Received: 7 June 2022 | Revised: 30 November 2022 | Accepted: 28 January 2023

DOI: 10.1002/eco.2525

RESEARCH ARTICLE

WILEY

Measurement of actual evapotranspiration in a páramo ecosystem using portable closed chambers: Comparison between giant rosettes, tussock grasses and shrubs

Barbara Meyers[1,2] | María Elena Gutiérrez-Lagoueyte[3,4] | Conrado Tobón[4]

[1]Department of Geobotany, Albert Ludwigs Universität Freiburg, Breisgau, Germany

[2]Maastricht Science Programme, Faculty of Science and Engineering, Maastricht University, Maastricht, Limburg, Netherlands

[3]Engineering and Basic Sciences school, Universidad EIA, Envigado, Colombia

[4]Department of Forestry Sciences, Universidad Nacional de Colombia-sede Medellín, Medellín, Colombia

Correspondence
Barbara Meyers, Department of Geobotany, Albert Ludwig Universität Freiburg, Breisgau, Germany.
Email: barbara.meyers@outlook.fr

Abstract

The páramos are Neotropical alpine tundra-like ecosystems that play a crucial role as biodiversity hotspots and also act as water sources for the inter-Andean regions and cities. Improving our understanding of hydrological processes, here evapotranspiration, is crucial, especially in the context of global changes. In páramos, most research have focused on estimating potential evapotranspiration (ETo) using the Penman–Monteith method. Only a few studies have quantified actual evapotranspiration using mostly the Eddy covariance method (EC) or volumetric lysimeters. Importantly, these studies focused only on tussock grass communities, and none have addressed the effect of other plant communities specific to páramos on the actual evapotranspiration of this ecosystem. In this research, portable closed chambers were installed for the first time in a páramo (in *Los Nevados* National Park, between 3900 and 4100 masl) to quantify actual evapotranspration (ETa) in March and May 2019 in three representative plant communities of the páramo (giant rosettes, shrubs and tussock grasses). The ETa rates measured were then compared with ETo estimated using the Penman–Monteith method. Also, environmental factors of solar radiation, temperature and relative humidity were recorded and their influence on ETa variation was analysed. Our results indicate that ETa daily rates were very low with a high daily variation (0.290 ± 0.266 mm day^{-1}). The shrubs showed higher ETa rates even though differences among communities were not significant. ETo rates calculated via the Penman–Monteith method were significantly higher (1.017 ± 0.468 mm day^{-1}) than those measured using the portable chambers. Portable closed chamber is a promising method to assess ETa at small spatial and time scales and under controlled environment; however, they should be improved to enable ETa measurements on longer time periods. This study confirms the highly variable and low evapotranspiration rate of the páramo vegetation, here confirmed across different plant communities and underlines the importance of solar radiation and temperature, which were positively correlated with evapotranspiration rates.

KEYWORDS
Calamagrostis, *Espeletia*, evapotranspiration, high altitude ecosystem, Penman–Monteith, *Pentacalia*, stomatal conductance

1 | INTRODUCTION

Páramos are Neotropical alpine ecosystems located between the tree line and the remaining glaciers of the Northern Andes, ranging from Northern Peru to Venezuela (Buytaert, Celleri, et al., 2006; Célleri & Feyen, 2009; Hofstede, Segarra, & Mena, 2003). Their altitudinal location varies with local geographical and climatic conditions, and in Colombia, they are commonly found between 3000 and 4600 m.a.s.l. These tropical alpine environments display particular abiotic conditions such as high daily temperature variations but low temperature seasonality, frequent light precipitation events, average temperature below 10°C, but they also display other unique conditions such as low oxygen and CO_2 pressure, strong winds, a high edaphic and topographic heterogeneity and high UV radiation (Azocar & Rada, 2006; Llambí & Sarmiento, 1998; Peyre, 2015; Ruiz-Carrascal et al., 2019). Due to climatic changes during the Pleistocene, which *promoted* the formation of continental islands and the extreme abiotic conditions to which the vegetation has been exposed to, the páramos now shelter an extremely diverse and adapted flora with characteristic growth forms and physiology (Flantua et al., 2019; Marín & Parra, 2015; Peyre, 2015).

Páramos provide crucial ecosystem services acting as a permanent water source for surrounding cities as well as supplying water for hydropower production and agricultural field irrigation (Buytaert, Celleri, et al., 2006; Célleri & Feyen, 2009; Hofstede, Segarra, & Mena, 2003; Peyre, 2015; Tobón & Arroyave, 2007). The storage and constant release of water from soils in páramos (mainly Andosols and Histosols) are possible given their high porosity and high water retention, the low temperature seasonality, and the cold and wet climate (Buytaert et al., 2005; Tobón, 2022a). Finally, the low evapotranspiration rates of vegetation (Tobón & Castro, 2022) is directly correlated to the high-water yield of the páramos (Buytaert, Iñiguez, et al., 2006; Cárdenas et al., 2018; Célleri & Feyen, 2009).

The vegetation of an ecosystem is intrinsically connected to the water cycle. On one hand, vegetation communities are influenced by precipitation, soil moisture and chemical composition of water. On the other, vegetation plays a key role in the hydrological cycle returning water to the atmosphere through transpiration and evaporation of intercepted water (Leguizamon & Tobón, 2017). In páramos, plant cover has shown to affect soil moisture (Pesantez et al., 2018) and water interception (Leguizamon & Tobón, 2017; Tobón 2022b). Together with meteorological conditions and air and soil moisture, the specific characteristics of the plant communities in the páramo such as xeromorphic traits and pubescent leaves have shown to regulate the low ET rates observed in these ecosystems (Buytaert, Iñiguez, et al., 2006; Cárdenas et al., 2018; Gutiérrez-Lagoueyte et al., Peyre, 2015).

Generally, it is difficult to quantify ET and there have been many models developed to address this. To measure or estimate ET, two approaches must be considered: (1) the physical character of this process using meteorological approaches and (2) the effect of vegetation characteristics such as plant physiology, species composition and stomatal properties (Jarvis & McNaughton, 1986; Kairu, 1991). Currently, the main estimation method used is the FAO Penman–Monteith which calculates reference ET (ETo) based on meteorological data (also described as FAO 56 PM method). This method has been previously applied to páramos (Buytaert, Iñiguez, et al., 2006; Cordova et al., 2015; Leguizamon & Tobón, 2017; Ochoa-Sanchez et al., 2019), as well as in other high altitude ecosystems (van den Bergh et al., 2013). Then, the main methods proposed in the literature to determine actual ETa (Damveld et al., 2018) are (1) the use of lysimeter (Coners et al., 2016; Ochoa-Sanchez et al., 2019; van den Bergh et al., 2013); (2) sapflow measurements (Duan et al., 2017; Granier & Loustau, 1994; Zhang et al., 1997); (3) the Eddy covariance method (Carrillo-Rojas et al., 2019; Gu et al., 2008; Ochoa-Sanchez et al., 2019); and (4) the use of either closed (McLeod et al., 2004) or ventilated (Denmead et al., 1993; Zhang et al., 2018) chambers encompassing an individual plant or a vegetation patch.

Actual evapotranspiration is a key process of the hydrological cycle and plays an important role on the ecohydrological processes of terrestrial ecosystems (Tobón & Castro, 2022). However, several difficulties arise when calculating actual evapotranspiration, mainly because of the high information requirements to apply energy balance models, the complexity of ecosystems, input data uncertainty (Chia et al., 2020; Ryken et al., 2022; Zhao et al., 2013) and the large spatial meteorological, edaphic, topographic and vegetation heterogeneity (Liu et al., 2022); therefore, simplified methods for calculating actual evapotranspiration are becoming widely used. Sap flow has been widely used method to determine actual evapotranspiration, however, it is mostly adapted to woody vegetation (Flo et al., 2019; Poyatos et al., 2021; Smith & Allen, 1996); therefore, in páramo ecosystems, they are only applicable (with adjustments) to *Espeletia* spp. and some shrub species (Cárdenas et al., 2018). Lysimeters and Eddy covariance have successfully been used in tussock grass communities in Ecuadorian páramos (Ochoa-Sanchez et al., 2019; Vásquez et al., 2022), however their installation remains complex and costly.

Furthermore, some studies have focused on measuring ET on tussock grass communities from Andean páramos (Ochoa-Sanchez et al., 2019; Vásquez et al., 2022), but none have been done in other types of páramo vegetation, such as shrubs and giant rosettes, although these are representative growth forms of worldwide páramos (Luteyn, 1999). Hence, there is still a need to measure and compare the contribution of the different specific vegetation cover to ETa and new approaches are required for assessing ETa at small time and spatial scale and under monitored environmental conditions to obtain a comprehensive understanding of ETa variations.

