareem et al., 2015). Wick lysimeters work well in structured clay soils with dominant preferential flow (Barzegar et al, 2004). To collect samples for isotopic analysis of water moving through the upper soil profile of each plot (reported in **Paper II)**, we installed wick at a depth of 50 cm (n = 6 per treatment: under the trees and below coffee shrubs only).

Sampling equipment and analysis

The process for sampling soils and handling them for isotopic analysis was as follows (**Paper II and III**).

Soil cores were collected under trees, below coffee shrubs, or below grass. From each core, two samples were taken for soil water isotopic analysis: one on of the superficial soil (0-15 cm), and one of the soil between the depths of 85 and 100 cm. Freshly-collected soil samples were placed in capped glass vials, wrapped in parafilm, and stored in a refrigerator (4˚C) until water extraction.

The lysimeters consisted of a PVC pipe (15 cm in diameter and 30 cm in length) with five openings (8 cm long by 5 cm wide) on the side directly in contact with the soil. PVC pipes were filled with soil, and with an 8-mm-diameter hygroscopic rope (Thermo-E glass fibre twisted rope- HKO Heat Protection Group, Germany) that was in direct contact with the soil. This type of lysimeter produces a hanging water column that exerts a negative pressure on the soil above the lysimeter (BrandiDohrn et al., 1996, Zhu et al., 2002), and collects water infiltrating to a depth of 50 cm. Water was collected from individual lysimeters after individual rain events, concurrently with soil sample collection (October 2013 – March 2014) (Figure 8 d).

3.2.4 Water dynamics: water in vegetation

Knowing the isotopic composition of a plant’s xylem water (for example, the water’s natural $^{2}H/^{1}H$ ($\delta^{2}H$) and $^{18}O/^{16}O$ ($\delta^{18}O$) ratios) enables researchers to quantify the relative proportions of water that the plant has drawn from each of its sources. More specifically, it is possible to match the isotopic signature of plant xylem water to a unique combination of the relative proportions of soil water drawn from different depths within the soil profile (Brunel et al., 1991, 1995; Dawson, 1993; Ehleringer and Dawson, 1992). In this thesis, all vegetation samples collected from trees were taken from non-photosynthetic twigs to avoid misinterpretations that can arise from evaporative enrichment of non-suberized tissues (Dawson and Ehleringer, 1993).

Practical sampling and analysis

I selected three sites, each of which represented one of the three dominant tree species (**Paper III**). At each site, I collected three twigs from each of three different representative trees located within a clump, together with three repetitions of grasses located underneath the trees. I also took three samples of grasses from the open area, at a distance equal to the height of the tallest tree (ca. 20 m) in the clump. Sampling was done in both the dry season (7-8 January 2013) and the wet season (9-10 June 2013).

The twigs that I collected were approximately 10 cm long, and were taken from three different positions on each selected tree. To prepare each twig for analysis, I cut it into pieces approximately 5 mm long by 3 mm in diameter. I placed each twig's pieces in a separate glass tube 70 mm long by 8 mm in diameter. Grass samples were taken from stems (the non-photosynthetic part of the stem at the joining part with the roots), collected from culms at two locations: one underneath the trees, and the other in the open area. I took three replications in each location. Grass samples were placed in tubes identical to those used for twig samples. To keep the vegetation samples tightly packed, I stuffed silk-wool into each tube, and then sealed the tubes with plastic lids to prevent air from entering. Samples were kept in the freezer (-4˚C) until water extraction. Each replication of vegetation samples was treated separately in the analysis (**Paper III**, **Paper II).**

Water was extracted from soil and vegetation samples using a cryogenic vacuum distillation line (Ehleringer et al., 2000). Water from soil and vegetation water was sampled as described in Sections 3.2.3 and 3.2.4. At two sites in Copan, where the top of the water table was three meters below ground level, we installed a PVC pipe in the ground for access to the groundwater. We sampled the groundwater by lowering a plastic glass hanging from a stick.

The extracted soil water was analysed to determine its isotopic composition (δ^{18}O and δD) using a Picarro L2130-i Cavity Ring-Down Spectrometer (CRDS) analyser coupled to an A0211 high-precision vaporization module (Picarro Inc., Santa Clara, CA, USA). Analyses were done in high precision mode. Raw data were corrected for analytical effects (i.e., memory and drift), and normalized to the Vienna Standard Mean Ocean Water (VSMOW) scale using the protocols proposed by van Geldern and Barth (2012). Isotopic signatures of water were calibrated using internal laboratory standards, which had in turn been calibrated against two International Atomic Energy Agency (IAEA) official standards: Greenland Ice Sheet Precipitation (GISP), and Standard Light Antarctic Precipitation (SLAP). Precisions of the isotopic measurements was certified as 0.05‰ for ^{18}O and 0.26‰ for ^{2}H, based on repeated analyses of known lab standards.

Gravimetric soil water content (SWC) was calculated as SWC = 100*(fresh weight – dry weight)/ (dry weight)] according to differences in sample weight before and after thorough water extraction at 105 °C for 1.5 h.

3.2.5 Isotopic analyses

The isotope ratio $\delta^{18}O$ of samples was calculated as

$\delta^{18}O(‰) = [(^{18}O/^{16}O)_{sample}/(^{18}O/^{16}O)_{standard}] -1 \times 1000$.

In **Paper II**, I used differences between the $^{2}H/^{1}H$ (δD) isotopic signature of soil water (δSW) and the local meteoric water line (LMWL; $\delta LMWL$) as a relative index of evaporation, based on similar methods such as the line condition excess (Lc-excess) approach described by Landwehr and Coplen (2006). More specifically, I used the measured $\delta^{18}O$ signature of surface soil water ($\delta^{18}O_{M}$) and the Aquiares site's LMWL ($\delta D = 8.7 (\delta^{18}O) + 17.9$; Sánchez-Murillo et al., 2016), to calculate the predicted $\delta^{2}H$ signatures of surface soil water samples: $\delta^{2}H_{P} = 8.7 (\delta^{18}OM) + 17.9$. As noted in Section 2.4, I report the lc excess as lc-excess = $\delta^{2}H_{M} – \delta^{2}H_{P}$, rather than the usual $\delta^{2}H_{P} – \delta^{2}H_{M}$, (i.e., rather than the version used by Landwehr and Coplen, (2006) because a positive value of $\delta^{2}H_{M} – \delta^{2}H_{P}$ indicates greater evaporation.

As evaporation proceeds, the water that is left behind remaining water becomes progressively more enriched with the heavier isotopes, resulting in evaporation lines with slopes of less than eight (Barnes and Allison, 1988, Kendall and Caldwell, 1998). Lc-excess values close to zero indicate little difference between the samples and local precipitation, whereas larger values indicate a greater degree of evaporation (Landwehr and Coplen, 2006).

