



INTERACTIONS BETWEEN LEAF AREA INDEX, CANOPY DENSITY AND EFFECTIVE PRECIPITATION OF A *POLYLEPIS RETICULATA* FOREST LOCATED IN A PARAMO ECOSYSTEM

INTERACCIONES ENTRE ÍNDICE DE ÁREA FOLIAR, DENSIDAD DEL DOSEL Y PRECIPITACIÓN EFECTIVA DE UN BOSQUE DE *POLYLEPIS RETICULATA* UBICADO EN UN ECOSISTEMA DE PÁRAMO

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Abstract

The measurement of vegetation cover is fundamental to quantify the precipitation percentage intercepted by it. The most widely techniques used to measure the cover *in situ* are the leaf area index (LAI) and the canopy density (CD). However, no attention has been paid to the differences recorded in the use of the two techniques or how these variables influence the hydrological balance on the throughfall (TF). For this reason, the objective of the study is to evaluate the relationship between vegetation cover measurements conducted by the LAI and CD methods and to identify how they relate with the TF, important for hydrological applications. The study was developed in a *Polylepis reticulata* forest of 15633 m², located at the Zhurucay Ecohydrological Observatory, south of Ecuador, in an altitudinal range of 3765 to 3809 m.a.s.l. The LAI was measured with the CI-110 Plant Canopy Imager equipment and CD with a spherical densiometer, covering a wide range of canopy cover values. The study site was instrumented with 9 tipping-bucket rain gauges to measure TF. The results indicate that LAI and CD averages are 2.43 m² m⁻² y 88% respectively; whose relationship is significant ($R^2 = 0.913$; $p < 0.05$). Mean annual TF is 773.2 mm, which tends to decrease with the increase of the LAI and CD; although, their relationship is not statistically significant ($p\text{-value} > 0.05$). This study shows the importance of characterizing the vegetation cover to understand the interaction with TF.

Keywords: *Polylepis reticulata*, leaf area index, canopy density, throughfall.

Resumen

La medición de la cobertura vegetal es fundamental para conocer qué porcentaje de la precipitación queda interceptada sobre la misma. Las técnicas más utilizadas para medir la cobertura *in situ* son el índice de área foliar (IAF) y la densidad del dosel (DD). Sin embargo, no se ha puesto atención en las diferencias registradas en el uso de las dos técnicas ni cómo estas variables influyen sobre el balance hidrológico particularmente sobre la precipitación efectiva (PE). Por tal motivo, el objetivo del estudio es evaluar la relación entre las mediciones de la cobertura vegetal realizadas por los métodos de IAF y DD e identificar cómo se relacionan con la PE, importante para aplicaciones hidrológicas. El estudio se desarrolló en un bosque de *Polylepis reticulata* de 15633 m², ubicado en el Observatorio Ecohidrológico Zhurucay, sur de Ecuador, en un rango altitudinal de 3765 a 3809 m s.n.m. El IAF se midió con el equipo CI-110 Plant Canopy Imager y la DD con un densiómetro esférico, cubriendo un amplio rango de valores de cobertura de dosel. Para medir la PE se instrumentó el sitio de estudio con 9 pluviógrafos. Los resultados indican que el IAF y DD son en promedio 2,43 m² m⁻² y 88%, respectivamente; cuya relación resulta ser significativa ($R^2 = 0,913$; $p < 0,05$). La PE media anual es de 773,2 mm, que tiende a disminuir con el incremento del IAF y DD; aunque su relación resulta estadísticamente no significativa (valores $p > 0,05$). Este estudio muestra la importancia de caracterizar la cobertura vegetal para entender la interacción con la PE.

Palabras clave: *Polylepis reticulata*, índice de área foliar, densidad del dosel, precipitación efectiva.

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1 Introduction

Vegetation cover is an essential factor in understanding ecosystems from a hydrological and ecological point of view, as it plays a significant role in forest-water relations (Levia et al., 2011), as well as in the transformation of solar energy into primary production (Hernández et al., 2003). In fact, forests with wide canopy coverage and high aerodynamic roughness cause high rates of potential evaporation (Gerrits et al., 2010), which means that the density of the cover, leaf area index, tilt angle and leaf shape affect hydrological processes such as interception (Crockford and Richardson, 2000; Fleischbein et al., 2005; Gerrits, 2010; Levia et al., 2011), evaporation, effective precipitation, and infiltration. The heterogeneous distribution of the canopy affects water availability in the forest area; in other words, in some places rain can reach the soil in higher quantities than in others, and it may exceed the amount of gross precipitation (Gerrits, 2010), because the canopy and the structure of the branches guide the rain into drip points that cause more intensity of local effective precipitation (Germer et al., 2006; Gerrits, 2010).

One of the most known forests of the high Andes is the *Polylepis* forests, which is seen as scattered ecotones. They are in altitudinal ranges from 3000 to 5000 m.a.s.l, especially in places protected by rocks or along the river banks (Domic et al., 2014), under extreme environmental conditions. Climate and topography have marked the existence of these forests as small isolated patches (Renison et al., 2006; Rangel and Arellano, 2010), which are forests that are sensitive to change due to their high endemism (Gareca et al., 2010), in the group of ecosystems with the highest threat (Herzog et al., 2002). Therefore, it is important to know its contribution to the water balance in the moorland, since the forest vegetation is able to collect more water than brush, including the one that comes from the mist (Nisbet, 2005).

Characterization of the forest canopy is essential because it plays a key role in the partitioning of gross precipitation (effective precipitation, cortical runoff, and interception) (Levia and Herwitz, 2005; Johnson and Lehmann, 2006; Park and Cameron, 2008), in the control of evaporation and storage of water (Levia et al., 2011). In addition, a detailed description of the canopy has facilitated the prediction

of water losses by interception (Moličová and Hubert, 1994). There are two basic measurement methods: (A) The leaf area index (LAI), which refers to the surface unit ($\text{m}^2 \text{m}^{-2}$) of the soil that is covered by the vertical projection of the canopy or leaf area (Jennings et al., 1999), (b) Canopy Density (CD) or Canopy Closure (%), which is the proportion observed from a single point of the sky that is darkened by vegetation (Jennings et al., 1999). These differ according to type of forest, density, spatial distribution of trees, type and structure of the canopy, phenological status of species, age and type of management (Lieberman et al., 1989; Pukkala et al., 1991). In the case of *Polylepis* forests, these variables have been determined as part of the research. For example, LAI has been associated with studies of leaf litter decay (Pinos et al., 2017). Meanwhile, CD has identified: the effect of canopy coverage on plant dynamics (Cierjacks et al., 2007), its influence on avifauna (Tinoco et al., 2013), or the structural complexity of the landscape (Renison et al., 2011), since a number of studies have focused on topics such as: distribution in the Andes (Gosling et al., 2009), history and causes of fragmentation (Kessler, 2002; Hoch and Körner, 2005; Valencia et al., 2018), morphological characteristics (Montalvo et al., 2018), floristic composition, and regeneration problems (Domic et al., 2014; Morales et al., 2018) with the purpose of understanding and knowing morphological differences among *Polylepis* species; also, knowing the ecological, climatic conditions in which these forests are developed and activities that have caused their fragmentation over time.