Accordingly, this research aimed at providing insights on ETa during one rainy period of the year in three representative plant communities in the páramo of Los Nevados National Park: shrubs (*Arbustal*), giant rosettes (*Frailejonal*) and tussock grass (*Pajonal*) (tussock grasses). This study also sought to test the applicability of portable closed chambers, an adaptable and small-scale method, to assess ETa in páramos. By installing chambers in páramos, the actual evapotranspiration of the vegetation was measured under homogeneous and monitored environmental conditions for a very short period. As these rates were measured under similar conditions, this enabled the comparison between ETa rates across vegetation communities. Moreover, this study also aimed at assessing the effect of environmental factors on ETa in these communities. Two main questions were answered: How do ETa rates vary among the three plant communities studied and how does this compare to Penman–Monteith calculations? Which meteorological variables affect ETa rates in páramo plant communities? How can portable closed chambers measurements improve our understanding of ETa in páramos?

2 | MATERIALS AND METHODS

2.1 | Study site and environmental conditions

The research took place in the páramo of *Los Nevados* National Park situated in the Andean central mountain range of Colombia, from March to May 2019. More specifically, the study sites were located in the upper part of the Claro River basin (between 04°48′–04°58′N and 75°30′–75°18′W, 3900–4100 m). Two meteorological stations were installed nearby the research plots to record temperature, relative air humidity, solar radiation wind speed and direction: a Davis® weather station (4°50′31.88″N; 75°22′34.64″W) and a Campbell® weather station combined with a temp/RH HOBO® sensor (4°51′33.61″N; 75°21′36.03″W). Measurements were recorded at 5 min intervals during the study period. The average annual precipitation in this area is 1400 mm with a bimodal distribution during the year, and the atmospheric pressure vary between 820 and 650 mb. The average climatic conditions recorded are presented in Table 1. The study period considered one of the rainy seasons observed in this area with an increased amount of precipitation as is shown by the data presented in Tables 1 and S1. Also, volumetric soil water contents (θ, cm^3 cm^{-3}) were automatically measured at five different soil depths, using SC625-type Time Domain Reflectometry (TDR) sensors, connected to a CR1000 datalogger (Campbell Scientific Ltd, Shepshed, UK) (4°50′31.88″N; 75°22′34.64″W). Field capacity and permanent wilting point were calculated based on water retention curves measured in undisturbed soil samples at the laboratory 2011. Field capacity was determined at 10 kPa according to that suggested by 2011 for soils with high organic matter content, as those from Los Nevados National Park, and permanent wilting point at 1500 kPa.

In páramos, plant species conform communities of well-defined floristic composition with uniform physiognomy distributed in the landscape (Salamanca et al., 2003). These communities are defined (and named) based on the dominant species which usually correspond to specific growth forms. In the páramo of Los Nevados National Park, five main communities have been described: giant-rosettes, tussock grasses, shrubs, cushion plants and mixed communities (Gutiérrez-Lagoueyte, 2017). From these, the three most representative communities (most abundant) were selected: giant-rosettes, shrubs and tussock grasses. The giant rosettes community is dominated by one-stem caulescent rosette of the species *Espeletia hartwegiana*, tussock grasses of *Calamagrostis* and herbs; the shrub community is mainly composed by woody species of limited growth and ramified stems, mostly dominated by shrub species of the genera *Pentacalia*, *Displostephium*, *Baccharis* and *Hypericum*, and in less abundance some grasses and herbs; and the tussock grass is defined mostly by the presence of tussocks of *Calamagrostis* and *Festuca*, and sparely by low abundant small shrubs and herbs. After identification of the community locations, five sites per community were randomly selected within these zones for the installation of the chambers.

2.2 | Chambers design and ETa measurements

The chambers to measure ETa were built directly in the field using PVC tubes (25 mm diameter), which were attached by PVC adapters to form a cubic chamber of 3.375 m^3 using tubes of 1.5 m long (Figure 1). Transparent polyethylene sheets were used to cover the chamber structure. Previous to the experiment, the chambers were tested in January 2019 and it was observed that, after approximately 10 min, relative humidity within the chamber stabilized and saturation was reached. Therefore, in March (23–28 March 2019) and in May 2019 (12–15 May 2019), the chambers were closed for 10 min every hour from 9:00 AM to 3:00 PM and were left open for the rest of the time. This allowed the relative humidity to reach the same humidity level as the surrounding environment before the next measurement. Due to the remote location of the sites, time slots could not be extended to measure ETa during a complete day (6:00 AM to

TABLE 1 Summary of weather conditions registered by the meteorological stations during the experimental period 1 March 2019 to 31 May 2019 (**Exp**. columns in the table); and the average monthly value from measurements of January 2018 to December 2020 (**Overall** columns in the table). Solar radiation was calculated based on data from 6:00 to 18:00.

	Temperature (°C)		Relative humidity (%)		Wind speed (m s^{-1})		Solar radiation (W m^{-2})		Precipitation (mm)	
	Exp.	Overall	Exp.	Overall	Exp.	Overall	Exp.	Overall	Exp.	Overall
Average	4.59	4.67	93	86	2.24	2.63	146.36	154.16	126.78	96.21
SD	2.1	2.6	6.17	0.11	1.6	1.8	247.71	237.81	7.21	29.37

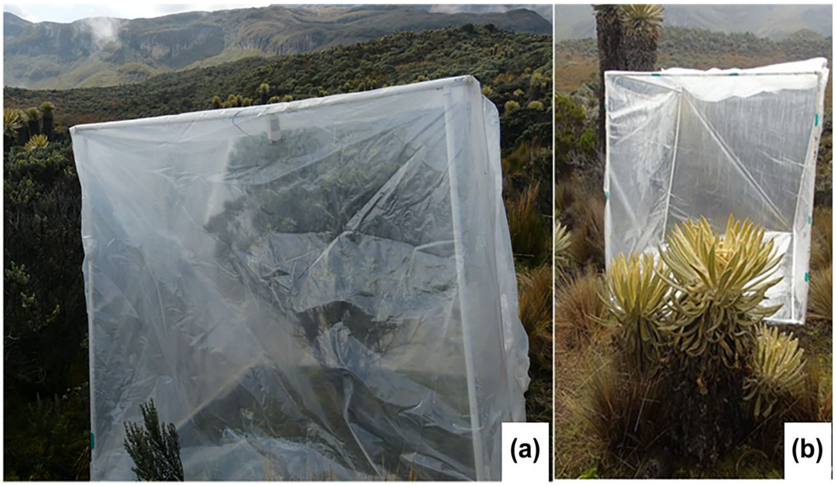


FIGURE 1 Closed (a) and open chambers (b) installed in the field.

6:00 PM). Inside the chambers as well as outside, HOBO Temperature/RH Data Loggers - MX2301A were installed. Temperature and relative humidity measurements were recorded every second during the study period.

Calculations of instantaneous hourly ETa rates and total daily ETa rates were developed using vapour density data as described by McLeod et al. (2004). The measurements of temperature and relative humidity inside the chamber were used to calculate the rate of vapour density. McLeod reported in 2004 the use of a calibration factor to account for the water absorption of the material of the chamber which was Perspex (showing hydrophilic properties). In this research, a calibration was not thought necessary, as the water absorption of polyethylene is very low (McLeod et al., 2004; Vasile et al., 2005).

To determine vapour density (ρv), we calculated saturation vapour pressure (e_s) and the partial vapour pressure (e) (Equation 1 and 2).

$$e_s = 6.11 \times \exp(17.27t/(241.2+t)) \tag{1}$$

where e_s is the saturation vapour pressure, t is temperature (°C) and 17.27 and 241.2 are constant values related to atmospheric pressure, which have been proposed by Bolton in 1980 and has been in other research in the mountain ranges of Colombia (Ruiz-Carrascal et al., 2019). This formula is elevation dependent as it follows temperature variations (Bolton, 1980).

$$e = (\mathrm{RH} \times e_s)/100 \tag{2}$$

where e (hPa) is the effective vapour pressure, RH is relative humidity (%) and e_s is saturation vapour pressure in hPa.

From these two values, the vapour density ρv (g/cm^3) was calculated (Equation 3).

$$\rho v = (0.622e/(287.04 \times t)) \times 10^5 \tag{3}$$

Then, vapour density inside the chambers was plotted over time. A linear trend was applied to the increasing section of the vapour density plot. The slope of this trend line (M) represents the vapour accumulation rate and was used in Equation (4) to calculate ETa rates per hour (mm h^{-1}).

$$ETa_{per\ hour} = 3.6 \times \frac{MV}{A} \tag{4}$$

where 3.6 is the factor to convert g m^{-2} s^{-1} into mm h^{-1}, M is the slope of the trend line (g m^{-3} s^{-1}), V is the volume of the chamber (m^3) and A is the area occupied by the chamber (m^2). Moreover, as day length in the páramos lasted on average 12 h, based on solar radiation measurements recorded by the meteorological stations, the ETa daily rates were then estimated using Equation (5).

$$ET_{\text{per day}} = \Sigma(ET_{\text{per hour}}) \times 12 \tag{5}$$

2.3 | Evapotranspiration rate calculation using the Penman–Monteith equation

Daily rates of reference evapotranspiration (ETo) were calculated from March to May 2019 using the Penman-Monteith equation (Allen, 2005) to compare with the ETa rates obtained via chamber measurements. Meteorological data were obtained from the field measurements, as indicated above, which included, wind speed, air temperature, net radiation (calculated from global radiation), relative air humidity and atmospheric pressure.