Please recall that one of the aims of this thesis was to estimate the relative proportions of water that vegetation draws, respectively, from the surface soil (< 10 cm deep), subsurface soil (100 cm deep), and groundwater (> 3m deep). Having determined the $\delta^{18}O_{M,P}$ and $\delta^{2}H_{M\cdot P}$ values for those sources, I calculated the relative proportions from the IsoSource mixing model (Phillips and Gregg, 2003). That model assumes that because ^{18}O and ^{2}H are stable isotopes, the isotopic composition of a plant's xylem water is the result of simple mixing of the water from each source. The linear system of mass-balance equations based upon that assumption can be solved by standard methods to estimate the relative proportions of water that the plant draws from each source. Note that only *n* isotopes are needed to identify, uniquely, the proportions drawn from *n*+1 sources (Phillips and Gregg, 2001).

To determine the relative proportions that trees and grass at Copan draw from surface, subsurface and groundwater sources, I used the IsoSource mixing model (Phillips and Gregg, 2003). In that model, the oxygen isotope ($\delta^{18}O$) of xylem water was compared to the $\delta^{18}O$ signature of soil water at two different depths (10 cm and 100 cm), and to groundwater (water table at 3 m depth). The output from this model provides the distribution of fractional contributions from each potential water source based upon isotopic mass balance constraints. The physical basis for that calculation is the conservation of each isotope's mass. Standard linear mixing models are used to solve the corresponding mass-balance equations to identify the unique combination of source proportions. That solution process works because *n* isotope systems can be used to determine the proportional contributions of *n*+1 sources to a mixture (Phillips and Gregg, 2001).

Additional statistical analyses of the calculated proportions were needed in order to determine whether each type of vegetation at the two sites used different water sources in the dry season than in the wet season. Those analyses treated surface water, subsurface water, and groundwater as "relatively independent" sources, after testing for statistically significant differences between the sources' respective isotopic signatures. The mixtures of sources drawn were defined for both seasons according to the mean $\delta^{18}O$ signature of the xylem water of the sampled vegetation type at each site.

3.2.6 Statistics

I used a combination of statistical tools in **Paper I**, according to the phenomena that I wished to investigate and the characteristics of their respective data. The paired t-test was used to compare infiltrabilities of samples taken from underneath the Aquiares site's trees and coffee bushes, because the data were normally distributed. In contrast, I needed to use median tests to compare the non-normally-distributed infiltrabilities of soils under Copan's trees and grasses. Principal-component analysis (Webster, 2001; Webster, 2007) was used to relate the different indices for preferential flow assessment in **Paper I**.

The normal distribution of data reported in **Paper II** allowed use of ANOVA to assess the variation of soil water content with soil depth, season, and treatment (tree or coffee).

A series of one-way ANOVA was used to (1) detect significant differences in SWC among treatments for each depth and season; (2) detect significant differences in lc-excess among the different soil depths, for each season and treatment; and (3) assess how rainfall intensity and treatment affected differences in lc-excess values of soil water collected from lysimeters at 50 cm depth. Lastly, **Paper II** used a least-squares regression to examine the relationship between SWC and lc-excess of surface soil water, and in this way to test the proposed conceptual model.

In **Paper III**, normally distributed data allowed me to use a general linear model with SWC as the response variable, and season, soil depth, and location/vegetation type as fixed explanatory variables. Site/tree species was used as block factor in order to test differences in soil moisture. The block factor proved to not be significant, so it was removed from the final statistical analysis. I explored the relation between soil water content (at 10 cm depth) and lc-excess through a general regression, with lc-excess as response variable and season (wet or dry) and location/vegetation type (i.e. under trees and open grass) as explanatory variables. I also tested the explanatory variables' interactions. Differences between lc-excess values of soil water at different depths were tested using a paired t-test.

To test the significance of differences between mean values of water-uptake proportions (i.e., of the relative proportions that vegetation draws from <10 cm, 100 cm, and groundwater), I used a general linear model. The response variable in my model was the mean proportion of water uptake from each feasible source. The explanatory fixed variables were vegetation type (tree, grass under trees and grass in open areas) and season. All data were tested for normal distribution and homogeneous variance using the Sharpiro-Wilkson test and the Levene statistic, respectively. The statistical software packages used were Minitab 16 (**Paper I**), Sigma Plot (**Paper II**), and Infostat (**Paper III**).

4 Results and Discussion

The three papers appended to this thesis investigated the relationship between tree cover and soil water dynamics in two contrasting tropical landscapes—a coffee agroforestry system located in permeable, stable volcanic soils in a humid tropical region, and a pasture landscape with scattered trees located in degraded, less-resilient soil in a seasonal tropical region. The purpose of the investigations was to disentangle the specific processes controlling this relationship. Below, I integrate the results from the three papers, and present my conclusions regarding the main processes. Further results and more-detailed discussions are provided in the appended papers (I—III).

4.1 Contrasting site- and context-dependent effects of trees upon infiltrability and preferential flow

4.1.1 The dynamics of infiltrability

Infiltrability varied strongly with distance from trees in both the Aquiares coffee agroforestry system and the Copan pasturelands (**Paper I)**. Comparisons of infiltrability rates measured by RSSSI in the coffee agroforestry system showed that only a few rainfall events surpass the infiltrability rates (always above 50 mm h^{-1}), corresponding to just 3% of the total rainfall falling during the study (Fig. 4a, **Paper I**). Thus, the infiltrability rates were sufficiently high to allow the infiltration of almost all rainfall events. This finding is consistent with earlier observations of Gómez-Delgado et al., (2011), whose combined experimentation and modeling at Aquiares found that coffee agroforestry seems to maintain the inherently high infiltrability levels of andisols. More specifically, that system maintained 92% of the soil's infiltration, according to

Gómez-Delgado et al.'s model. Thus, this agroforestry system in volcanic soil has the potential to conserve water effectively and prevent erosion.

In the Copan site's pasture landscape, soils had infiltration rates sufficient to absorb all rainfall with lower intensities lower than 20 mm h^{-1}. Nevertheless, 30% of the typical rainfall events in this region have intensities higher than 20 mm h^{-1}, which represented 25% of the measured infiltration rates at pasture locations 22–30 m from trees. Therefore, one can expect substantial surface runoff in areas without tree cover. I also inferred surface runoff during my rainfall simulations at 20 mm h^{-1} (Fig 4b, **Paper I**). These results are consistent with those from a study of Panamanian pastures by Hassler et al., (2011), who compared K_{sat} (soil hydraulic conductivity at saturation) with the amount of rain that falls during 30 minutes at maximum intensity, and concluded that pastures in a tropical region with a distinct dry season were prone to overland flow. These authors conducted their study by comparing pastures in different states of forest succession. In general, they found that after conversion to pasture, forests require more than eight years of succession to reach the pre-pasture levels of K_{sat}.