At the canopy scale, two hydrological processes as important as precipitation occur: A) throughfall (TF), which is the amount of water that reaches the soil through the canopy and/or which falls by drip after being in contact with the foliage (Levia and Frost, 2006), and b) interception, which is water retained by leaves and branches of vegetation, reducing the amount of water that reaches the soil (Gerrits, 2010). The properties of the rain also affect these processes (Crockford and Richardson, 2000; Murakami, 2006); for example, a sequence of events with dry period intervals can intercept more water than a storm, as some of the water retained in the canopy is evaporated, creating space for more storage (Levia et al., 2011). Some authors have found that TF varies from 60% to 95% of gross precipitation (Germer et al., 2006; Zimmermann et al., 2007; Berger

et al., 2008; Brauman et al., 2010), while interception may represent a variation of 10 to 50% (Zhang et al., 2006; Roth et al., 2007). This variability affects infiltration, runoff, flow and water storage, which are consecutive processes to complete the hydrological cycle (Tsiko et al., 2012). Few studies have shown the role of *Polylepis* forests in hydrology, such as that carried out by Alfaro (2015) in Peru and that of Harden et al. (2013) in Ecuador, which indicate the influence of *Polylepis racemosa* forests (introduced and managed species) on water infiltration into the soil. Research on effective precipitation and water interception in the canopy has had more emphasis on high Andean forests (Ramos Franco and Armenteras, 2019), low montane forests (Fleischbein et al., 2005; Wullaert et al., 2009), tropical montane forests (Zimmermann et al., 2007; Gomez et al., 2008) and temperate tropical forest (Oyarzún et al., 2011), facilitating the understanding of the hydrological balance. There is little information on the relationship between the characteristics of the canopy and the amount of water that reaches the soil in High Andean forests and even more so in forests that are at the tree boundary; therefore, the role of the vegetative cover in *Polylepis* forests in hydrological processes at the canopy scale is unknown. For this reason, the aim of this research is to evaluate the relationship between the measurements of vegetative cover made using the LAI and CD methods, and to identify how they relate to TF, which is important for hydrological applications.

2 Materials and Methods

2.1 Study area

The study was carried out at the Zhuruca ecohydrological observatory where there is a *Polylepis* forest of 15633 m², which has an altitudinal range from 3765 to 3809 m.a.s.l., with slopes ranging from 10 to 50%. The dominant plant species is *Polylepis reticulata*, finding other tree species such as *Escallonia myrtiloides*, *Oreopanax sp.*, *Weinmannia sp.*, *Gynoxys sp.*, species of the Melastomataceae family and shrubs such as *Valeriana sp.* *Polylepis reticulata* trees can reach a height of 15 m, have tortuous trunks with several branches, a height diameter of 33.58 cm and a basal area of 925.64 cm². Leaves are alternating and measure up to 2.5 cm long, grow as clusters at the ends of the branches, and are made

up of 3 or 5 elliptical leaflets.

The climate is influenced by the Pacific moisture and continental air masses coming from the Amazon basin (Córdova et al., 2013). The interannual precipitation is characterized by being highly uniform, and it is slightly higher from January to July; the average annual precipitation is 1300 mm (Ochoa et al., 2018). Precipitation often occurs as drizzle, representing 80% of rainy days (Padrón et al., 2015). The average daily temperature range is 0.4 °C to 14.2 °C, with an annual average of 6.1 °C. The average annual relative humidity is 93.6%. The level of solar radiation is 4942 MJm⁻² year⁻¹ with a daily average of 13.73 MJm⁻² day⁻¹. Wind speed follows a seasonal pattern with a monthly average of 3.21 m s⁻¹ from October to March and 4.77 m s⁻¹ from June to September (Carrillo et al., 2019). This area has an annual reference evapotranspiration of 723 mm at an altitude of 3780 m.a.s.l. (Córdova et al., 2015) and an annual current evapotranspiration (ETa) of 622 mm (average daily rate of 1.7 mm) (Ochoa et al., 2019).

2.2 Study design

A number of activities were carried out for the location of sites for measuring TF, LAI and CD in the *Polylepis* forest:

1. The forest area was divided into a 20 m × 20 m grid to determine the CD percentage at each point of the intersection (proportion of sky covered by vegetation) with a concave spherical densitometer at the height of the buds (1.20 m above the ground) and at a distance of 30 cm from the operator, method described in section 3.2.
2. The values obtained characterized the spatial CD variability of forest. Several interpolation methods were used to identify the best characterization, and the errors of each were analyzed; the methods used were: Ordinary kriging (spherical model), inverse distance weighting (IDW) and Thiessen polygons.
3. The spatial location of 9 sampling sites distributed in low, medium, and high CD values was identified, considering the edge effect (Figure 1).

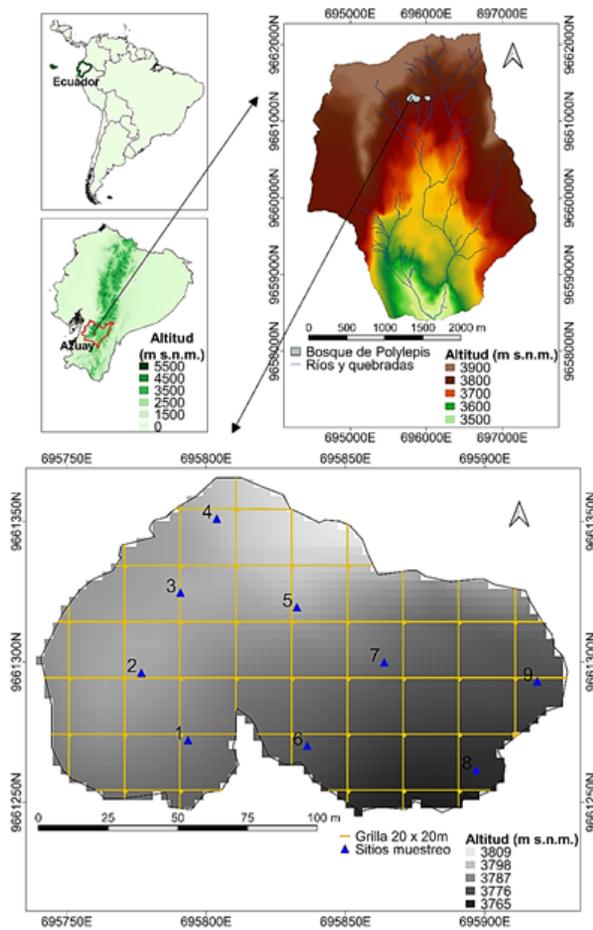


Figure 1. Study area located in the Zhurucay ecohydrological observatory in the south of Ecuador.

2.3 Measurement of the canopy density

Once the sampling sites for the TF measurement have been established, the CD percentage on each rain gauge was measured. A spherical densitometer consisting of a spirit level and a concave mirror divided by a grid of 24 square cells that reflected the incident light at an angle of 180° was used to determine this variable. Each reading consists of the mental subdivision of each cell into 4 squares that are represented by an imaginary point in the center, giving a total of 96 central points, which when found covered by the reflection of the plant cover are counted. An average value of four readings per site (direction of cardinal points) was obtained, the same as for the canopy percentage is multiplied by 1.04 (1/96*100) (Lemmon, 1956, 1957; Cook et al., 1995).

2.4 Leaf area index measurement

LAI measurement ($\text{m}^2 \text{m}^{-2}$) was performed at each site where CD was measured. The optical equipment CI-110 Plant Canopy Imager, consisting of an 8-megapixel camera equipped with a 170° angle hemispheric (fisheye) lens was used. The software is based on the calculation of the fraction of the visible sky under the canopy using the Gap-Fraction Inversion procedure (Norman and Campbell, 1989), according to three main equations: Transmission coefficient for diffuse radiation ingress, canopy extinction coefficients (LAI), and the average of the slope angle of the foliage. Canopy images are divided into zenith and azimuthal divisions (canopy sectors). The sky fraction (solar beam transmission coefficient) visible in each division is analyzed by counting the sky portion of the pixels in the image. The machine captures wide-angle images of the

canopy while estimating the LAI and measuring photosynthetically active radiation (PAR) levels per sampling site. Images are updated live on the built-in monitor, providing instant data for verification and analysis with the built-in software. LAI is represented by values ranging from 0 to 10, where 0 is equivalent to an area without a canopy or bare soil and 10 represents a dense canopy (Bio-Science, 2016). Optimal sky conditions for measurements should be under a uniform cloud cover in the morning or late afternoon (amount of low radiation) (Bio-Science, 2016).