$$\mathrm{ETo} = \frac{\Delta(R_n - G) + \left(\frac{\rho C_p}{r_a}\right)(e_s - e_a)}{\lambda \rho_w \left(\Delta + \gamma\left(1 + \frac{r_s}{r_a}\right)\right)} \tag{6}$$

where:

- ETo: evapotranspiration (mm day^{-1})
- Δ: slope of the saturation vapour pressure versus temperature curve (kPa °C^{-1})

- R_n: Net radiation flux at the surface (MJ m^{-2})
- G: Sensible heat exchange from the surface to the soil (MJ m^{-2})
- ρ: Dry air density (kg m^{-3})
- C_p: Specific heat of air at constant pressure (J kg^{-1} K^{-1})
- (e_s-e_a): Vapour pressure deficit (kPa)
- γ: Psyhometric constant (kPa °C^{-1})
- r_s: surface resistance (s m^{-1})
- r_a: aerodynamic resistance (depending on leaf boundary layer) (s m^{-1})
- λ: Latent heat of vaporization or the energy require to vaporize liquid water into water vapour (J kg^{-1})
- ρ_w: Density of liquid water (kg m^{-3})

The slope of saturation vapour pressure (Δ) was calculated following Equation (7).

$$\Delta = \frac{4098\left[0.6108e^{\frac{17.27T}{T+237.3}}\right]}{(T+237.3)^2} \tag{7}$$

where

- Δ: slope of saturation vapour pressure (at air temperature T) (kPa °C^{-1})
- T: air temperature (°C)

Dry air density (ρ) was calculated following Equation (8). The average air pressure in the páramo over the period studied was 0.76 Pa.

$$\rho_{\text{dry air}} = \frac{p}{R \times T} \tag{8}$$

where

- $\rho_{\text{dry air}}$: density of dry air (kg m^{-3})
- p: air pressure (Pa)
- R: specific gas constant for dry air, 287.05 J kg^{-1} K^{-1}
- T: Temperature (°K)

The psychometric constant (γ) was calculated following Equation (9).

$$\gamma = \frac{P \times C_p}{\varepsilon \times \lambda} \tag{9}$$

where:

- P: atmospheric pressure (kPa)
- λ: latent heat of vaporization, 2.45 (MJ kg^{-1}°C^{-1})
- C_p: specific heat at constant pressure, 1.013.10^{-3} (MJ kg^{-1}°C^{-1})
- ε: ratio molecular weight of water vapour/dry air, 0.622

The published thermodynamics values for specific heat (C_p) at the average temperature measured in the páramo were retrieved from (Hilsenrath, 1955).

Stomatal resistance was calculated using the average stomatal conductance (mmol m^{-2} s^{-1}) per community converted to s m^{-1} (Equation 10), and the LAI was measured during the studied period (Table S3).

$$Sc\,(\text{s m}^{-1}) = \frac{Sc * 0.001}{a\left(\frac{P}{101.3}\right)\left(\frac{273.15}{273.15+T}\right)} \tag{10}$$

where

- Sc: Stomatal conductance (mmol m^{-2} s^{-1}) measured in the field as explained below
- a: 44.6 $\left(\frac{mol}{m^3}\right)$
- T: Temperature (°K)

The surface resistance (r_s) is a function of stomatal resistance (r) and leaf dimension expressed by the Leaf Area Index (Table S3) (Stone & Plante, 2014) (Equation 11).

$$r_s = \frac{r}{\textit{effective LAI}} \tag{11}$$

where:

- r: Stomatal resistance (s m^{-1})
- *effective* LAI: 0.5 × LAI

Aerodynamic resistance (r_a) was calculated based on Equation (12) (Allen, 2005).

$$r_a = \frac{\ln\left(\frac{z_m - d}{z_{om}}\right) \times \ln\left(\frac{z_h - d}{z_{oh}}\right)}{k^2 \times u_z} \tag{12}$$

where

- r_a: aerodynamic resistance (s m^{-1})
- z_m: height of wind measurements (m)
- z_h: height of humidity measurements (m)
- d: zero plane displacement height (m)
- z_{om}: roughness length governing momentum transfer (m)
- z_{oh}: roughness length governing transfer of heat and vapour (m)
- k: von Karman's constant, 0.41 (—)
- u_z: wind speed at height z (m s^{-1})

Heights at which wind and humidity sensors were placed were measured in the field (2.07 and 1.5 m, respectively). Then, d, z_{om} and z_{oh} and d were calculated following Equations (13)–(15) (Allen, 2005).

The average plant height (h) was calculated per community based on measurements done in the field (Table S2).

$$d = \frac{2}{3} \times h \quad (13)$$

$$z_{om} = 0.123 \times h \quad (14)$$

$$z_{oh} = 0.1 \times z_{om} \quad (15)$$

where:

h: plant height (m)

2.4 | Stomatal conductance

Stomatal conductance was measured to estimate ETo for each community studied using the Penman–Monteith equation. At each chamber location, stomatal conductance (µmol m^{-2} s^{-1}) was measured on the abaxial side of the leaves of two individuals from the dominant species at each community (Table S4) by using a SC-1 leaf porometer (Meter Environment®). Three leaves (at three different heights) per individual were randomly selected and measured during the studied period, every hour between 10:00 AM and 1:00 PM only for sunny and dry days. Based on the leaf measurements, the mean value by individual was calculated. To obtain average stomatal conductance per community, the measurements were weighted using the mean abundance of each species by community observed in the plots (Table S4). Importantly, although porometers have been used in tussock grass and pasture grasses (Baruch et al., 1985; Ramírez et al., 2006), it has been discussed that high relative humidity of the incoming air (more than 80% RH) can generate significant errors in the porometer measurement (Mcdermitt, 1990). For that reason, the porometer was calibrated daily and the silica gel was also changed regularly, and no measurements were made when the humidity was too high for the porometer to correctly calibrate.

2.5 | Data analysis

All data analyses were performed using R programming (R Core Team, 2018) and Microsoft Excel. Average ETa hourly rates and standard deviation were first calculated for the three communities. Based on the ETa hourly rates obtained during the studied period, a comparison was made between communities. To achieve this, a one-way ANOVA test was performed to check for significant differences between communities. Data was checked for homogeneity using the Levene test and for normality using a Shapiro test. Significant level was set at 0.05. Finally, a Tukey multiple comparison test was applied to compare the differences between each community. The Penman–Monteith ETo rates were also compared among communities using the non-paramteric Kruskal Wallis and Withney–Wilcoxon tests. Finally, to assess the strength of the correspondence between the results obtained via the Penman–Monteith and the closed chamber method, a linear regression was applied to the daily ET rates measured with the two methods at the same times and days.

To understand which variables were most important in the variation of ETa rates at the closed chambers measurements, a principal component analysis (PCA) was performed. The PCA also enabled to ordinate communities according to their ETa rates and environmental co-variables. The analysis was carried out using the Factoextra and the FactoMineR packages (Le & Husson, 2008). Correlation between ETa rates and each environmental factors was also tested via spearman correlation tests.

The environmental variables included in the analysis were solar radiation, temperature and relative humidity. Precipitation was also added for its effect on soil moisture and air humidity. Finally, a redundancy analysis was carried to extract and summarize the variation in the ET rates using these environmental variables.

3 | RESULTS

Average hourly and daily ETa rates per community are presented in Table 2. Average ETa rates were very low (with an average of 0.018 mm h^{-1} for the three communities) and presented a relatively high variation (with rates varying from 0 to 0.1 mm h^{-1}). The ANOVA test showed no significant difference ($p = 0.07$) among the three communities (Figure 2). Based on the multiple comparison procedures (Tukey's test), shrubs ETa rates differed most from the two other communities, though none of these comparisons were significant. Also, it was observed that the time needed for the chamber to saturate was different between vegetation communities as chambers installed in the tussock plant community showed the fastest saturation. Moreover, during the preparation of the experiment in the field, water

TABLE 2 Average hourly and daily rates of ETa (± SE) for each community measured via the portable closed chamber and calculated via the Penman–Monteith equation (ETo).