My two study locations differed markedly in their DRSSI-derived infiltrability rates. These measurements were more repeatable than those from the RSSSI experiment. Still DRSSI-derived infiltrability rates in the coffee agroforestry system were the same in locations near trees as in locations away from them (DRSSI values, Fig. 5a, **Paper I**; p = 0.105; distant tree mean =1124 mm h^{-1}, near tree mean = 898 mm h^{-1}). Several key factors can explain these results, one being the inherently high permeability of andisols (Cattan et al., 2009; Dorel et al., 2000; Gómez-Delgado et al., 2011; Nanzyo, 2002), besides, this soil have 73 and 70 % of total porosity, and more than 58 and 55 % of sand at 10 and 100 cm depth respectively, both contributing to that high permeability. Another factor is the use of a no-tillage soil management (Beer, 1988) where an unpruned perennial understory of coffee trees with extensive roots (Defrenet, 2016) leaves organic residues on top of the soil.

The soil properties of the Copan pastureland are quite different. There, infiltrability rates close to trees were about three times greater than those in the open pasture (Mood median test, p = 0.009; clump of trees median = 146 mm h^{-1}, open-pasture median = 47 mm h^{-1}, Fig. 5b, **Paper I**). Therefore, while trees improved the soil macroporosity in the pasture landscape, the coffee agroforestry systems' soil macroporosity is sufficiently high even without shade trees. Other authors, too, have found higher infiltration and K_{sat} values in agroforestry systems than in crop systems (Siriri et al., 2006). However, my results for the agroforestry system on andisols contrast with reviews confirming that trees generally improve infiltrability within agroforestry or afforestation schemes (Ilstedt et al., 2007). In the studies analyzed in the meta-analysis carried out by Ilstedt et al., (2007), the soils belong to two classes, ultisol and alfisols, they were grass and mostly crops before afforestation, and tree species used for afforestation were *Tectonia grandis, Cassia spectabilis, Sesbania sesban, Gliricidia sepium*, among others.

Another review found that biomass and infiltration capacity are positively correlated under water-limited conditions in a site with varying vegetation (Thompson et al., 2010), but are not significantly correlated under humid conditions. However, it is important to note that that review excluded studies that investigate effect of disturbances; e.g. from agriculture. The pasture landscape in Copan had an extended dry season (six months), and was affected by grazing. Trees under agroforestry parklands improve soil hydraulic properties by influencing groundwater recharge in semiarid tropics of Burkina Faso (Bargues-Tobella et al., 2014). Similarly, Belsky et al., (1993) found that trees increased infiltrability in a mesic savanna in Kenya, and Ellis et al., (2006) observed the same effect in open areas of an Australian pasture that is trampled by animals.

4.1.2 Preferential flow patterns

At both sites (Aquiares and Copan), preferential flow indices were higher near trees than away from them. The difference was greater in Copan. Perkins et al. (2012) found the same phenomenon in Hawaii: preferential flow is higher in areas of native tree species (individually and in various combinations) than in nearby degraded grasslands.

Matrix flow showed a different trend: it dominated in the open-pasture sections of Honduran transects. Furthermore, at Copan the measured steady-state infiltrability rates correlated significantly with distance from trees, as did the various preferential-flow indices (**Paper I**). In contrast, preferential flow was present in both sections of the Aquiares transects; that is, beneath the canopy trees that defined the transects' origins (Fig. 2a, **Paper I**), and also in the transects' coffee-only sections (Fig. 2b, **Paper I**).

That conclusion was based upon the significantly lower ($p = 0.01$) lc-excess in deeper soil water (100 cm) as compared to near-surface soil water (**Paper II**) These lower lc-excess values occur because under preferential flow, water moves rapidly through the vadose zone, and thus suffers less evaporative loss. As a result, preferential flow causes the isotopic signature of deep soil water to be similar to that of recent precipitation. (I.e., the deep-soil water was less enriched in ^{2}H than the surface water, making its lc-excess closer to zero).

During the dry season, lc-excess values in near-surface water under trees were greater than in water from deeper soil. That finding, which was true for water under coffee ($p = 0.04$) as well as beneath shade trees ($p = 0.07$; Fig. 4B, **Paper II**) reveals the presence of preferential flow. The isotopic approach used in **Paper II** was useful because that approach's measurements are indicative of flow during real moisture conditions, in contrast to blue-dye measurements that are made during saturated conditions. A pre-requisite for the presence of preferential flow is soil moisture, together with pore structure. Therefore, the isotopic approach was a good complement to the indirect dye and pore structure indices used in Paper I. In **Paper III,** I presented isotopic analyses showing that at Copan, a preferential flow was present under trees, but not in open grassland: compared to values for near-surface water, the lc-excess values were lower for the subsoil water under trees, but not in the open, grass-covered areas. This difference was significantly larger during the wet season (i.e., lc-excess was 2.6 times higher in water from the surface soil: 30.24‰ vs. 11.25‰; $p=0.03$). During the dry season, the difference was almost significant (Figures 8A and 8B, **Paper III**).

Relatively few studies compare the effects of trees upon preferential flow. However, a Honduran case in which a greater preferential flow was linked with trees, in contrast to degraded pasture, was reported in Honduras by Hanson et al., (2004). Another case where trees' presence favored a preferential flow is in semiarid parkland in Burkina Faso (Bargues-Tobella et al., 2014). Both of these studies showed a strong, positive relationship between preferential flow and tree cover. Specifically in the study of Burkina Faso, the authors reported that in small open areas, where tree influence is higher, the soil's physical properties are more spatially variable, with more macropores occurring at points where tree roots can reach and fewer in locations where there are no roots.

4.1.3 Soil water content (SWC)

In Aquiares, SWC was generally higher under coffee than underneath shade trees ($p < 0.001$), and roughly 33% higher in the wet season than in the dry season ($p < 0.001$; Fig. 3; Table S1, **Paper II**). At 15 cm depth, SWC was higher in the wet season than in the dry season ($p < 0.001$), but the canopy-cover effect (trees vs. coffee) was significant only during the dry season ($p = 0.001$; Fig. 3A, **Paper II**). At the 100-cm depth, SWC was higher in the wet season ($p < 0,001$), and was higher coffee than underneath shade trees in both seasons ($p < 0.05$; Fig. 3B, **Paper II**).

During the dry season in the Copan pasture landscape, SWC at the 10-cm depth was ca. 1.3 times higher under trees ($p=0.004$) than in open areas (Figure

3A, **Paper III).** However SWC at that depth during the wet season was similar under trees and away from them. During the dry season, the SWC at 100 cm was ca. 1.6 times higher (p=0.013) under trees than in open areas. Again, the canopy type made little difference during the wet season (Figure 3B, **Paper III**).