2.5 Effective Precipitation Measurement

Nine automatic 0.2 mm resolution rain gauges were installed at a ground height of 1.20 m. Rain gauges were calibrated *in situ* and a plastic mesh was placed on each one to collect the leaf litter and thus avoid its plugging. The download of data, maintenance and cleaning of the equipment was carried out weekly from March 9, 2019 until March 8, 2020.

Records were added to have a database every 5 minutes. The amount of TF obtained corresponds to the daily and annual accumulation of the values recorded by the rain gauges at each sampling point within the forest. In case of data loss due to download failure or plugging, a daily data filling was performed using the linear regression method of the rain gauge values that showed data loss with

the gauge that presented the best correlation.

2.6 Relationship between CD, LAI, and TF

CD was first compared with LAI by correlation using Pearson method in order to know whether these two variables show the same information regarding canopy coverage. Linear correlations and regressions of CD and LAI were then performed with TF to determine which variable allows the identification of TF variability in the forest canopy.

3 Results

3.1 Canopy density

The spatial variability of the modeled canopy demonstrated better fit and accuracy with the characteristics of the area when using interpolation with the Kriging method compared to IDW and Thiessen polygons (37 points, 20 × 20 m grid). The method was better suited to the data, presenting the lowest errors.

Figure 2 shows that CD in the *Polylepis* forest has a range between 62.5% and 95.2% of spatial variation. In certain areas, values between 87 and 91% predominate, representing approximately an area of 550 m².

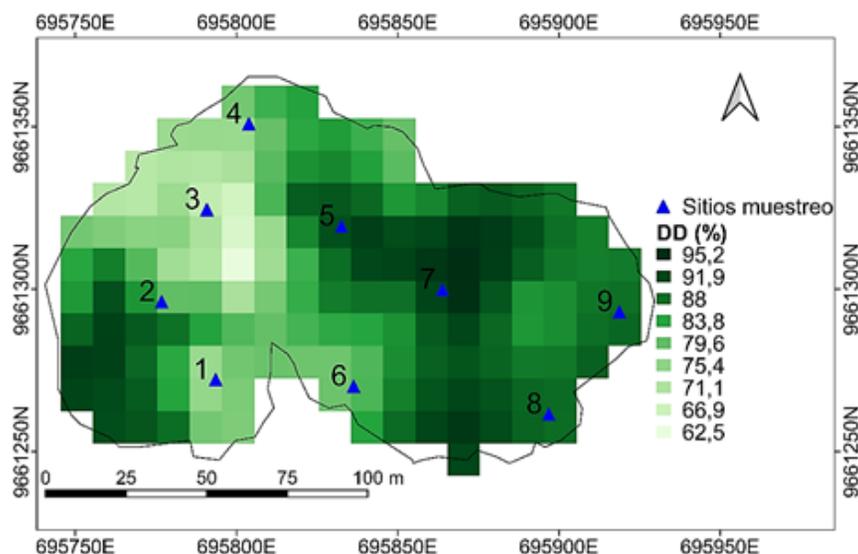


Figure 2. Spatial variability of canopy density by Kriging interpolation method and effective precipitation sampling sites.

As indicated in section 3.4, 9 sampling sites were considered for TF, where CD and LAI were measured (Figure 2). Figure 3 shows that the CD percentage at the 9 sites varies from 79% (site 1) to 96% (site 5). The average value of the CD percentage was $88 \pm 5.8\%$. The variation coefficient was low, without exceeding 10%, indicating homogeneity in the data.

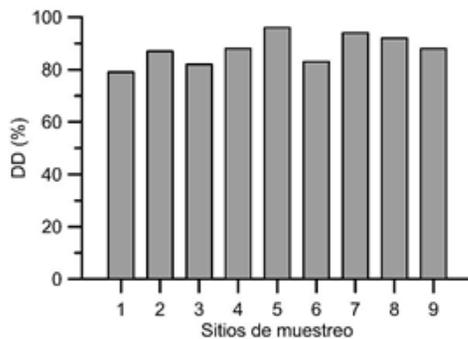


Figure 3. Percentage of canopy density

3.2 Leaf area index

As shown in Figure 4, the estimated LAI at the 9 sampling sites varies between $2.05 \text{ m}^2 \text{ m}^{-2}$ (site 1) and $2.79 \text{ m}^2 \text{ m}^{-2}$ (site 5), with an average of $2.43 \pm 0.25 \text{ m}^2 \text{ m}^{-2}$. Similarly with CD, the variation coefficient was 10%, confirming a low variability of LAI in the forest.

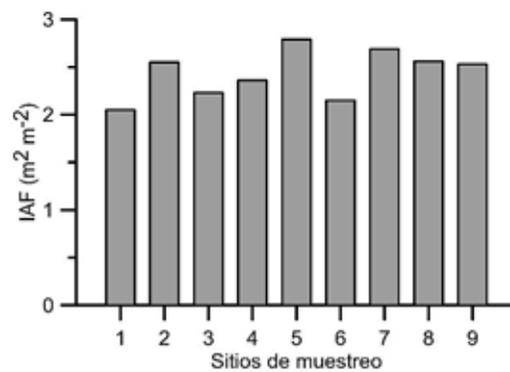


Figure 4. Leaf area index

3.3 Effective Precipitation

It was found that the rain gauge of site 2 had the highest lost data percentage of TF with 3.6% data to be filled in. It should be emphasized that this procedure did not affect the results because it did not exceed the acceptable limit of lost values (10%).

The average annual TF estimated by rainfall at 9 sites in the *Polylepis* forest was $773.2 \text{ mm year}^{-1} \pm 212.6$ with a daily average of $2.1 \pm 0.58 \text{ mm day}^{-1}$ (Table 1). The annual quantity of TF varies between 484.9 and $1191.6 \text{ mm year}^{-1}$, and the annual average daily quantity varies from 1.3 to 3.3 mm day^{-1} ; these values correspond to site 9 and 1, respectively (Table 1 and Figure 5).

Table 1. Annual effective precipitation (TF), annual daily mean, annual daily standard deviation (σ), and annual daily variation coefficient (CV).

Sampling site	Annual TF (MM year^{-1})	Annual TF daily average (MM day^{-1})	σ annual daily	CV annual daily (%)
1	1191.6	3.3	5.2	160
2	825.4	2.3	4.1	180
3	694.5	1.9	3.2	170
4	743.0	2.0	3.5	170
5	592.7	1.6	2.9	180
6	862.5	2.4	4.1	170
7	944.9	2.6	4.7	180
8	619.1	1.7	2.9	170
9	484.9	1.3	2.3	170
\bar{x}	773.2	2.1		
σ	212.6	0.58	3.8	
CV	28	28		180

The variation coefficient for both annual values and annual daily average values for all sites represents 28% variability. When analyzing the annual daily TF at each sampling site, it is observed that the data report a CV of 160% (site 1) to 180% (sites 2, 5 and 8), indicating that TF has high heterogeneity in the forest under study.

Figure 5 shows that the box diagrams show outliers that are concentrated above the upper limit, maybe in response to specific precipitation events, which in this case are daily events exceeding 10 mm.