	Chamber		Penman–Monteith	
Community	mm h^{-1}	mm day^{-1}	mm h^{-1}	mm day^{-1}
Overall	0.018 ± 0.018	0.290 ± 0.266	0.062 ± 0.039	1.017 ± 0.468
Shrubs	0.023 ± 0.022	0.323 ± 0.290	0.081 ± 0.038	0.981 ± 0.456
Tussock grasses	0.016 ± 0.018	0.272 ± 0.286	0.091 ± 0.040	1.069 ± 0.461
Giant rosettes	0.016 ± 0.014	0.276 ± 0.223	0.081 ± 0.038	0.976 ± 0.427

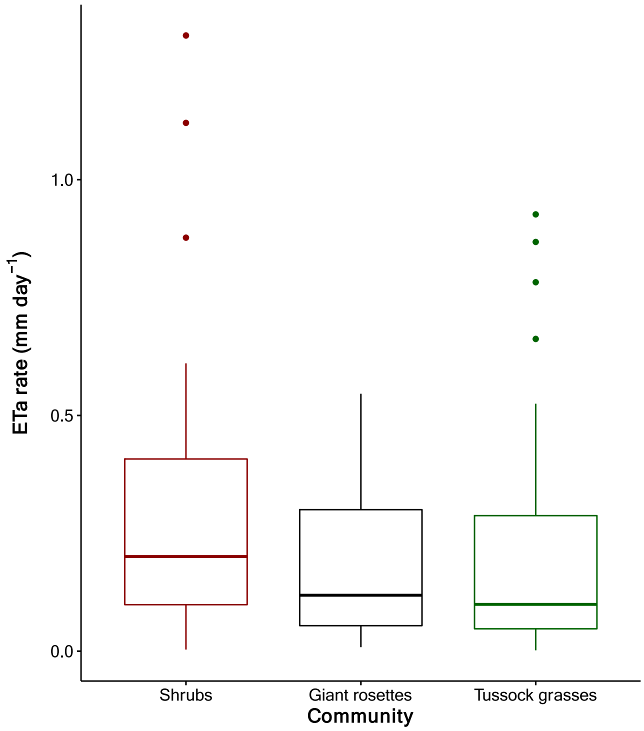


FIGURE 2 Evapotranspiration rates (mm day^{-1}) measured via the chamber method (ETa) for the three plant communities studied during the experimental period.

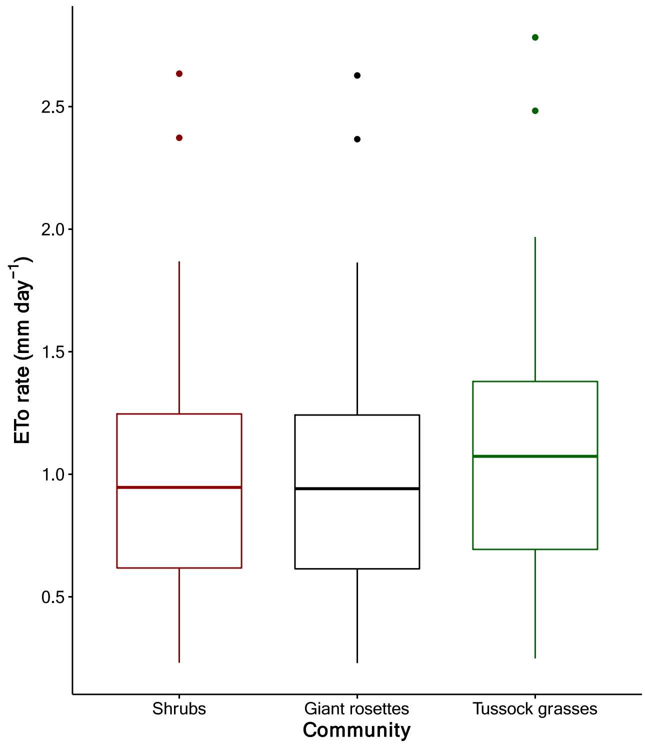


FIGURE 3 Evapotranspiration rates (mm day^{-1}) calculated via the Penman–Monteith equation (ETo, right) for the three plant communities studied during the experimental period.

condensation was observed on the chamber walls early in the morning, with a consequent increase of air humidity inside the chambers, therefore it was decided that no measurements would be made until all condensed water inside was removed.

The hourly and daily average ETo rate calculated using the Penman–Monteith equation during the experimental periods are also presented in Table 2. The stomatal conductance measurements used in this equation are presented in Figure 5. A high variation in daily and hourly ETo rates was observed with a maximum of 2.69 mm day^{-1} and a minimum daily rate of 0.244 mm day^{-1}. Although the ANOVA test was not significant, tussock grasses showed a highest ETa daily rate (1.069 ± 0.461 mm day^{-1}) compared to shrubs (0.981 ± 0.456 mm day^{-1}) and giant rosettes (0.976 ± 0.427 mm day^{-1}) (Figure 3).

There was a significant linear relationship (F statistics; $p < 0.05$) between the chamber daily ETa measurements and the calculated PM ETo rates with an adjusted R^2 value was 0.37 as shown in Figure 4. The results obtained via the PM equation were nearly 25% higher than the ET rates measured using the portable chambers.

3.1 | Stomatal conductance

The weighted stomatal conductance from the measurements (at the abaxial side of leaves) in the individuals at the three communities are presented in Figure 5: tussock grasses (*Calamagrostis recta*), giant rosettes (*Espeletia hartwegiana*), and shrubs (*Diplostephium schultzii* and *Pentacalia vernicosa*). The stomatal conductance was significantly different among communities ($p < 0.05$) when using a one-way ANOVA test. The multiple comparison (Tukey's test) showed that these differences were significant only between shrubs and giant rosettes communities ($p < 0.05$), but not between giant rosettes and tussock grasses or shrubs and tussock grasses. Giant rosettes had the highest stomatal conductance.

3.2 | Control of climatic factors on ET rates

According to PCA analysis, temperature was the climatic variable which explained most of the variation (55.2%). between the environmental variables (relative humidity, temperature, solar radiation and precipitation) and ETa rate from the chamber measurements (Figure 6). Moreover, ETa rates were significantly positively correlated with solar radiation and temperature ($p < 0.05$) and negatively correlated with relative humidity ($p < 0.05$).

The redundancy analysis performed showed that solar radiation, temperature, precipitation and relative humidity have a significant effect on ETa hourly rates variation and these factors were significantly explaining ET hourly rates variation (Table 3). The adjusted R^2 for the model selected was 0.52.

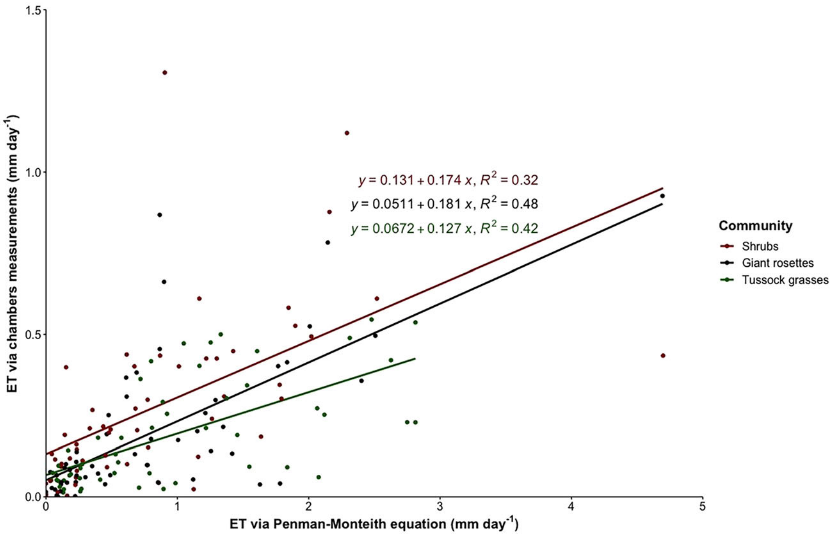


FIGURE 4 Comparison of the daily ETa rates measured via the chambers and via the Penman–Monteith equation (ETo) for the experimental period and for the three communities studied (Shrubs [dark red], Giant rosettes [black] and Tussock grasses [dark green]).

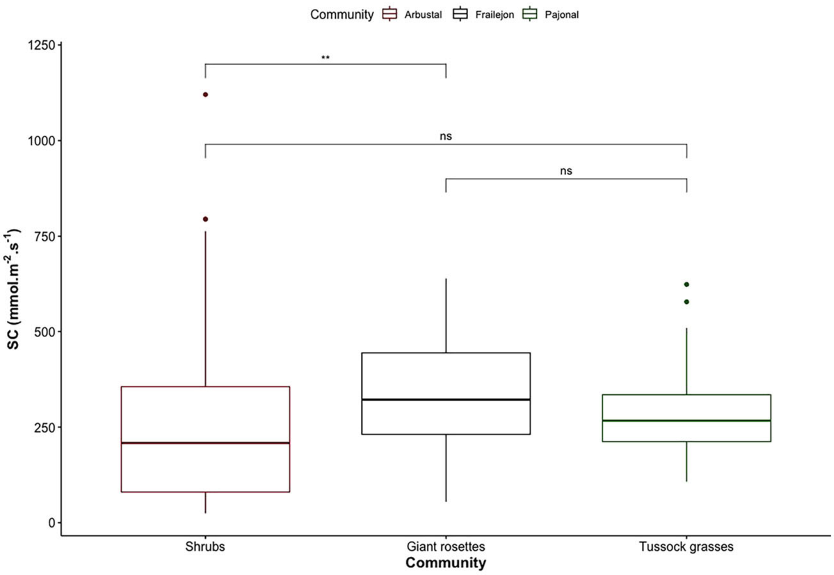


FIGURE 5 Weighted stomatal conductance (mm m^{-2} s^{-1}) measured for the three communities studied during the experimental period.