Tree canopies are known to affect soil evaporation in contrasting ways. For instance, a study conducted by Wallace et al., (1999) on *Grevilea robusta* trees in Kenya found that on average, the presence of a tree canopy reduced soil evaporation by 157 mm of water per year (an amount equal to 21% of annual rainfall) compared to bare soil. In a previous experiment at the same site, Jackson and Wallace (1999) found that soil evaporation was lower under dense (LAI = 2.2), unpruned tree canopies. According to Wallace et al., (1999), this canopy effect was proportionally greater in dry years, during which the amount of rainfall was 33% of annual precipitation. In contrast, they also inferred (from modeling and analysis) that the amount of rainfall intercepted by canopy trees can be greater than the amount that they save via reduction in soil evaporation. In those cases, trees would reduce surface soil moisture.

Trees can also reduce surface soil moisture by root abstraction of water from upper soil layers. That phenomenon is common in climates where either annual rainfall or rainfall intensities are high (> 1000 mm and >~3-4 mm h^{-1}; respectively). Similarly, Ong and Leakey (1999) concluded, in their literature analysis, that canopy trees reduced soil moisture by transpiration as well as by interception in tropical agroforestry systems with high tree density and high LAI. Furthermore, Padovan et al., (2015) found that continued water uptake by deep-rooted trees in a coffee agroforestry system actually increased water use, compared to that in a full-sun coffee system. That increase overshadowed the benefits (for coffee production) offered by the agroforestry system's superior exploitation of the whole soil profile.

The situation described by Padovan et al. occurred during a long and particularly severe dry season (almost six months, with a total rainfall of only 10 mm). Coffee growing in full sun used less water at the beginning of the dry season; therefore, water was still available from the deeper soil layers as the drought continued. That caveat having been stated, the fact remains that throughout Padovan et al.'s investigation, SWC during dry seasons was higher under full-sun coffee than under trees, throughout the soil profile.

Additional data of relevance were published by Lin (2010), who found low soil moisture under a coffee agroforestry system in southern Mexico that had medium tree canopy cover (10–30%). This canopy cover is comparable to that of the coffee agroforestry system studied in **Papers I and II** (15 % canopy projection, Taugourdeau et al., 2014). However, other researchers have reported that soil moisture is higher under canopy trees, rather than lower. Mazzarino et al., (1993) found that effect in the humid tropics of Costa Rica, where they compared two alley-cropping systems, involving leguminous trees, to two cropping systems that did not contain trees. A similar effect of trees on soil moisture was found in southern Costa Rica by van Kanten and Vaast (2006). These authors reported on a four-year-old coffee agroforestry system with sub-optimal ecological conditions for coffee growth: low latitude (640 m.a.s.l, mean daytime air temperature above 26°C, and large diurnal variations in relative humidity and vapor pressure deficit, especially during the lowest period of soil water availability. From studies of two tree-coffee combinations, van Kanten and Vaast found that independently of the period, SWC was the highest in the combination of coffee and *E. poeppigiana*. Improved SWC and related properties (e.g., nutrients and belowground productivity) under trees have been reported in savanna ecosystems in Africa (Weltzin and Coughenour, 1990; Belsky et al., 1993), as well as in Mediterranean rangelands (Joffre and Rambal, 1993) and tropical ecosystems in America (Nepstadt et al., 1996).

The main factors affecting soil water and related properties in landscapes with scattered trees, or in schemes of trees outside forest, are (1) the size of the gaps between trees, and (2) the distance from trees to canopies. Gap size is a key reference of tree densities: large open areas mean lower tree densities, whereas small open areas indicate higher tree densities. As trees densities increase, crowns and roots will overlap, thus reducing the resources available for herbaceous layer (Obot, 1998; Belsky, 1994). That phenomenon explains why Weltzin and Coughenour (1990) found that total herbaceous biomass is higher around tree stems and lower in the tree interspaces in a savanna type system in northwestern Kenya: temperature and water stress are lower under tree canopies in that system, and nutrient concentrations are higher. Moreover, in an African savanna, water infiltrated deeper and more rapidly into zones below isolated trees than in open grassland (Belsky et al., 1993). Nevertheless, smaller gaps within a dense canopy cover could also show a lower SWC. This effect was reported by Holl (1999) for a humid tropical region of Costa Rica. Holl found that soil moisture was higher in the forest, as well as in the forest gaps, than in the pasture. However, the pasture vegetation in Holl’s study can be considered medium-sized gaps, given that it consisted of non-native grasses with isolated trees, and that pasture-vegetation plots were located at least 4 m from the edges of the canopies of isolated trees.

Similar results were reported by Nepstadt et al., (1996) in tropical Amazonia. In their study, surface soil water was depleted more in abandoned pasture than in forest habitats during the dry season. Nepstadt et al. attributed this finding to the higher root length density in the abandoned pasture’s surface soil. It is important to note that in their study, the pasture had been abandoned 12 years before the experiment. Therefore, it had 1–2 m tall “islands” of trees and shrubs covering about 10% of the studied pasture. Thus, this abandoned pasture is equivalent to an early succession stage. Information on spatio-temporal variation of SWC during mid-successional stages is found in Joffree and Rambal (1988), who studied Mediterranean rangelands (dehesas) in southern Spain (van Uytvanck et al., 2008). There, water-holding capacity and nutrient content were higher under woody canopies of scattered evergreen oak trees, and soil bulk density was lower.

4.2 Relationship between transpiration, evaporation, rainfall interception, and SWC

Using the new conceptual model based on relationships between lc-excess and surface SWC (**Paper II**), I identified contrasting mechanisms by which canopy trees and coffee shrubs may influence small-scale soil water dynamics, and thereby elucidated how and when some mechanisms dominate. Predictions inferred from the model were explored in both study sites.

One of the key mechanisms in the model is rainfall interception, which occurs before canopy throughfall and stemflow. The model suggests that when interception is a dominating process, spatial variations in the SWC will be positively correlated to lc-excess (Figure 3 B) because in the process of evaporation and exchange with the atmospheric vapor of rain water that has been intercepted by foliage, the canopy throughfall and stemflow water usually become enriched with the heavier ^{18}O isotope (compared to open-sky rainfall) before entering the soil (Saxena, 1986; Brodersen et al., 2000). However, the mechanism of throughfall enrichment may, potentially, be a combination of (1) in-canopy fractionation, and (2) selective canopy storage of rainfall from the ends of events that have decreasing ^{18}O (Dewalle and Swistock, 1994). Although throughfall enrichment is likely to occur in many situations, it may not occur in others (Scholl et al., 2011), especially under high humidity and in closed forest contexts. For instance, throughfall with a depleted isotopic signature was reported under conditions of high humidity, as in the Black Forest in Germany, specifically at the periphery of the crowns (Brodersen et al., 2000).