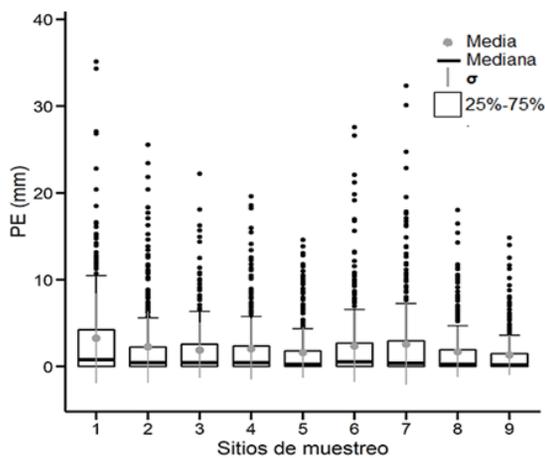


Figure 5. Effective daily precipitation

3.4 Relationship between CD, LAI, and TF

As expected, the correlation between LAI and CD is highly significant with a p value < 0.05 and a R² coefficient of 0.913. Figure 6 shows that CD tends to increase when LAI increases.

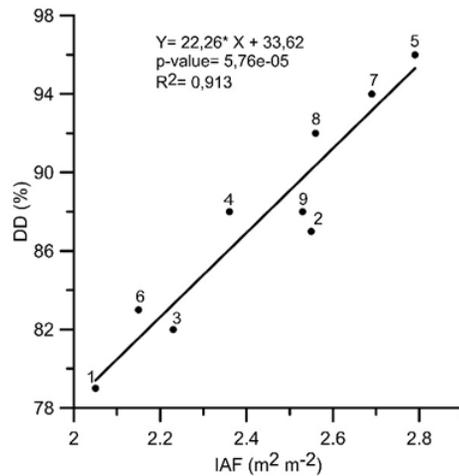


Figure 6. Relationship between leaf area index (LAI) and canopy density (CD) (1-9 sampling sites)

Correlation coefficients indicate an inverse relationship between leaf coverage variables (LAI and CD) and TF, reporting values of -0.535 and -0.524 , respectively; as expected, TF tends to decrease when CD or LAI increase (Figure 7).

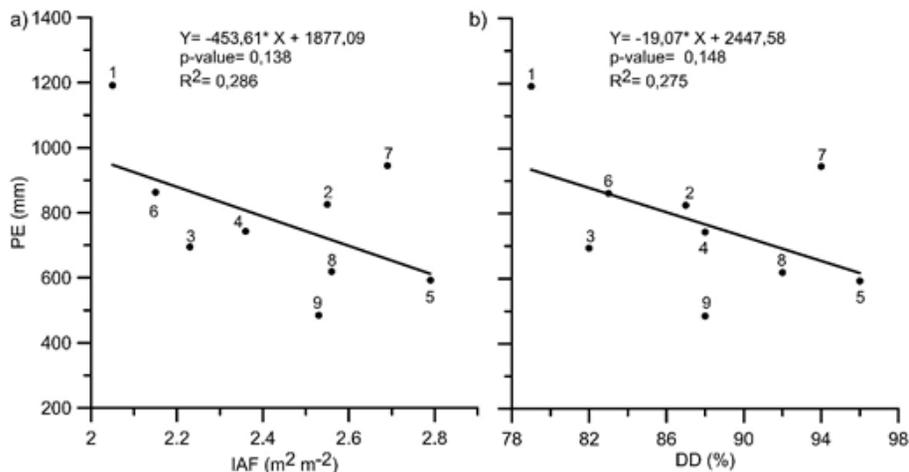


Figure 7. Relationship between (a) leaf area index (LAI), (b) canopy density (CD) and effective precipitation (TF) (1-9 sampling sites)

However, p values > 0.05 indicate that the ratio is not significant. When applying the linear regression method, low R^2 coefficients of 0.286 and 0.275 were found, which indicate little dependence or response of TF to these canopy coverage variables.

4 Discussion

Information about the LAI, CD, TF and the relationship between such variables for the analyzed *Polylepis reticulata* forest represents important information for the High Andean forests, since it facilitates understanding and establishes a foundation on the role of vegetation in hydrological processes that occur in moorland forests.

4.1 Characterization of canopy coverage

Researches conducted in Andean ecosystem forests have shown values of LAI and CD (Table 2), and have characterized canopy coverage and the relationship with different ecological functions.

4.1.1 Leaf area index studies

LAI values of the *Polylepis* forest studied are within the lower values reported by Pinos et al. (2017) for *Polylepis reticulata* forests in the Cajas National Park, which have a LAI between 2.60 to 6.17 $\text{m}^2 \text{m}^{-2}$ (mean of 3.96 $\text{m}^2 \text{m}^{-2}$). This difference may be due to the method used for determining LAI, as the author used specific foliar area and tree density per study plot. In studies carried out on pine plantations established in moorland ecosystems, Alvarado and Muñoz (2017) report a LAI from 0.23 to 2.22 $\text{m}^2 \text{m}^{-2}$ (mean of 0.92 $\text{m}^2 \text{m}^{-2}$), values that are lower than those found in this study, possibly due to the shape of leaves and density of the plantation. Likewise, Jadán et al. (2019) recorded very low LAI values (0.2 $\text{m}^2 \text{m}^{-2}$) in plantations of similar species and a LAI of 5.5 $\text{m}^2 \text{m}^{-2}$ in high montane forests, which is higher than the one found in this research. In a study carried out in high and low montane evergreen forests located in southern Ecuador, Alvarado and Cobos (2019) reported LAI results with less variability than the present study. Fleischbein et al. (2005) indicate that a low montane forest in southern Ecuador has a LAI between 5.2 and 9.3 $\text{m}^2 \text{m}^{-2}$ (mean of 7.3 $\text{m}^2 \text{m}^{-2}$), higher than those identified in the present study. Moser et al. (2007) in tropical montane forests in the south of Ecuador indicate

that as the altitude increases the size of the leaves is smaller, therefore, the LAI decreases. Gomez et al. (2008) in tropical montane forests of Peru found that LAI is 2.5 ± 0.7 to $2.9 \pm 0.2 \text{ m}^2 \text{m}^{-2}$, values that are higher than those found in the *Polylepis* forest.

4.1.2 Canopy density studies

Studies conducted in *Polylepis* forests have determined CD percentages; as is the case with the study conducted by Cierjacks et al. (2007) in *Polylepis pautata e incana*, forests, in which values of 46.7% were found near the border and 65 - 75% in the inner part of the forest, data that appear to be lower than those of this study near the border (79.83 and 88%; sites 1, 6 and 9) as well as in the inner forest (94 - 96%; site 7 and 5).

Similarly, Renison et al. (2011) in a *Polylepis australis* forest identified CD variability that is lower than in the present study with percentages of 8, 23, 54, and up to 72%. This may be because the results of the studies present a subjectivity bias because they were determined visually, a method that depends entirely on the experience of the technician. In pine plantations located in moorland ecosystems, Alvarado and Muñoz (2017) reported that these forests have a CD range from 5.5 to 74.7% (mean 44.5%). Similarly, Quiroz et al. (2019) presented CD percentages (19.3% - 64.8%) lower than those found at the study site. In high and low montane evergreen forests located in the south of Ecuador, CD averages were $53 \pm 4\%$ and $72 \pm 3.2\%$ lower than those found in this study (Alvarado and Cobos, 2019). The research carried out by Gomez et al. (2008), in a tropical montane forest in Peru has similarities in CD values ($87.9\% \pm 6.2$ to $90.7\% \pm 1.6$) with data reported from *Polylepis* forest.