3.3 | Control of soil water content on ETa rates

Temporal dynamics of soil water content from 5- to 80-cm depth in studied sites are shown in Figure 7. Soil moisture at these sites were near field capacity during the entire measured period, and far above the permanent wilting point (horizon A: 0.25 cm^3 cm^{-3}). These soil moisture values imply a large water availability for plant transpiration. At soil surface (5 cm) water content was more variable than at deeper soil depths, which is connected to dynamics of precipitation, soil water uptake by roots and soil drainage 2011. The average soil water content for the period studied was at 0.59 cm^3 cm^{-3}. Overall, the amount of water present in soils was stable over the study period and did not decrease much below the field capacity.

4 | DISCUSSION

This research provides evidence of a low and consistent actual evapotranspiration rate across three plant communities specific to páramo vegetation. This low ETa is primarily driven by the low relative humidity observed in this ecosystem, especially during the rainy season. Nonetheless, some differences are observed among communities and can be explained by differences in leaf traits and water use strategies (Frenck et al., 2018; Maxwell et al., 2018; Zhang et al., 2018).

Shrubs, which showed the highest ETa, have small to very small leaves (compared with tussock grasses and giant rosettes) with a high density of stomata (mostly on the abaxial side) and varying trichome densities; these traits can reduce water losses, but other specific adaptations of tussock grasses and giant rosettes potentially explain the lower ETa rates in these two communities (Gutiérrez-Lagoueyte et al., 2023. Indeed, dominant species *Espeletia hartwegiana* of the giant rosettes community presents pubescent leaves (Gutiérrez-Lagoueyte et al., 2023), which diminish the impact of wind and solar radiation on evapotranspiration and increase the diffusive resistance of the leaf boundary layer (Azocar & Rada, 2006; Cárdenas et al., 2018; Mora Osejo, 2001). Furthermore, about 75% of standing leaves of tussock grasses are necromass, and only 25% of leaves are potentially available for transpiration also lowering evapotranspiration

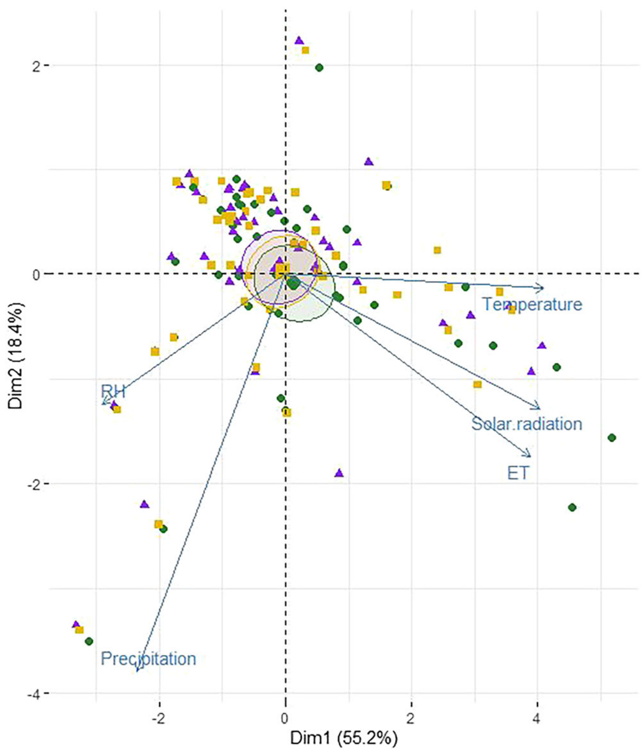


FIGURE 6 Principal component analysis (PCA) analysis including relative humidity, precipitation, temperature, solar radiation and evapotranspiration hourly rates (ETa) measured in chambers (green: shrubs, purple: giant rosette and yellow: tussock grasses).

TABLE 3 Redundancy analysis including ETa hourly rates (response) and climatic factors measured in the field ($R^2 = 0.52$).

	Variance	*F*	Pr (>*F*)
Temperature	$1.505e^{-04}$	112.895	0.001
Relative humidity	$9.306e^{-06}$	6.976	0.019
Precipitation	$5.902e^{-05}$	4.424	0.036
Solar radiation	$3.618e^{-04}$	27.123	0.001

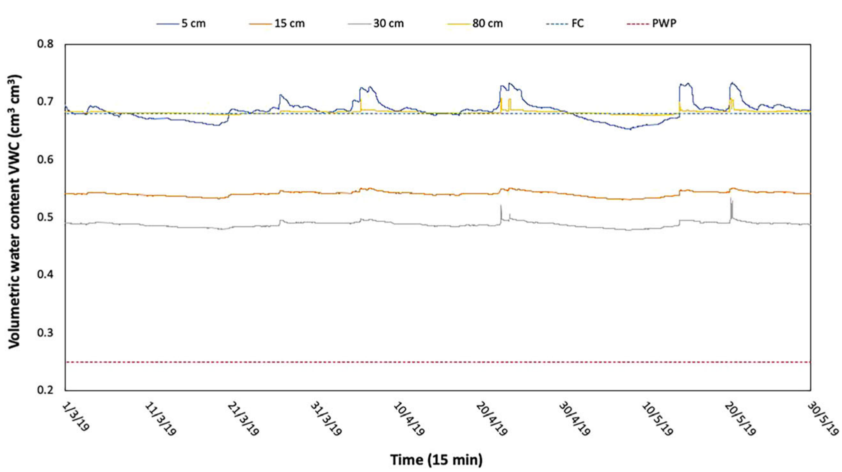
(Azocar & Rada, 2006; Buytaert, Iñiguez, et al., 2006; Gutiérrez-Lagoueyte et al., 2023). In this research, the results also underline the high variability of the evapotranspiration rates that can be explained by the high diurnal temperature variations commonly occurring in páramo environments (Azocar & Rada, 2006; Peyre, 2015; Ruiz-Carrascal et al., 2019).

Using the Penman–Monteith equation, the differences among communities are driven by differences in LAI, height and stomatal conductance but do not include any other aspects of the communities. The relatively higher LAI measured in tussock grasses combined with their low height and higher stomatal resistance explain the higher rates calculated as shown by similar results obtained by Gutiérrez-Lagoueyte (2022).

Stomatal conductance varied among communities (although not significantly) suggesting physiological differences among species in their regulation of stomata. Contrarily to the ET rates measured in the chambers, the average stomatal conductance was higher in *Espeletia hartwegiana* (giant rosettes) than in tussock grass species and shrub species. The lower SC observed in shrubs could be due to the high interspecific variation in stomatal conductance within the shrub community reducing the average SC measured for shrubs (Figure S4). Moreover, a high stomatal conductance has not shown to be directly correlated to a higher ET in the páramos (Jarvis & McNaughton, 1986; Martin et al., 1999). The higher stomatal conductance of giant rosettes could be explained by the presence of a reservoir of water in the stem pith, which helps with the regulation of the water potential gradient and allows a higher control on the water loss through stomata; therefore, the species has the ability to continuously move water and transpire (Cárdenas et al., 2018; Mora Osejo, 2001; Rada et al., 2012).

Dissimilarities in the evapotranspiration of plant communities have already been found in alpine ecosystems (McLeod et al., 2004; van den Bergh et al., 2013; Zhang et al., 2018); however, comparisons made on plant communities located at different altitudes and consequently environmental conditions were also different (e.g., temperature and solar radiation) (van den Bergh et al., 2013). In

FIGURE 7 Soil volumetric water content at 5-, 15-, 30- and 80-cm depth recorded from 1–31 May 2019, and field capacity values, as found from the water retention curve Tobón, 2022c.



Andean páramos, vegetation communities have evolved under similar environmental conditions and the high saturation of the air reducing the evapotranspiration during the wet season studied makes the discrimination across communities more complex (Flantua et al., 2019; Peyre, 2015). Also, the different results obtained among methods is expected as the models and the scale underlying each methods differ: the chambers measure the evapotranspiration of a vegetation patch while the porometer gives information at the leaf level and Penman–Monteith estimates ET at the ecosystem scale (Allen, 2005; Gutiérrez-Lagoueyte, 2022).

4.1 | ET through closed chamber compared with Penman–Monteith approach

The average ETa rates obtained via the chamber measurements are very low (average daily rate of 0.223 ± 0.224 mm day^{-1}) and are comparable with minimum ETa rates obtained in several studies done in similar ecosystems. Importantly, ETa rates measured by the chamber and ETo estimation are linearly correlated supporting that they are able to measure similar processes, only at different scales. For example, a study led in Ecuador showed that the actual evapotranspiration measured via the Eddy covariance method was 1.74 mm day^{-1} with minimal events of 0.3 mm a day and maximal events of 5.1 mm day^{-1} (622 mm year^{-1}) (Carrillo-Rojas et al., 2019; Ochoa-Sanchez et al., 2019). Moreover, in the Tibetan plateau, average ET rates between 0.4 and 2.2 mm day^{-1} were measured with high seasonal effect on these rates (Gu et al., 2008). Also, a study in the south part of the National Park Los Nevados (páramo de Romerales), potential evapotranspiration was calculated using Penman–Monteith and frequent daily rates of lower than 0.8 mm day^{-1} and a yearly evapotranspiration rate of approximately 327.8 mm were found (Valencia-Leguizamon & Tobon, 2017). On the other hand, average daily rates obtained via the Penman–Monteith method (average daily rate of 2.9 ± 3.5 mm day^{-1}) corresponds to the highest values measured previously in these ecosystems (Ochoa-Sanchez et al., 2019; Tobón & Castro, 2022; Vásquez et al., 2022). For instance, in the East Cordillera of Colombia, in the páramo of Chingaza, frequent events of lower than 0.6 mm day^{-1} and maximum ET rates of 2.4 mm day^{-1} were calculated (approximately 223.6 mm per year) (Valencia-Leguizamon & Tobon, 2017). Therefore, compared with the research mentioned above, it appears that Penman–Monteith calculation could overestimate evapotranspiration while the chamber method underestimates it.