Another example of depleted isotopic signatures in throughfall was found in mountains with evergreen forest under a rainy temperate climate in Valdivia, Chile (Hervé-Fernández et al., 2016). In this case, the authors attributed their results to the water-mixing process, but also to processes not fully understood. However, Allen et al., (2017), in their extended review, concluded that the isotopic differences between throughfall and open precipitation are generally small and positive. (I.e., isotopic enrichment of throughfall). They also pointed out that it is possible to find that such differences between throughfall and open precipitation vary in magnitude and direction, which likely responds to the exchange or selective transmittance of temporally varying rainfall.

The differences cited above are consistent with the new conceptual model, and should manifest themselves as a varying influence of interception. I inferred, from the positive correlation between SWC and lc-excess, that canopy throughfall and stemflow were the main processes influencing surface soil moisture when LAI was high, and for heavy rains occurring during times of high potential evapotranspiration. In contrast, SWC and lc-excess were negatively correlated when enhanced soil evaporative water losses occurred under conditions of reduced LAI, which may enhance the soil energy budget and the potential evapotranspiration.

My field data indicated that soil evaporation can be higher under defoliated shade tree. Specifically, the negative correlation between SWC and lc-excess was nearly significant ($p = 0.09$; $r^2 = 0.67$, Figure 9). In contrast, I found a significant positive relationship between the SWC and lc-excess of surface soil water under evergreen coffee during the dry season ($p= 0.05$; $r^2 = 0.77$, Figure 9). That positive relationship probably resulted from isotopic enrichment of intercepted rainfall during its evaporation, and before canopy throughfall and stemflow. Conversely enhanced soil evaporation when the tree has shed its leaves suggests greater evaporative water losses beneath trees: lc-excess values of surface soil water were 20 % higher under shade trees than under evergreen coffee (23.8 ± 5.9 ‰ and 19.6 ± 4.7 ‰, respectively). The latter two results are from the dry season. I recognize that this relationship under shade trees was largely driven by one data point with an extremely high lc-excess value, yet based on multiplying the interquartile range by a factor of 2.2 we determined that this data point was not an outlier (Hoaglin and Iglewicz, 1987).

During the wet season, lc-excess and SWC showed no correlation, regardless of cover (shade tree or coffee). That finding indicates either that transpiration dominated the other processes of soil evaporation and rainfall interception, or that the previous mechanisms compensated for each other. Although not tested, a possible reason why wet seasons show weaker trends could be that topography affected water movement in the soil. Future research might address such uncertainties through spatial analysis and inclusion of stratification in the sampling plan. In addition, the new conceptual model could be expanded to include topographic influences.

In the pasture landscape in Honduras, I found an almost-significant negative relationship between lc-excess and SWC for grasses during the dry season

(**Paper III).** That negative relationship was not seen under trees. If this difference is real, it indicates that soil evaporation is lower under trees, a phenomenon which would be consistent with the higher SWC under trees than under open grass. Nevertheless, the model is limited because I did not measured evaporation directly in the field. An apparent shift of trees' water use toward groundwater sources, together with a potential reduction in transpiration due to partial defoliation (Sarmiento et al., 1985), could also explain why SWC is higher underneath trees. In contrast to the relationship below trees during the dry season, I found a positive relationship between lc-excess and the SWC under the trees during the wet season, indicating throughfall and stemflow following interception by leaves and stems (Figure 10).

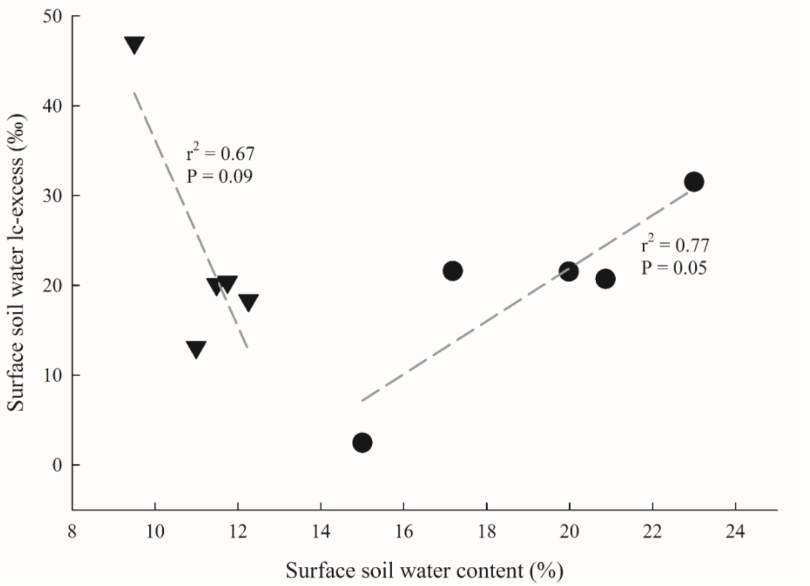

Figure 9. Relationship between lc-excess and SWC in a coffee agroforestry system in Turrialba, Costa Rica, during the dry season. Triangles represent samples collected under trees, and circles represent samples collected under coffee.

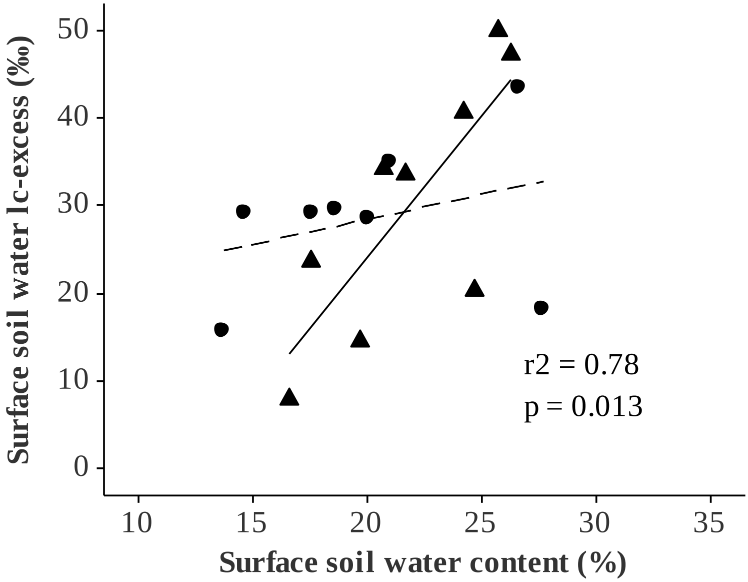

Figure 10. Relationship between surface soil water lc-excess and surface SWC in a pasture landscape in Copan, Honduras. Triangles and circles represent (respectively) samples collected under trees, and under grass. Values of r^2 and p are for the combined significant relationships of trees and grasses, during the wet season.