According to the observed, the low similarity of the LAI and the CD percentage between forests is because such variables depend on the specific conditions of the area, which generally influence the development and characteristics of each tree species. Influential parameters are: leaf size, tree density per surface unit, architecture and structure of branches and topography; therefore, they can vary significantly from one site to another, even so it is the same forest species.

The close relationship between LAI and CD is

observed by regression analysis, revealing a strong proportionality between the two variables, which is consistent with the study carried out by Buckley et al. (1999), in which they report a R^2 of 0.93 and 0.99 in oak and pine forests, stating that this happens because the forests studied have a uniform structure. However, these authors also comment that the relationship between variables can change when there are differences between forest species, treetop architecture and development stage.

Table 2. LAI and CD of forests located in Andean ecosystems

Ecosystem and Type of forest	Study site and height (m.a.s.l)	LAI measurement ($m^2 m^{-2}$)	CD Measurement (%)	Reference
Moorland: <i>Polylepis reticulata</i> Forest	Ecuador, Zhurucay River Basin, (3765 – 3809)	2.05 – 2.79	79 – 96	Present study
Moorland: <i>Polylepis reticulata</i> Forest	Ecuador, Parin Boxes, (3735 – 3930)	2.60 – 6.17		Pinos et al. (2017)
Moorland: <i>Polylepis pauta</i> and <i>incana</i>	Ecuador, Papallacta, (3500 – 4100)		46.7 - 75	Cierjacks et al. (2007)
Moorland: <i>Polylepis australis</i> forest	Argentina, Córdoba, (1400 – 2500)		8-72	Renison et al. (2011)
Moorland: Pine plantation	Ecuador, Azuay, (3500 – 3700)	0.23 – 2.22	5.5 – 74.7	Alvarado and Muñoz (2017)
Moorland: Pine plantation	Ecuador, Azuay, (3600 – 3800)		19.3 – 64.8	Quiroz et al. (2019)
Moorland: Pine plantation High montane forest	Ecuador, Azuay, (3800 y 2500)	5.5 and 0.2		Jadán et al. (2019)
High and low montane evergreen forests	Ecuador, Azuay, (2000 – 3800)	1.6 – 2.5	53 – 72	Alvarado and Cobos (2019)
Low montane forest	Ecuador, Loja - Zamora, (1900 – 2000)	5.2 – 9.3		Fleischbein et al. (2005)
Tropical montane forest	Ecuador, Loja, (1050 – 3060)	5.1 – 2.9		Moser et al. (2007)
Cloudy tropical montane forest	Peru, Yanachaga-Chemillén National Park, (2815 – 2468)	2.5 – 2.9	87.9 – 90.7	Gomez et al. (2008)

4.2 Variability of effective precipitation and relationship with canopy coverage

This study showed that TF in the *Polylepis* forest was heterogeneous. The literature does not report another TF study conducted in *Polylepis* forests. Studies in premontane tropical forests (Teale et al., 2014), low montane forest (Fleischbein et al., 2005) and mixed oak forest (Staelens et al., 2006) also found that TF is very variable. These studies explain that this variable may be influenced by the shape of the canopy, morphological characteristics of the leaves and in some cases by a higher epiphyte load on the canopy that can generate more dripping points, which increases TF variability. Similarly, the study conducted by Zimmermann et al. (2007) explains that spatial variability depends mainly on the complexity of the canopy and is influenced by the number of species per area, irregular height, epiphytic presence, age, structure and arrangement of trees. Another possible explanation is that TF also depends on the precipitation depth, reason for which the spatial variability of TF increases, suggesting that spatial patterns of TF volume can be independent of the ecosystem. Germer et al. (2006) and Roth et al. (2007) show that there are characteristics such as species diversity, vegetation size and structure that result in rain distribution, dripping and storage points located in the lower canopy, producing spatially heterogeneous patterns. Zimmermann et al. (2009) and Macinnis et al. (2014) show similar results in their studies, since vegetation influences the movement of water through the canopy, and certain forms or its distribution within the forest area can create dripping points. In addition, other studies such Zimmermann et al. (2008) indicate that TF is affected by background canopy conditions such as moisture. In this study, the annual daily variation coefficient turns out to be higher than the annual. Carlyle and Price (2007) explain that when TF is observed at a time resolution of lower aggregation, such as daily aggregation or event aggregation, this value is influenced by the intensity conditions of gross precipitation, and it even depends on wind conditions. The variation coefficient in TF may increase or decrease when the intensity of rain is its main change factor (Weiqing et al., 2007).

Although the correlations found between the variables LAI, CD and TF are not statistically significant in this study, the results show an inverse

proportionality between the canopy cover variables and TF, which is consistent with previous research in which TF tends to decrease as LAI increases (Llorens and Gallart, 2000; Loescher et al., 2002; Nadkarni and Sumera, 2004). Similarly, Holwerda et al. (2006) indicate that TF in a Puerto Rico forest was higher in areas with low canopy amounts, because a smaller canopy surface correlates with a smaller amount of intercepted water. In the study conducted by Fleischbein et al. (2005) a negative correlation between LAI and TF (Pearson $r = -0.49$) was reported, being slightly lower than the coefficient found in this study. However, when compared to interception, Fleischbein et al. (2005) show that LAI accounts for only 12% of the variation, stating that the area of plant cover measured on TF rain gauges is higher than the area of the gauge. Thus, the difference in the capture area of the TF meters and the area covered by the LAI and CD equipment could explain the variability of the interception, or in the case of this study, TF variation in similar LAI values and the low determination coefficients between the canopy cover variables with TF. When comparing the results with the study conducted by Teale et al. (2014) in a forest in Costa Rica, it is confirmed that the relationship between LAI and TF is statistically non-significant, probably because locations with similar LAI may have different leaf type, wood coverage, orientation of foliage and branches, among other features that create retention points and drip points. For this reason, it is clear that vegetation influences the way water moves through the canopy; while TF is generally lower than gross precipitation, certain arrangements and vegetation forms can create dripping points, thereby exceeding precipitation. Overall, the results of studies that attempted to relate canopy coverage or vegetation characteristics with TF have been limited (Keim et al., 2005). Similarly, Zimmermann et al. (2009) when talking about the relationship between the canopy opening and TF at the measuring points, say that it is weaker as the magnitude of the precipitation event increases. In a study conducted by Molina et al. (2019) in pine and oak forests, it is indicated that TF is not significantly related when CD values are lower than 60%. However, when increasing this variable over a range of 60 to 100% a significant pattern of TF reduction with increased CD is observed, showing a negative correlation of 0.51 and 0.61, respectively. Authors such as Park and Cameron (2008) found that there is an interac-

tion between impacts produced by canopy characteristics in TF with the influence of precipitation; however, statistical analysis could not identify any pattern. (Levia et al., 2011) indicate that spatial patterns of TF vary significantly between ecosystems, so it is not possible to identify a relationship between the canopy and TF.

As mentioned before, the possible explanation for the non-significant relationship between canopy cover variables and TF is that this hydrological process does not only depend on CD or LAI, but on other factors such as vegetation (structure, branch architecture, density, age, angle of inclination of the leaves) and climate (intensity of rain and wind).

On the other hand, studies carried out in deciduous forests indicate the effect of foliage dynamics on TF, because they present remarkable periods of leaf loss, which is the opposite in perennial forests such as *Polylepis*. However, it is clear that its foliage presents a dynamic that consists on the clearing and renewal of leaves, as indicated by Pinos (2014), when reporting that *Polylepis* forests have 0.61 year^{-1} overshoot rates and the foliar renewal period occurs 1.75 years. For this reason, this dynamic should be taken into account for future research with more measurement points, at different times or seasons of the year.