Several factors can explain Penman–Monteith overestimation observed in this study. First, this equation aims at calculating the reference evapotranspiration (ETo) which has shown to be 13% higher than the actual ETa measured by chambers (Ochoa-Sanchez et al., 2019). Then Penman–Monteith has shown to overestimate ETa as this method assumes that water is an unlimited resource, freely available in the leaf and that vegetation grows under stress-free conditions (Allen, 2005; Rodríguez-Iturbe & Porporato, 2005). The use of calibration factors has been advised as the equation also overestimates ETa by 22% (Ochoa-Sanchez et al., 2019). Furthermore, the Penman–Monteith equation follows a single layer or 'big leaf' approach which implies that the transport properties of the vegetation surface is represented by a single-surface resistance and a single aerodynamic resistance (Allen, 2005). This approach has shown to be adequate in most ecosystems such as temperate forests; however, it might not be adequate for páramo vegetation because of the frequency of low clouds, fog conditions and very high RH conditions (Cordova et al., 2015; Tobón, 2022d).

The measurements of ETa using the chambers underline that the ETa rates of the vegetation of the páramo might be lower than what has been previously estimated in other páramos (Carrillo-Rojas et al., 2019; Ochoa-Sanchez et al., 2019). However, ETa rates measured in this study are also low due to the short study period and the high humidity observed during the rainy season. Indeed, increased frequency of precipitation and fog events during this period have shown to significantly decrease ET rates (Tobón, 2022). Underestimation of ETa measured using closed chambers could be due to several factors: first, most of the studies mentioned above calculated these daily averages on longer time periods (usually 1 year or more). However, although the analysed data corresponds to a small period of the year, it does reflect the dynamics of the ET variation for an hourly scale and under controlled conditions. Closed chambers might result in lower ETa mainly due to (1) the difference on radiation wavelength entering the chamber, (2) the absence of wind inside the chambers, (3) the high relative humidity measured during the study period in the páramo and (4) the formation of a specific micro-climate inside the chambers through the increase of temperature and humidity, thus suppressing ETa (Hewitt et al., 2018; McLeod et al., 2004). Importantly, the models and techniques previously applied to páramos, include the presence of open-water surfaces such as lagoons in the páramos, while the chambers focuses on water lost by plant and soil in small areas (Kairu, 1991). Indeed, if looking at the global water cycle, transpiration from the biota only represent 0.003% of the land water reservoir, while surface waters represent 0.6% therefore having a higher contribution to the evapotranspiration of the land ecosystems (Chahine, 1992). The chambers offer a potential affordable and portable method to compare ETa between plant communities in remote and heterogeneous ecosystems however they should be improved to be installed for longer period.

4.2 | Environmental control on ET

This study showed that soil water content was not a limiting factor as it remained quite high (above FC) for the whole period. This is different from other páramos such as in Venezuela, where soil water content variations was the environmental factor which control the most ET rates (Mora Osejo, 2001). Contrary, in this study, energy availability represented by solar radiation and temperature seemed to be the controlling factors of ET, which was also found in Ecuadorian páramo, where higher solar radiation led to higher evapotranspiration (Ochoa-Sanchez et al., 2019). Solar radiation has proved to trigger stomatal opening therefore increasing ET (Mora Osejo, 2001; Pearcy et al., 2000). Relative humidity also played a role in lowering ET rates as no additional water vapour can be added to the atmosphere at high relative humidity (Musy & Higy, 2011). Importantly, deforestation of the Andean forest added to the future warmer and drier climate expected in montane cloud belts worldwide, could reduce the occurrence of fog therefore decreasing the relative humidity and increasing solar incidence (Alvarado-Barrientos et al., 2014). Based on the data obtained in this study this might eventually increase ET therefore decreasing the water yield of páramos.

5 | CONCLUSIONS

To conclude, this study underlines that the rates of ETa could be lower than initially calculated using ETo methods, at least in humid páramos as found in the Northern Andes. The closed chambers were useful at comparing ETa on small areas in a Colombian páramo under similar monitored environmental conditions among plant communities during the rainy season and they provided a better understanding of the water use strategies of vegetation communities in this ecosystem. The low ETa rates measured for the different plant communities further confirm the hypothesis that páramos vegetation plays a crucial role in lowering the overall evapotranspiration of this ecosystem and help improve the water retention capacity of this ecosystem, due to the low evapotranspiration rates. Also, a high variation in the daily ET rates was observed and was correlated with the large fluctuations of daily solar incidence and temperature. These results therefore underline the importance of these environmental factors in determining ET rates by different plant communities in Andean páramos. Finally, this study highlights the need to develop more accurate and low-cost ET measuring methods and adapting estimation methods to tropical ecosystems such as the páramos.

SIGNIFICANCE STATEMENT

This article aims at improving the understanding of evapotranspiration in high altitude Andean ecosystems that is crucial as they act as a permanent water source for surrounding cities. Here, evapotranspiration was measured using portable closed chambers and the results confirmed the importance of the vegetation in reducing water losses. Based on this method, ETa of the local biota might be even lower than initially estimated for Colombian páramos. Moreover, the importance of solar radiation and temperature in controlling evapotranspiration rates was underlined bringing important insight on the water cycle responses to climate change in these ecosystems. This article also stresses the need to develop more suitable and accessible methods to measure evapotranspiration rates in tropical high-altitude ecosystems.

ACKNOWLEDGEMENTS

The authors would like to thank Dr. Daniel Ruiz-Carrascal, associate research scientist at Columbia University for his help with the Penman–Monteith calculations and his advice on the interpretation of the results obtained in relation with the climatic measurements. Also, the authors thank the other members of the *Hidrología y Modelación de Ecosistemas* research group at the Universidad Nacional sede Medellin, especially Lina Marcela Camelo Mendoza, Manuel Felipe Leandro Arevalo and Juan Simon Rodas Lopera for their support during the field work. Finally, the authors also thank the University of Maastricht and Dr. Roy Erkens for supporting and encouraging this thesis research project. Open Access funding enabled and organized by Projekt DEAL.

DATA AVAILABILITY STATEMENT

Data are available on demand and are in the process of being made openly available on a public repository.

REFERENCES

Allen, R. (2005). Penman-Monteith equation. In *Encyclopedia of soils in the environment, Elsevier*, (pp. 180–188).

Alvarado-Barrientos, M. S., Holwerda, F., Asbjornsen, H., Dawson, T. E., & Bruijnzeel, L. A. (2014). Suppression of transpiration due to cloud immersion in a seasonally dry Mexican weeping pine plantation. *Agricultural and Forest Meteorology*, *186*, 12–25. https://doi.org/10.1016/j.agrformet.2013.11.002

Aparecido, L. M. T., Teodoro, G. S., Mosquera, G., Brum, M., Barros, F. D., Pompeu, P. V., Rodas, M., Lazo, P., Müller, C. S., Mulligan, M., Asbjornsen, H., Moore, G. W., & Oliveira, R. S. (2018). Ecohydrological drivers of Neotropical vegetation in montane ecosystems. *Ecohydrology*, *11*(3), 17. https://doi.org/10.1002/eco.1932

Azocar, A., & Rada, F. (2006). *Ecofisiología de Plantas de Páramo: Universidad de los Andes*. Inst. de Ciencias Ambientales y Ecologicas.