The new conceptual model proposed in this thesis made accurate predictions of correlations between SWC and lc-excess for two contrasting sites, in contrasting seasons, under different vegetation types. Those successes provide support for continuing exploration and testing of the conceptual model. If used in more cases and contexts, it could provide insights into the influence of various vegetation on the spatial variation of SWC.

4.3 Vertical partitioning of water sources

At Copan **(Paper III),** the main difference in vertical water partitioning between trees and grasses was seen in the sub-soil and groundwater. In contrast, the proportions of water taken from topsoil by grass, trees, and grass under trees were the same in the wet season as in the dry season. However, the proportional contribution of topsoil water to tree and grass transpiration (Figure 5, top panel in **Paper III)** was approximately 2.7 times higher ($p<0,0001$) during the wet season (66%) than in the dry season (24%). In the latter season, grasses and trees drew 45% and 14%, respectively, of their water from the subsoil at a depth of 100 cm ($p=0.0016$), while trees used a higher proportion of groundwater than the grasses (72% vs 28%, respectively; p<0,0001).

Results from the dry season provide evidence for the below-ground partitioning of water use, in contrast to several studies that found-contrary to Walter's two-layer hypothesis- no evidence for the below-ground partitioning of soil resources between woody and herbaceous vegetation in tropical savannas. Those studies did not include groundwater as a source, although they did compare proportions of water drawn from various soil depths. For instance, Le Roux et al. (2005) compared proportions drawn from soil depths at 10-cm intervals up to 200 cm. Mordelet et al., (1997) compared proportions from depths up to 120 cm, at 10-cm intervals, and Kulmatiski et al., (2010) did so for depths up to 140, at 20-cm intervals

A potential source (e.g., groundwater) should not be neglected unless there is sufficient reason to believe that it does not contribute significantly to the relevant mixtures (in this, case, to xylem water). As explained by Phillips et al. (2005), a partitioning model that omits a significant source can bias the proportions attributed to the sources that the model does include. To quantify the difference that neglect of groundwater would have made in the present study, I used the IsoError tool (Philip and Gregg, 2001). The result was that top soil water was accessed at lower proportions both by trees and grasses, and therefore that both used higher proportion of water from soil at the 100-cm depth. However, the opposite was true during the wet season. Thus, the "biased" results, like the unbiased ones, predicted that trees and grasses would partition topsoil and subsoil water during the wet season, and that the partitioning would be more-pronounced under trees. (These results are not shown in **Paper III**).

Moustakas (2013) found evidence that seasonal changes in factors such as climate and grazing pressure can cause interactions to switch, temporarily, between positive and negative at a given location in a pasture landscape that contains scattered trees. This type of seasonally-varying interaction was also found by Ward et al., (2013) and Priyadarshini et al., (2015). During the wet season, I found very similar water uptakes for trees and pasture, skewed toward soil surface water extraction. This result indicated that moisture partitioning or the niche hypothesis did not apply when water was not a limiting factor. Similarly, Midwood et al., (1998), who studied a savanna parkland in southern Texas, did not find isotopic evidence for vertical partitioning of soil moisture in co-occurring woody plants during the late summer and early fall.

Such an absence of vertical soil moisture partitioning is suggested by several authors' reports of overlap between the rooting zones and uptake of trees and grasses. Those cases studied root distribution and nutrients (Verweij et al., 2011; February and Higgins, 2010; Ludwig et al., 2004; Mordelet et al., 1997), as well as SWC and water stable isotopes (Le Roux et al., 1995; Le Roux and Bariac, 1998). However, overlap between rooting zones during the wet season can also be explained by the observation that plants minimize energy use when water is limited, but increase their root growth in areas where soil water is more easily available (Adiku et al., 1996). For instance, Oliveira et al. (2005) found that *Campo sujo*—grassy vegetation with interspersed small shrubs with a maximum height of around 2.5 m—is dominated by shallow-rooted grasses that have above-ground biomass production coupled with the drying and rewetting cycles of upper soil horizons.

From the preceding discussion, it can be seen that the vertical partitioning of soil moisture can be site- and season-dependent. That is, the root profile's shape is determined by the distribution of the incoming rainfall pulses and infiltration depths, which means that rooting systems are deeper where the soils coarse-textured, and that the evaporative demand slightly exceeds precipitation (Laio et al., 2006; Guswa, 2008). But how could such seasonal transitions in water source explain partitioning?

The explanation may be that although roots overlap in the top soil, trees nevertheless draw more water from the ground water because (1) they have easier access to it, and (2) withdrawal of groundwater is easier than withdrawal of water from soil. In contrast, grasses' shallower roots tend to restrict them to competing for the sub-soil water. In this scenario, water-source partitioning would occur because roots expand and die seasonally. That is, deep roots may allow plants access to a water source available after upper soil layers have dried out, enabling them to decouple the timing of growth from rainfall events, and to persist after neighbouring species have died or become dormant (Casper y Jackson, 1997).

Especially in dry lands or seasonal tropical weather, groundwater is a reliable but spatially restricted source to a small number of highly specialized, phreatophytic species. Thus, plants in dry lands may tap into these pools, differing in their use of water in wet and dry seasons (Chesson et al., 2004). The details of this general behaviour will depend on roots' shapes, phenologies, and growth forms (Schenk & Jackson 2002). Nevertheless, differences in timing of resource consumption are not, by themselves, sufficient for coexistence. Two other factors are involved in the storage effect: (1) long-term persistence of species in the location, and (2) patterns of covariance between environment and competition; i.e. covariance, over time or in degree, between the environmental response of the species whose phenology enables it to dominate in resource consumption, and the limitation on resource consumption to intra- and interspecific competition (Chesson et al., 2004).

According to Knoop and Walker (1985), different ratios of grasses to woody plants result from the different ratios of topsoil to subsoil water. These authors studied the interactions of trees and grasses in a Southern African savanna, through trenches and root-counting, and concluded that woody plants are dominant where the ratios of topsoil to subsoil water are low. Conversely, grass exists in the same location because of its faster response to wetter periods, and because the roots of woody plants do not fully occupy the topsoil. In wet environments, with a higher ratio of topsoil water to subsoil water, the opposite is true: the root depth of woody plants generally decreases with increasing wetness, and shows greater sensitivity to changes in rainfall frequency than to rainfall intensity (Guswa, 2008).