5 Conclusions

This study is a pioneer in comparing measurements of LAI and CD and their relationship with TF in *Polylepis* forests, which are characterized as part of moorland ecosystems. LAI and CD are variables that differ according to the conditions the forests are exposed to during their growth, for example, soil nutrients, water, wind, precipitation, temperature; as well as characteristics typical of the species that make up the forest such as: leaf shape and size, architecture and branch structure, height, age, among others.

A strong relationship was found between the measured canopy variables, which in turn provide similar coverage information, concluding that any technique could be used to estimate canopy coverage. However, due to its greater comfort, ease of operation and low cost, the technique of measuring

the CD percentage using the spherical densitometer method is the most optimal for this activity.

When studying effective precipitation, it was observed that it is not only influenced by the variables mentioned above, but by the set of characteristics and distribution of forest species that increase plant complexity in the forest and the heterogeneity of TF. In addition, the finer the temporal resolution used in the TF estimation (daily, schedule, minutes), possibly the more influenced by environmental conditions such as the intensity and duration of precipitation, wind, solar radiation, background conditions, dry or canopy moisture.

The non-significant relationship between LAI and CD with TF can be due to the difference in measuring areas of the 2 variables (canopy cover and precipitation), since the area covered by rain gauges is much smaller than the area projected by the equipment used to measure canopy coverage. Therefore, measurements of plant cover – with any technique – are limited to properly characterize the variability of TF in the ecosystem studied.

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References

Alfaro, G. (2015). Caracterización de la infiltración en bosques de *Polylepis spp.*, de 11 y 29 años, parque nacional huascarán, quebrada quilcayhuanca, huaraz, ancash. Tesis de grado, Universidad Agraria La Molina. Online: <https://bit.ly/3ooQaZh>, Perú.

- Alvarado, A. and Muñoz, L. (2017). Evaluación de la regeneración natural y su relación con la altitud y cobertura de dosel en plantaciones no manejadas de *Pinus patula* en zonas alto andinas, en la provincia del azuay. Tesis de grado, Universidad de Cuenca. Online: <https://bit.ly/3ol1YvI>, Cuenca, Ecuador.
- Alvarado, I. and Cobos, C. (2019). Relaciones entre la estructura y cobertura arbórea con el carbono almacenado en bosques montanos andinos en el macizo del cajas, azuay-ecuador. Tesis de grado, Universidad de Cuenca. Online: <https://bit.ly/3yc33dL>, Cuenca, Ecuador.
- Berger, T., Untersteiner, H., Schume, H., and Jost, G. (2008). Throughfall fluxes in a secondary spruce (*Picea abies*), a beech (*Fagus sylvatica*) and a mixed spruce-beech stand. *Forest Ecology and Management*, 255(3-4):605–618. Online: <https://bit.ly/3ftBtQD>.
- Bio-Science (2016). *Manual CI-110 / 120 Plant Canopy Imager*.
- Brauman, K., Freyberg, D., and Daily, G. (2010). Forest structure influences on rainfall partitioning and cloud interception: A comparison of native forest sites in kona, hawai'i. *Agricultural and Forest Meteorology*, 150(2):265–275. Online: <https://bit.ly/3ot1jrY>.
- Buckley, D., Isebrands, J., and Sharik, T. (1999). Practical field methods of estimating canopy cover, par, and lai in michigan oak and pine stands. *Northern Journal of Applied Forestry*, 16(1):25–32. Online: <https://bit.ly/3brumXW>.
- Carlyle, D. and Price, A. (2007). Modelling canopy interception loss from a madrean pine-oak stand, northeastern mexico. *Hydrological Processes: An International Journal*, 21(19):2572–2580. Online: <https://bit.ly/2Rdx7Fr>.
- Carrillo, G., Silva, B., Rollenbeck, R., Célleri, R., and Bendix, J. (2019). The breathing of the andean highlands: Net ecosystem exchange and evapotranspiration over the páramo of southern ecuador. *Agricultural and Forest Meteorology*, 265:30–47. Online: <https://bit.ly/2SS1odg>.
- Cierjacks, A., Iglesias, J., Wesche, K., and Hensen, I. (2007). Impact of sowing, canopy cover and litter on seedling dynamics of two *Polylepis* species at upper tree lines in central ecuador. *Journal of Tropical Ecology*, pages 309–318. Online: <https://bit.ly/3hwp78i>.
- Cook, J., Stutzman, T., Bowers, C., Brenner, K., and Irwin, L. (1995). Spherical densimeters produce biased estimates of forest canopy cover. *Wildlife Society Bulletin*, 23(4):711–717. Online: <https://bit.ly/3uTrieF>.
- Córdova, M., Carrillo, G., and Célleri, R. (2013). Errores en la estimación de la evapotranspiración de referencia de una zona de páramo andino debidos al uso de datos mensuales, diarios y horarios. *Aqua-LAC*, 5(2):14–22. Online: <https://bit.ly/3fem8mM>.
- Córdova, M., Carrillo, G., Crespo, P., Wilcox, B., and Célleri, R. (2015). Evaluation of the penman-monteith (fao 56 pm) method for calculating reference evapotranspiration using limited data. *Mountain Research and Development*, 35(3):230–239. Online: <https://bit.ly/3bplNwH>.
- Crockford, R. and Richardson, D. (2000). Partitioning of rainfall into throughfall, stemflow and interception: effect of forest type, ground cover and climate. *Hydrological processes*, 14(16-17):2903–2920. Online: <https://bit.ly/3buU0ei>.
- Domic, A., Camilo, G., and Capriles, J. (2014). Small-scale farming and grazing reduce regeneration of *Polylepis tomentella* (rosaceae) in the semiarid andes of bolivia. *Biotropica*, 46(1):106–113. Online: <https://bit.ly/33INigu>.
- Fleischbein, K., Wilcke, W., Goller, R., Boy, J., Valarezo, C., Zech, W., and Knoblich, K. (2005). Rainfall interception in a lower montane forest in ecuador: effects of canopy properties. *Hydrological Processes: An International Journal*, 19(7):1355–1371. Online: <https://bit.ly/3eMJGjI>.
- Gareca, E., Hermy, M., Fjeldså, J., and Honnay, O. (2010). *Polylepis* woodland remnants as biodiversity islands in the bolivian high andes. *Biodiversity and conservation*, 19(12):3327–3346. Online: <https://bit.ly/3osFHvW>.
- Germer, S., Elsenbeer, H., and Moraes, J. (2006). Throughfall and temporal trends of rainfall redistribution in an open tropical rainforest, southwestern amazonia (rondônia, brazil). *Hydrology*