Baruch, Z., Ludlow, M. M., & Davis, R. (1985). Photosynthetic responses of native and introduced C4 grasses from Venezuelan savannas. *Oecologia*, *67*, 388–393. https://doi.org/10.1007/BF00384945

Bolton, D. (1980). The computation of equivalent potential temperature. *Monthly Weather Review*, *108*, 1046–1053. https://doi.org/10.1175/1520-0493(1980)108<1046:TCOEPT>2.0.CO;2

Buytaert, W., Celleri, R., De Bievre, B., Cisneros, F., Wyseure, G., Deckers, J., & Hofstede, R. (2006). Human impact on the hydrology of the Andean páramos. *Earth-Science Reviews*, *79*(1–2), 53–72. https://doi.org/10.1016/j.earscirev.2006.06.002

Buytaert, W., Iñiguez, V., Celleri, R., De Bièvre, B., Wyseure, G., & Deckers, J. (2006). Analysis of the Water Balance of Small Páramo Catchments in South Ecuador. Environmental Role of Wetlands in Headwaters, 271–281. https://doi.org/10.1007/1-4020-4228-0_24

Buytaert, W., Wyseure, G., De Bièvre, B., & Deckers, J. (2005). The effect of land-use changes on the hydrological behaviour of Histic andosols in South Ecuador. *Hydrological Processes*, *19*(20), 3985–3997. https://doi.org/10.1002/hyp.5867

Cárdenas, M. F., Tobón, C., Rock, B. N., & del Valle, J. I. (2018). Ecophysiology of frailejones (Espeletia spp.), and its contribution to the hydrological functioning of páramo ecosystems. *Plant Ecology*, *219*(2), 185–198. https://doi.org/10.1007/s11258-017-0787-x

Carrillo-Rojas, G., Silva, B., Rollenbeck, R., Celleri, R., & 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. https://doi.org/10.1016/j.agrformet.2018.11.006

Célleri, R., & Feyen, J. (2009). The hydrology of tropical Andean ecosystems: Importance, knowledge status, and perspectives. *Mountain Research and Development*, *29*(4), 350–355. https://doi.org/10.1659/mrd.00007

Chahine, M. T. (1992). The hydrological cycle and its influence on climate. *Nature*, *359*(6394), 373–380. https://doi.org/10.1038/359373a0

Chia, M. Y., Huang, Y. F., Koo, C. H., & Fung, K. F. (2020). Recent advances in evapotranspiration estimation using artificial intelligence approaches with a focus on hybridization techniques-a review. *Agronomy*, *10*(1), 101. https://doi.org/10.3390/agronomy10010101

Coners, H., Babel, W., Willinghöfer, S., Biermann, T., Köhler, L., Seeber, E., Foken, T., Ma, Y., Yang, Y., Miehe, G., & Leuschner, C. (2016). Evapotranspiration and water balance of high-elevation grassland on the Tibetan plateau. *Journal of Hydrology*, *533*, 557–566. https://doi.org/10.1016/j.jhydrol.2015.12.021

Cordova, M., Carrillo-Rojas, G., Crespo, P., Wilcox, B. P., & Celleri, R. (2015). Evaluation of the Penman-Monteith (FAO 56 PM) method for calculating reference evapotranspiration using limited data application to the wet páramo of southern Ecuador. *Mountain Research and Development*, *35*(3), 230–239. https://doi.org/10.1659/mrd-journal-d-14-0024.1

Damveld, J. H., van der Reijden, K. J., Cheng, C., Koop, L., Haaksma, L. R., Walsh, C. A. J., Soetaert, K., Borsje, B. W., Govers, L. L., Roos, P. C., Olff, H., & Hulscher, S. (2018). Video transects reveal that tidal sand waves affect the spatial distribution of benthic organisms and sand ripples. *Geophysical Research Letters*, *45*(21), 11837–11846. https://doi.org/10.1029/2018gl079858

Denmead, O. T., Dunin, F. X., Wong, S. C., & Greenwood, E. A. N. (1993). Measuring water use efficiency of eucalypt trees with chambers and micrometeorological techniques. *Journal of Hydrology*, *150*(2), 649–664. https://doi.org/10.1016/0022-1694(93)90130-2

Duan, L. M., Lv, Y., Yan, X., Liu, T. X., & Wang, X. X. (2017). Upscaling stem to community-level transpiration for two sand-fixing plants: Salix gordejevii and Caragana microphylla. *Water*, *9*(5), 12. https://doi.org/10.3390/w9050361

Flantua, S., O'Dea, A., Onstein, R., & Hooghiemstra, H. (2019). The flickering connectivity system of the north Andean páramos. *Journal of Biogeography*, *46*(8), 1808–1825.

Flo, V., Martinez-Vilalta, J., Steppe, K., Schuldt, B., & Poyatos, R. (2019). A synthesis of bias and uncertainty in sap flow methods. *Agricultural and Forest Meteorology*, *271*, 362–374, ISSN 0168-1923. https://doi.org/10.1016/j.agrformet.2019.03.012

Frenck, G., Leitinger, G., Obojes, N., Hofmann, M., Newesely, C., Deutschmann, M., Tappeiner, U., & Tasser, E. (2018). Community-specific hydraulic conductance potential of soil water decomposed for two Alpine grasslands by small-scale lysimetry. *Biogeosciences*, *15*(4), 1065–1078. https://doi.org/10.5194/bg-15-1065-2018

Granier, A., & Loustau, D. (1994). Measuring and modeling the transpiration of a maritime pine canopy from sap-flow data. *Agricultural and Forest Meteorology*, *71*(1–2), 61–81. https://doi.org/10.1016/0168-1923(94)90100-7

Gu, S., Tang, Y., Cui, X., du, M., Zhao, L., Li, Y., Xu, S., Zhou, H., Kato, T., Qi, P., & Zhao, X. (2008). Characterizing evapotranspiration over a meadow ecosystem on the Qinghai-Tibetan plateau. *Journal of Geophysical Research-Atmospheres*, *113*(D8), D08118. https://doi.org/10.1029/2007JD009173

Gutiérrez-Lagoueyte, M. (2017). Dinámica ecohidrológica de la vegetación de páramo asociada a sus rasgos funcionales, bajo condiciones climáticas actuales y proyectadas (unpublished thesis proposal) Universidad Nacional de Colombia, sede Medellín.

Gutiérrez-Lagoueyte, M. E. (2022). Chapter 5. Evapotranspiration in the canopy of plant communities [Unpublished Phd's thesis]. Universidad Nacional de Colombia.

Gutiérrez-Lagoueyte, M. E., Leandro, M., & Tobón, C. (2023). Rasgos funcionales de las especies de flora dominantes en el páramo, Parque Nacional Natural Los Nevados. En:. In C. Tobón (Ed.), *Los páramos de Colombia: Caractéristiques biofisícas, Ecohidrología y Cambio Climático* (p. 489). Universidad Nacional de Colombia.

Hewitt, I. C., Fernald, A. G., & Samani, Z. A. (2018). Calculating field-scale evapotranspiration with closed-chamber and remote sensing methods. *JAWRA Journal of the American Water Resources Association*, *54*(4), 962–973. https://doi.org/10.1111/1752-1688.12654

Hilsenrath, J. (1955). *Tables of thermal properties of gases: Comprising tables of thermodynamic and transport properties of air, argon, carbon dioxide, carbon monoxide, hydrogen, nitrogen, oxygen, and steam*. US Dept. of Commerce, National Bureau of Standards.

Hofstede, R., Segarra, P., & Mena, P. (2003). *Los Páramos del Mundo. Proyecto Atlas Mundial de los Páramos*. Global Peatland Initiative/NC-IUCN/EcoCiencia.

Jarvis, P. G., & McNaughton, K. G. (1986). Stomatal control of transpiration: Scaling up from leaf to region. In A. MacFadyen & E. D. Ford (Eds.), *Advances in ecological research* (Vol. 15) (pp. 1–49). Academic Press.

Kairu, E. N. (1991). A review of methods for estimating evapotranspiration: Particularly those that utilize remote sensing. *GeoJournal*, *25*(4), 371–376. https://doi.org/10.1007/BF02439487

Le, S., & Husson, F. (2008). SENSOMINER: A PACKAGE FOR SENSORY DATA ANALYSIS. *Journal of Sensory Studies*, *23*(1), 14–25. https://doi.org/10.1111/j.1745-459X.2007.00137.x

Leguizamon, J. V., & Tobón, C. (2017). Influencia de la vegetación en el funcionamiento hidrológico de cuencas de humedales de alta montaña tropical. *Revista Ecosistemas*, *26*(2), 10–17.

Liu, Y., Qiu, G., Zhang, H., Yang, Y., Zhang, Y., Wang, Q., Zhao, W., Jia, L., Ji, X., Xiong, Y., & Yan, C. (2022). Shifting from homogeneous to heterogeneous surfaces in estimating terrestrial evapotranspiration: Review and perspectives. *Science China Earth Sciences*, *65*, 197–214. https://doi.org/10.1007/s11430-020-9834-y

Llambí, L. D., & Sarmiento, L. (1998). Biomasa microbiana y otros parámetros edáficos en una sucesión secundaria de los páramos venezolanos. *Ecotropicos*, *11*, 1–14.

Luteyn, J. (1999). Páramos: A checklist of plant diversity, geographical distribution, and botanical literature. *Memoirs of the New York Botanical Garden*, *84*, 278.

Marín, C., & Parra, S. (2015). *Bitácora de flora*. Instituto de Investigación de Recursos Biológicos-Alexander von Humboldt.