5 Conclusions

In this thesis, I studied the effects of scattered trees on soil water dynamics in two sites with contrasting soil, management, and climate. The main processes analysed that determine soil water dynamics were infiltration, preferential and matrix flow, SWC, macroporosity, water-holding capacity, and uptake. Through a new conceptual model, I studied evaporation, transpiration, and throughfall/stemflow, all of which are each key determiners of soil water dynamics. I explained contrasts between these processes by relating them to soil type, vegetation characteristics, rainfall intensities or rainy seasons, and the trees' arrangement in the agroecosystem (i.e., coffee agroforest in Turrialba, Aquiares, Costa Rica, and pasture with scattered trees in Copan, Honduras).

In conclusion, with reference to my specific hypotheses (Section 2.6), I found that:

1. Trees favoured higher infiltrability in agroecosystems with signs of soil degradation, but made no difference in the highly porous (and only slightly degraded) andisol of the densely-rooted coffee agroforestry system (**Paper I**).

2. At Aquiares, SWC measurements indicated considerably lower surface soil moisture under shade trees than underneath coffee due to the trees' greater transpiration (**Paper II**). In contrast, the scattered trees in the Copan pasture landscape led to reduced soil evaporation plus higher infiltration and preferential flow, thereby increasing SWC underneath trees compared to that under open grasses, particularly when water may be limited (as in the dry season) (**Paper III**).

3. In the pasture landscape, preferential flow was higher near trees due to a higher macroporosity, and because tree leaves increase the

conduction of intercepted water via throughfall and stemflow. These processes produce a higher SWC, which also facilitated the initiation of preferential flow, particularly near scattered trees in the pasture landscape during the wet season (**Paper III**). However, in the case of a coffee agroforestry system, where trees also produce greater tree transpiration during the wet and fully-leafed season, SWC was lower under trees than under coffee. Conversely, the preferential flow was greater under coffee shrubs than under neighbouring canopy trees, particularly during the dry season. The difference is attributable to the higher canopy throughfall and stemflow of intercepted water under evergreen coffee, together with the coffee farm’s highly permeable soils. All of those factors increase soil moisture, and thereby help to initiate preferential flow (**Paper II**).

4. The relationship between SWC’s variation and its corresponding isotopic signature (lc-excess) is influenced by the dominant hydrological processes affecting the system. The presence of trees influenced the magnitude and direction of this relationship (**Papers II and III**). Thus, the proposed new conceptual model specifically indicated that (1) Evaporation drives the contrasting relationships between lc-excess and surface soil moisture. A negative trend between SWC and lc-excess of surface soil water under shade trees during the dry season was confirmation of enhanced evaporative soil water losses under defoliated shade trees in the agroforest. In contrast, a positive trend between the surface SWC and lc-excess values present under coffee shrubs supported an increase in canopy interception and throughfall, particularly during the dry season (**Paper II**); (2) During the wet season, SWC and lc-excess of surface soil water showed no obvious correlation regardless of the canopy cover. Therefore, the above-mentioned spacial variation between SWC and its corresponding isotopic signature (lc-excess) was largely the result of transpiration (**Paper II**); and (3) Isotopically enriched soil water (i.e., higher lc-excess values) at lower soil depths suggest a matrix flow, whereas similar isotopic values between subsoil water and precipitation indicate a preferential flow. The latter was evidenced by smaller lc-excess values in the subsoil and groundwater than in surface soils. That difference was substantially larger under trees than underneath open grass in the pasture landscape. Under grasses in that landscape, lc-excess and SWC were apparently uncorrelated.

However, they were positively correlated under trees in that landscape, but only during the wet season. That result is a sign of variations in the interception potential, and consequently in the throughfall and stemflow of intercepted water by leaves and stems. Those processes, in turn, drive spatial variations in soil water (**Paper III**).

5. Soil water partitions vertically between trees and grasses in grasslands. Thus, facilitation or complementarity process act in that ecosystem during the dry season, when soil water is more rare, although not limited (**Paper III**). In the pasture landscape with scattered trees, soil water dynamics were affected by vertical partitioning of soil water in the following ways: (1) Wetter soils in the dry season underneath trees were linked to preferential groundwater use by the trees, with a consequent potential reduction of competition for surficial water resources when this resource is most needed. In contrast, grasses used a large proportion of subsurface water during the dry season, without reaching groundwater. (2) During the wet season-a period when water is not a limiting factor-surface soil is the main water source for both trees and grasses. Thus, the relationship between trees and grasses in the pastureland is always facilitative (**Paper III**), even though their respective primary sources of water changed with the seasons. This result expands and deepens our understanding of how grasses and scattered trees coexist in pasture landscapes.

In summary, results from this thesis indicate that in tropical agroecosystems, scattered trees can increase both the capture of rainfall and the retention of soil moisture. Therefore, the presence of trees-especially in degraded pasture landscapes-may help make some Central American agroecosystems more resilient to two expected consequences of climate change: increases in heavy precipitation events, and reduction in rainfall.

6 Future research directions

A better understanding of trees' effects on soil water dynamics is fundamental to formulating better measures for mitigating the effects of climate change upon society. Those measures might include forest restoration, along with incentives (financial or otherwise) that link conservation of trees to payments for environmental services.

This thesis contributed to the necessary understanding by introducing a new conceptual model that relates roles of evaporation, interception, transpiration, and preferential flow processes to isotopic signatures of soil water and groundwater. The model provides an alternative and simple method for understanding soil water dynamics in agroecosystems, including the effects of varying tree cover. Because it made good predictions of correlations between SWC and lc-excess for two contrasting sites, in contrasting seasons, under different vegetation types, the new conceptual model also warrants further testing in other heterogeneous and open agroforestry systems, or systems with trees outside the forest, particularly in humid and seasonally tropics. However these tests will be accompanied by additional measurements of soil evaporation with isotopics analyses in order to validate the model itself. The findings of this thesis also make clear the need for additional wide-ranging efforts that use water stable isotope analyses in combination with traditional field-based methods (i.e., infiltrometers, soil moisture measurements, and runoff plots). In such studies, each type of method can compensate for the characteristic difficulties and deficiencies of others, thereby helping to answer key remaining questions about trees' effects upon soil water dynamics.

The new conceptual model guided me in formulating experiments that provided qualitative evidence of processes through which trees affect groundwater recharge. The next step in developing and validating that model would be to quantify the actual recharge, as well as the other fluxes that are included in the model (evaporation, interception, transpiration). Possible options for tackling that challenge include micrometeorology, measurement of sap flow, collection of throughfall and transpiration water for isotopic analyses, and isotopic tracer analyses (for transpired water). Having collected such quantitative data, a logical continuation would be to model and simulate the relevant fluxes, with the goal of developing a specific model. That development would, preferably, use existing visually-based systems-modelling software, such as SIMILE (Simulistics Ltd) or STELLA (Isee Systems, Inc., 2005). Such tools are accessible and transparent to researchers and others without programming knowledge.