- and *Earth System Sciences*, 10(3):383–393. Online: <https://bit.ly/3oie8FJ>.
- Gerrits, A., Pfister, L., and Savenije, H. (2010). Spatial and temporal variability of canopy and forest floor interception in a beech forest. *Hydrological Processes*, 24(21):3011–3025. Online: <https://bit.ly/2RYbo4g>.
- Gerrits, M. (2010). *The role of interception in the hydrological cycle*. Doctoral thesis, Technische Universiteit Delft. Online: <https://bit.ly/3omnEr7>, Delft, Netherlands.
- Gomez, D., Oberbauer, S., McClain, M., and Philippi, T. (2008). Rainfall and cloud-water interception in tropical montane forests in the eastern andes of central peru. *Forest Ecology and Management*, 255(3-4):1315–1325. Online: <https://bit.ly/3tWXhJx>.
- Gosling, W., Hanselman, J., Knox, C., Valencia, B., and Bush, M. (2009). Long-term drivers of change in *Polylepis* woodland distribution in the central andes. *Journal of Vegetation Science*, 20(6):1041–1052. Online: <https://bit.ly/3eXxCfQ>.
- Harden, C., Hartsig, J., Farley, K., Lee, J., and Bremer, L. (2013). Effects of land-use change on water in andean páramo grassland soils. *Annals of the Association of American Geographers*, 103(2):375–384. Online: <https://bit.ly/2RuPGVp>.
- Hernández, M., Granados, D., and Sánchez, A. (2003). Productividad de los ecosistemas en las regiones áridas. *Revista Chapingo. Serie Ciencias Forestales y del Ambiente*, 9(2):113–123. Online: <https://bit.ly/33O6XLO>.
- Herzog, S., Cahill, J., Fjeldså, J., Kessler, M., Yensen, E., Tarifa, T., Capriles, J., Fernández, E., Hensen, I., Ibsch, P., Loayza, I., Renison, D., Dellacassa, E., Flores, E., Cingolani, A., Lorenzo, D., Matthysen, E., Schinner, D., Soria, R., Troncoso, A., Ståhl, B., and Vilaseca, A. (2002). Ecology and conservation of high-andean *Polylepis* forests. *Ecotropica*, 8:93–95. Online: <https://bit.ly/3hB4WL0>.
- Hoch, G. and Körner, C. (2005). Growth, demography and carbon relations of *Polylepis* trees at the world's highest treeline. *Functional Ecology*, 19(6):941–951. Online: <https://bit.ly/3fjdZHD>.
- Holwerda, F., Scatena, F., and Bruijnzeel, L. (2006). Throughfall in a puerto rican lower montane rain forest: A comparison of sampling strategies. *Journal of Hydrology*, 327(3-4):592–602. Online: <https://bit.ly/3ymj1lO>.
- Jadán, O., Cedillo, H., Pillacela, P., Gualpa, D., Gordillo, A., Zea, P., Díaz, L., Bermúdez, F., Arciniegas, A., Quizhpe, W., and Vaca, C. (2019). Regeneración de árboles en ecosistemas naturales y plantaciones de *Pinus patula* (pinaceae) dentro de un gradiente altitudinal andino (azuay, ecuador). *Revista de Biología Tropical*, 67(1):182–195. Online: <https://bit.ly/3f12psa>.
- Jennings, S., Brown, N., and Sheil, D. (1999). Assessing forest canopies and understorey illumination: canopy closure, canopy cover and other measures. *Forestry: An International Journal of Forest Research*, 72(1):59–74. Online: <https://bit.ly/2RwoANR>.
- Johnson, M. and Lehmann, J. (2006). Double-funneling of trees: Stemflow and root-induced preferential flow. *Ecoscience*, 13(3):324–333. Online: <https://bit.ly/3tUJzqG>.
- Keim, R., Skaugset, A., and Weiler, M. (2005). Temporal persistence of spatial patterns in throughfall. *Journal of Hydrology*, 314(1-4):263–274. Online: <https://bit.ly/3wd4CGD>.
- Kessler, M. (2002). The “*Polylepis* problem”: where do we stand. *Ecotropica*, 8(2):97–110. Online: <https://bit.ly/3ymoHw0>.
- Lemmon, P. (1956). A spherical densiometer for estimating forest overstorey density. *Forest science*, 2(4):314–320. Online: <https://bit.ly/3eNKKDW>.
- Lemmon, P. (1957). Using forest densiometers. *Journal of Forestry*, 55(9):1–2. Online: <https://bit.ly/33LBfyP>.
- Levia, D. and Frost, E. (2006). Variability of throughfall volume and solute inputs in wooded ecosystems. *Progress in Physical Geography*, 30(5):605–632. Online: <https://bit.ly/2RV0MmL>.
- Levia, D. and Herwitz, S. (2005). Interspecific variation of bark water storage capacity of three deciduous tree species in relation to stemflow yield and solute flux to forest soils. *Catena*, 64(1):117–137. Online: <https://bit.ly/3eOMgFR>.

- Levia, D., Keim, R., Carlyles, D., and Frost, E. (2011). *Forest Hydrology and Biogeochemistry*, chapter Throughfall and Stemflow in Wooded Ecosystems, pages 425–443. Online: <https://bit.ly/3ynopVt>. Springer.
- Lieberman, M., Lieberman, D., and Peralta, R. (1989). Forests are not just swiss cheese: canopy stereogeometry of non-gaps in tropical forests. *Ecology*, 70(3):550–552. Online: <https://bit.ly/3w4TN9i>.
- Llorens, P. and Gallart, F. (2000). A simplified method for forest water storage capacity measurement. *Journal of hydrology*, 240(1-2):131–144. Online: <https://bit.ly/3uREiBH>.
- Loescher, H., Powers, J., and Oberbauer, S. (2002). Spatial variation of throughfall volume in an old-growth tropical wet forest, costa rica. *Journal of Tropical Ecology*, pages 397–407. Online: <https://bit.ly/3bwU8d7>.
- Macinnis, C., Flores, E., Müller, H., and Schwendenmann, L. (2014). Throughfall and stemflow vary seasonally in different land-use types in a lower montane tropical region of panama. *Hydrological Processes*, 28(4):2174–2184. Online: <https://bit.ly/2Rne4bB>.
- Moličová, H. and Hubert, P. (1994). Canopy influence on rainfall fields' microscale structure in tropical forests. *Journal of Applied Meteorology*, 33(12):1464–1467. Online: <https://bit.ly/3ydzWXB>.
- Molina, A., Llorens, P., Garcia, P., de Las Heras, M., Cayuela, C., Gallart, F., and Latron, J. (2019). Contributions of throughfall, forest and soil characteristics to near-surface soil water-content variability at the plot scale in a mountainous mediterranean area. *Science of the Total Environment*, 647:1421–1432. Online: <https://bit.ly/3fqMMZX>.
- Montalvo, J., Minga, D., Verdugo, A., López, J., Guazhambo, D., Pacheco, D., Siddons, D., Crespo, A., and Zárate, E. (2018). Características morfológico-funcionales, diversidad arbórea, tasa de crecimiento y de secuestro de carbono en especies y ecosistemas de *Polylepis* del sur de ecuador. *Ecología Austral*, 28(1-bis):249–261. Online: <https://bit.ly/33KSQXI>.
- Morales, L., Sevillano, C., Fick, S., and Young, T. (2018). Differential seedling regeneration patterns across forest–grassland ecotones in two tropical treeline species (*Polylepis* spp.). *Austral Ecology*, 43(5):514–526. Online: <https://bit.ly/3ykOMLS>.
- Moser, G., Hertel, D., and Leuschner, C. (2007). Altitudinal change in lai and stand leaf biomass in tropical montane forests: a transect study in ecuador and a pan-tropical meta-analysis. *Ecosystems*, 10(6):924–935. Online: <https://bit.ly/33NC6z3>.
- Murakami, S. (2006). A proposal for a new forest canopy interception mechanism: Splash droplet evaporation. *Journal of Hydrology*, 319(1-4):72–82. Online: <https://bit.ly/3yfx6Bn>.
- Nadkarni, N. and Sumera, M. (2004). Old-growth forest canopy structure and its relationship to throughfall interception. *Forest Science*, 50(3):290–298. Online: <https://bit.ly/3tTlMr0>.
- Nisbet, T. (2005). Water use by trees. *Forestry Commission*, 65:1–8. Online: <https://bit.ly/33Lk14T>.
- Norman, J. and Campbell, G. (1989). *Plant physiological ecology*, chapter Canopy structure, pages 301–325. Springer. Online: <https://bit.ly/2SLlwfO>.
- Ochoa, A., Crespo, P., Carrillo, G., Sucozhañay, A., and Célleri, R. (2019). Actual evapotranspiration in the high andean grasslands: A comparison of measurement and estimation methods. *Frontiers in Earth Science*, 7:1–16. Online: <https://bit.ly/3ols2GS>.
- Ochoa, A., Crespo, P., and Célleri, R. (2018). Quantification of rainfall interception in the high andean tussock grasslands. *Ecohydrology*, 11(3):e1946. Online: <https://bit.ly/33KbQpo>.
- Oyarzún, C., Godoy, R., Staelens, J., Donoso, P., and Verhoest, N. (2011). Seasonal and annual throughfall and stemflow in andean temperate rainforests. *Hydrological Processes*, 25(4):623–633. Online: <https://bit.ly/3hCi7vc>.
- Padrón, R., Wilcox, B., Crespo, P., and Célleri, R. (2015). Rainfall in the andean páramo: new insights from high-resolution monitoring in southern ecuador. *Journal of Hydrometeorology*, 16(3):985–996. Online: <https://bit.ly/3yffYHa>.