Martin, T. A., Hinckley, T. M., Meinzer, F. C., & Sprugel, D. G. (1999). Boundary layer conductance, leaf temperature and transpiration of Abies amabilis branches. *Tree Physiology*, *19*(7), 435–443. https://doi.org/10.1093/treephys/19.7.435

Maxwell, T. M., Silva, L. C. R., & Horwath, W. R. (2018). Integrating effects of species composition and soil properties to predict shifts in montane forest carbon–water relations. *Proceedings of the National Academy of Sciences*, *115*(18), E4219–E4226. https://doi.org/10.1073/pnas.1718864115

Mcdermitt, D. (1990). Sources of error in the estimation of stomatal conductance and transpiration from Porometer data. *HortScience*, *25*, 1538–1548. https://doi.org/10.21273/HORTSCI.25.12.1538

McLeod, M. K., Daniel, H., Faulkner, R., & Murison, R. (2004). Evaluation of an enclosed portable chamber to measure crop and pasture actual evapotranspiration at small scale. *Agricultural Water Management*, *67*(1), 15–34. https://doi.org/10.1016/j.agwat.2003.12.006

Mora Osejo, L. E. (2001). *Contribuciones al estudio comparativo de la conductancia y de la transpiración foliar de especies de plantas del páramo, Academia Colombiana de Ciencias exactas, Fisicas y Naturales*.

Musy, A., & Higy, C. (2011). Hydrology: a science of nature. https://doi.org/10.1201/b10426

Ochoa-Sanchez, A., Crespo, P., Carrillo-Rojas, G., Sucozhanay, A., & Celleri, R. (2019). Actual evapotranspiration in the high Andean grasslands: A comparison of measurement and estimation methods. *Frontiers in Earth Science*, *7*, 55. https://doi.org/10.3389/feart.2019.00055

Pearcy, R. W., Schulze, E. D., & Zimmermann, R. (2000). Measurement of transpiration and leaf conductance. In R. W. Pearcy, J. R. Ehleringer,

H. A. Mooney, & P. W. Rundel (Eds.), *Plant physiological ecology: Field methods and instrumentation* (pp. 137–160). Springer Netherlands.

Pesantez, J., Mosquera, G. M., Crespo, P., Breuer, L., & Windhorst, D. (2018). Effect of land cover and hydro-meteorological controls on soil water DOC concentrations in a high-elevation tropical environment. *Hydrological Processes*, *32*(17), 2624–2635. https://doi.org/10.1002/hyp.13224

Peyre, G. (2015). Plant diversity and vegetation of the Andean Páramo (PhD), University of Barcelona.

Poyatos, R., Granda, V., Flo, V., Adams, M. A., Adorján, B., Aguadé, D., Aidar, M. P., Allen, S., Alvarado-Barrientos, M. S., Anderson-Teixeira, K. J., & Aparecido, L. M. (2021). Global transpiration data from sap flow measurements: The SAPFLUXNET database. *Earth System Science Data*, *13*, 2607–2649. https://doi.org/10.5194/essd-13-2607-2021

R Core Team. (2018). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Rada, F., Azócar, A., & Rojas-Altuve, A. (2012). Water relations and gas exchange in Coespeletia moritziana (Sch. Bip) Cuatrec., a giant rosette species of the high tropical Andes. *Photosynthetica*, *50*(3), 429–436. https://doi.org/10.1007/s11099-012-0050-6

Ramírez, D. A., Valladares, F., Blasco, A., & Bellot, J. (2006). Assessing transpiration in the tussock grass Stipa tenacissima L.: The crucial role of the interplay between morphology and physiology. *Acta Oecologica*, *30*, 386–398. https://doi.org/10.1016/j.actao.2006.06.006

Rodríguez-Iturbe, I., & Porporato, A. (2005). *Ecohydrology of water-controlled ecosystems: Soil moisture and plant dynamics*. Cambridge University Press.

Ruiz-Carrascal, D., Gutiérrez-Lagoueyte, M., & Zuluaga-Pulgarín, M. (2019). El clima de los páramos en Colombia: variables climáticas esenciales_Manuscript in preparation.

Ryken, A. C., Gochis, D., & Maxwell, R. M. (2022). Unravelling groundwater contributions to evapotranspiration and constraining water fluxes in a high-elevation catchment. *Hydrological Processes*, *36*(1), e14449. https://doi.org/10.1002/hyp.14449

Salamanca, S., Cleef, A. M., & Rangel-Ch, O. (2003). The páramo vegetation of the volcanic Ruiz-Tolima massif. In T. van der Hammen & A. D. Santos (Eds.), *Studies on tropical Andean ecosystems, the Colombian central cordillera, Los Nevados National Natural Park Transect* (Vol. 5) (pp. 1–77), J.Cramer.

Smith, D. M., & Allen, S. J. (1996). Measurement of sap flow in plant stems. *Journal of Experimental Botany*, *47*(12), 1833–1844. https://doi.org/10.1093/jxb/47.12.1833

Stone, M. M., & Plante, A. F. (2014). Changes in phosphatase kinetics with soil depth across a variable tropical landscape. *Soil Biology and Biochemistry*, *71*, 61–67. https://doi.org/10.1016/j.soilbio.2014.01.006

Tobón, C. (2022a). El clima de los páramos de Colombia. En:. In C. Tobón (Ed.), *Los páramos de Colombia. Características biofísicas, Ecohidrología y Cambio Climático* (p. 631). Universidad Nacional, de Colombia.

Tobón, C. (2022b). Interceptación de la precipitación por la vegetación de los páramos. En:. In C. Tobón (Ed.), *Los páramos de Colombia. Características biofísicas, Ecohidrología y Cambio Climático* (p. 631). Universidad Nacional, de Colombia.

Tobón, C. (2022c). Los suelos de los páramos en Colombia y sus propiedades hidrofísicas. En:. In C. Tobón (Ed.), *Los páramos de Colombia. Características biofísicas, Ecohidrología 34 y Cambio Climático* (p. 631). Universidad Nacional, de Colombia.

Tobón, C. (2022d). Contribución de la niebla a la ecohidrología de los páramos en Colombia. In C. Tobón (Ed.), *Los páramos de Colombia. Características biofísicas, Ecohidrología y Cambio Climático*. En: (p. 631). Universidad Nacional, de Colombia.

Tobón, C., & Arroyave, F. (2007). Inputs by fog and horizontal precipitation to the páramo ecosystems and their contribution to the water balance. Paper presented at the Proceedings Fourth International Conference on Frog Collection and Dew.

Tobón, C., Bruijnzeel, L.A., Frumau, K.F.A. & Calvo, J.C. (2011). Changes in soil hydraulic properties and soil water status after conversion of tropical montane cloud forest to pasture in northern Costa Rica. In: Bruijnzeel, L. A., Scatena, F. N., & Hamilton, L. S. (Eds.). (2011) *Tropical Montane Cloud Forests*. https://doi.org/10.1017/cbo9780511778384

Tobón, C., & Castro, E. (2022). Funcionamiento ecohidrológico de los páramos en Colombia: Balance hídrico, rendimiento y regulación hídrica. En:. In C. Tobón (Ed.), *Los páramos de Colombia. Características biofísicas, Ecohidrología y Cambio Climático* (p. 631). Universidad Nacional, de Colombia.

Valencia-Leguizamon, J., & Tobon, C. (2017). Influence of vegetation on the hydrological functioning of tropical high mountain wetlands basins. *Ecosistemas: Revista Cietifica Y Tecnica de Ecologia Y Medio Ambiente*, *26*(2), 10–17. https://doi.org/10.7818/ecos.2017.26-2.02

van den Bergh, T., Inauen, N., Hiltbrunner, E., & Körner, C. (2013). Climate and plant cover co-determine the elevational reduction in evapotranspiration in the Swiss Alps. *Journal of Hydrology*, *500*, 75–83. https://doi.org/10.1016/j.jhydrol.2013.07.013

Vasile, C., Pascu, M., & Rapra Technology, L. (2005). *Practical guide to polyethylene*. Rapra Technology Ltd.

Vásquez, C., Célleri, R., Córdova, M., & Carrillo-Rojas, G. (2022). Improving reference evapotranspiration (ETo) calculation under limited data conditions in the high tropical Andes. *Agricultural Water Management*, *262*, 107439, ISSN 0378-3774. https://doi.org/10.1016/j.agwat.2021.107439

Zhang, H., Simmonds, L. P., Morison, J. I., & Payne, D. (1997). Estimation of transpiration by single trees: Comparison of sap flow measurements with a combination equation. *Agricultural and Forest Meteorology*, *87*(2–3), 155–169. https://doi.org/10.1016/S0168-1923(97)00017-8

Zhang, R., Xu, X., Liu, M., Zhang, Y., Xu, C., Yi, R., & Luo, W. (2018). Comparing evapotranspiration characteristics and environmental controls for three agroforestry ecosystems in a subtropical humid karst area. *Journal of Hydrology*, *563*, 1042–1050. https://doi.org/10.1016/j.jhydrol.2018.06.051

Zhao, L., Xia, J., Xu, C. Y., Wang, Z., Sobkowiak, L., & Long, C. (2013). Evapotranspiration estimation methods in hydrological models. *Journal of Geographical Sciences*, *23*, 359–369. https://doi.org/10.1007/s11442-013-1015-9

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Meyers, B., Gutiérrez-Lagoueyte, M. E., & Tobón, C. (2023). Measurement of actual evapotranspiration in a páramo ecosystem using portable closed chambers: Comparison between giant rosettes, tussock grasses and shrubs. *Ecohydrology*, e2525. https://doi.org/10.1002/eco.2525