One of the remaining questions is, “Which tree densities, in agroecosystems that include different trees densities in different environments, will give the best balance between hydrological services and mitigation of climate change?” Mitigating climate change through tree planting involves alters several elements of the hydrological cycle: flows of water and sediment, levels of evapotranspiration, and vapour flows. Increases in evapotranspiration occur by interception, and because carbon fixation through biomass production increases leaf area, vapour flows, and water consumption. Thus, less water is available for other uses.

However, increased evapotranspiration or vapour flows may also decrease the movement of water and sediments off-site. As a result, inclusion of trees may be either beneficial or detrimental to water resources. This issue deserves further investigation, with the specific goal of determining which tree densities, in dry areas, will give the optimum balance between infiltration and evapotranspiration (i.e. maximum infiltration effect and minimum transpiration+rainfall-interception effect). That question might be answered through modelling at the whole-plot-scale, taking into account the heterogeneity of tree distribution.

As actual quantitative water recharge was not measured in my thesis, efforts to complete the conceptual model and the analysis of how trees influence soil water dynamics should include a module describing how water moves at levels all the way down to the water table. Again, water stable isotopic analyses of groundwater, combined with constant flow measurements (e.g. with pressure transducer sensors) could be a good methodological design.

Revived efforts to restore landscapes, especially in the countries where I conducted this thesis (Costa Rica and Honduras), require more data on trees’ positive effects (e.g., increased SWC, infiltrability, and preferential flow) and negative effects (e.g., high evapotranspiration and water uptake) upon soil and groundwater recharge. It is known that those effects depend upon the conditions extant. Further investigation is needed of the species-dependence of trees’ effects upon interception and transpiration. In the case of silvopastoral systems, more work is also needed on the species-dependence of soil degradation, and to identify optimum land-use management practices for various species. Equally important is testing whether there is a limiting grazing pressure (animal load) beyond which trees may not be able to provide any benefits.

In this thesis, I studied the effects of trees upon infiltrability, preferential flow, and the main processes governing soil water dynamics. To complete this line of research, I recommend a coordinated program that (1) measures the potential groundwater recharge during different seasons, on appropriately contrasting sites; (2) conducts experiments of the sort described in this thesis, to understand the dynamic effects of trees upon recharge; (3) collects the actual draining water underneath trees (during long-term lysimetric studies), and analyses it for comparison with water collected from adjacent treeless areas; and (4) measures trees' water use (sap flow) (Ilstedt et al., 2016) at least once every month. From the results of that study, researchers could calculate groundwater recharge (i.e., the difference between rainfall and trees' water use) for specific tree species of interest, with a time resolution of one month. That information will allow climate-change scenarios to be incorporated into such datasets. Researches will then be able to predict how trees might affect groundwater recharge under pessimistic or optimistic climate-change scenarios.

The need is urgent for basic research that can indicate how to assess ecosystem services. Among the needed research is a long-term (>1 year) study of how different species of trees partition their water consumption among available sources (especially groundwater) in different climates, locations, soils, and hydrologic conditions. That study should capture data on seasonal and transitional responses, so that researchers may then calibrate models of local water balances. By including plant-form interactions as well, such models may provide important insights into trees' effects upon local water availability: for example, in humid savannas. The models could also identify the extent to which crops in drylands and seasonal tropics harm ecosystem functioning by using more water than the natural vegetation.

In general, existing knowledge of the roles of trees in watersheds is not sufficiently extensive, deep, or detailed for accurate quantification of the hydrological resources needed for good management of ecosystems. Knowing how much water can be provided or lost by the trees is crucial for a robust design of schemes of payments or incentives to maintain ecosystem services.

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Popular science summary

Water is essential for sustaining our productive systems, as well as for the functioning of the whole environment. In this thesis, I studied how isolated trees affect soil water and groundwater in a degraded, heavily-grazed pastureland and in a coffee farm. I found that in the pastureland, several effects of trees increase infiltration of water into the soil. For example, their deep roots leave vertical channels in the soil when they die, and decomposed organic litter from trees' fallen leaves and branches mixes into the soil, thereby loosening it.

In contrast, trees did not affect water infiltration significantly in the coffee farm, which was a well-managed agroforestry operation on inherently good volcanic soils. This is not to say that trees are not very important in such systems: they provide other benefits like clean air, nutrients for the soil, and food for birds and other wildlife.

In this study I also confirmed that in the pastureland, the relationship between trees and grasses is facilitative (rather than competitive) because trees and grasses do not draw water from the same levels of soil, especially during the dry season, when the need for water is greatest.

More generally, my study contributed to understanding the different water pathways and functions derived from trees. For example, how they capture water, consume it during growth, and facilitate its movement deeply into the soil. I studied those phenomena by relating them to compositional characteristics (specifically, those involving what are known as isotopes) of water contained in the soil.

The findings and new understandings that have come from this thesis will help us design better strategies for managing our landscapes as we restore them and populate them with more trees.

Resumen popular

El agua es esencial para mantener nuestros sistemas productivos así como para todo el funcionamiento de la naturaleza. En esta tesis pude comprobar que mantener árboles en pasturas degradadas por sobrepastoreo resulta en mejoras en la infiltración de agua en el suelo. Esto es posible porque los árboles tienen raíces más profundas comparadas con los pastos, cuando mueren algunas raíces forman grietas en el suelo y espacios más grandes para que el agua se mueva, hay más restos de hojas que al mezclarse con el suelo lo aflojan y todo esto en conjunto favorece que el agua entre en el suelo. Sin embargo, cuando el suelo tiene buenas propiedades y el sistema productivo está bien manejado, como en la finca de café con árboles que yo estudié, no tenemos dicha diferencia. Pero esto no significa que los árboles no son importantes en aquellos sistemas. Podemos promoverlos por los otros beneficios que obtenemos de los árboles como aire puro, alimento para aves y otros animales silvestres, nutrientes para el suelo, entre otros.

En este estudio también confirmé que los árboles y los pastos viven juntos en un ambiente facilitador porque el agua utilizada por los árboles no es la misma que la utilizada por os pastos, especialmente cuando es más necesaria durante la época seca. Entonces ellos no compiten por agua.

En un contexto más amplio, mi estudio contribuye a entender los diferentes caminos del agua en el suelo y las funciones derivadas de los árboles como cuando estos captan agua, cuando solo la consumen para crecer y cuando favorecen el movimiento profundo el agua en el suelo, entre otros. Para esto, relacioné características específicas de la composición del agua (llamadas isótopos) con el agua contenida en el suelo.

Todos estos hallazgos y nuevo entendimiento derivados de mi investigación buscan contribuir al ajuste y diseño de mejores estrategias para manejar nuestras tierras al mismo tiempo que las restauramos con más árboles en el paisaje.

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