- Park, A. and Cameron, J. (2008). The influence of canopy traits on throughfall and stemflow in five tropical trees growing in a panamanian plantation. *Forest Ecology and Management*, 255(5-6):1915–1925. Online: <https://s.si.edu/2RYcVqS>.
- Pinos, J. (2014). Biomasa foliar, desfronde y descomposición de la hojarasca en los rodales de *Polylepis reticulata* del parque nacional cajas. Tesis de grado, Universidad de Cuenca. Online: <https://bit.ly/3uRJg1d>, Cuenca, Ecuador.
- Pinos, J., Studholme, A., Carabajo, A., and Gracia, C. (2017). Leaf litterfall and decomposition of *Polylepis reticulata* in the treeline of the ecuadorian andes. *Mountain Research and Development*, 37(1):87–96. Online: <https://bit.ly/3hARMxX>.
- Pukkala, T., Becker, P., Kuuluvainen, T., and Oker, P. (1991). Predicting spatial distribution of direct radiation below forest canopies. *Agricultural and Forest Meteorology*, 55(3-4):295–307. Online: <https://bit.ly/33LmEnh>.
- Quiroz, C., Marín, F., Arias, R., Crespo, P., Weber, M., and Palomeque, X. (2019). Comparison of natural regeneration in natural grassland and pine plantations across an elevational gradient in the páramo ecosystem of southern ecuador. *Forests*, 10(9):1–30. Online: <https://bit.ly/2SVwUHL>.
- Ramos Franco, A. and Armenteras, D. (2019). Interceptación y escorrentía del bosque altoandino en la reserva forestal protectora “el malmo”. *Acta Biológica Colombiana*, 24(1):97–108. Online: <https://bit.ly/3hruCKc>.
- Rangel, O. and Arellano, H. (2010). *Colombia Diversidad Biótica X. Cambio Global (Natural) y Climático (Antrópico) en el páramo colombiano*. Bogotá, chapter Bosques De Polylepis: Un Tipo de vegetación condenado a la extinción, pages 443–478. Instituto de Ciencias Naturales-Facultad de Ciencias-Universidad Nacional de Colombia. Online: <https://bit.ly/3yoWpki>.
- Renison, D., Hensen, I., and Suarez, R. (2011). Landscape structural complexity of high-mountain *Polylepis australis* forests: a new aspect of restoration goals. *Restoration Ecology*, 19(3):390–398. Online: <https://bit.ly/2RlsUze>.
- Renison, D., Hensen, I., Suarez, R., and Cingolani, A. (2006). Cover and growth habit of *Polylepis* woodlands and shrublands in the mountains of central argentina: human or environmental influence? *Journal of Biogeography*, 33(5):876–887. Online: <https://bit.ly/3ojlLM6>.
- Roth, B., Slatton, K., and Cohen, M. (2007). On the potential for high-resolution lidar to improve rainfall interception estimates in forest ecosystems. *Frontiers in Ecology and the Environment*, 5(8):421–428. Online: <https://bit.ly/2QsQda8>.
- Staelens, J., De Schrijver, A., Verheyen, K., and Verhoest, N. (2006). Spatial variability and temporal stability of throughfall deposition under beech (*Fagus sylvatica* L.) in relationship to canopy structure. *Environmental Pollution*, 142(2):254–263. Online: <https://bit.ly/33LDl1R>.
- Teale, N., Mahan, H., Bleakney, S., Berger, A., Shibley, N., Frauenfeld, O., Quiring, S., Rapp, A., Roark, E., and Washington, R. (2014). Impacts of vegetation and precipitation on throughfall heterogeneity in a tropical pre-montane transitional cloud forest. *Biotropica*, 46(6):667–676. Online: <https://bit.ly/3hzDIKj>.
- Tinoco, B., Astudillo, P., Latta, S., Strubbe, D., and Graham, C. (2013). Influence of patch factors and connectivity on the avifauna of fragmented *Polylepis* forest in the ecuadorian andes. *Biotropica*, 45(5):602–611. Online: <https://bit.ly/2RmA4mY>.
- Tsiko, C., Makurira, H., Gerrits, A., and Savenije, H. (2012). Measuring forest floor and canopy interception in a savannah ecosystem. *Physics and Chemistry of the Earth, Parts A/B/C*, 47:122–127. Online: <https://bit.ly/2RmAgTe>.
- Valencia, B., Bush, M., Coe, A., Orren, E., and Gosling, W. (2018). *Polylepis* woodland dynamics during the last 20,000 years. *Journal of Biogeography*, 45(5):1019–1030. Online: <https://bit.ly/33UhWn1>.
- Weiqing, Z., Zhiqiang, Z., Jun, W., and Jinqiang, X. (2007). Spatial variability of throughfall in a chinese pine (*Pinus tabulaeformis*) plantation in northern china. *Frontiers of Forestry in China*, 2(2):169–173. Online: <https://bit.ly/3uUfo4b>.
- Wullaert, H., Pohlert, T., Boy, J., Valarezo, C., and Wilcke, W. (2009). Spatial throughfall heterogeneity in a montane rain forest in ecuador: extent, temporal stability and drivers. *Journal of Hydrology*, 377(1-2):71–79. Online: <https://bit.ly/3eRSBk1>.

- Zhang, G., Zeng, G., Jiang, Y., Huang, G., Li, J., Yao, J., Tan, W., Xiang, R., and Zhang, X. (2006). Modelling and measurement of two-layer-canopy interception losses in a subtropical evergreen forest of central-south china. *Hydrology and Earth System Sciences*, 10(1):65–77. Online: <https://bit.ly/3eOg71c>.
- Zimmermann, A., Germer, S., Neill, C., and Krusche, A. and Elsenbeer, H. (2008). Spatio-temporal patterns of throughfall and solute deposition in an open tropical rain forest. *Journal of Hydrology*, 360(1-4):87–102. Online: <https://bit.ly/3hwkrnt>.
- Zimmermann, A., Wilcke, W., and Elsenbeer, H. (2007). Spatial and temporal patterns of throughfall quantity and quality in a tropical montane forest in ecuador. *Journal of Hydrology*, 343(1-2):80–96. Online: <https://bit.ly/3tS49rM>.
- Zimmermann, A., Zimmermann, B., and Elsenbeer, H. (2009). Rainfall redistribution in a tropical forest: Spatial and temporal patterns. *Water Resources Research*, 45(11):1–18. Online: <https://bit.ly/3huuc5H>.