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Ecophysiology of frailejones (*Espeletia* spp.), and its contribution to the hydrological functioning of páramo ecosystems

María Fernanda Cárdenas · **Conrado Tobón** · **Barret N. Rock** · **Jorge Ignacio del Valle**

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Abstract Páramos are high elevation tropical ecosystems in northern Andes, with large water yield and water regulation. One of the main and representative species growing in these páramos is the genus *Espeletia*, known as frailejones. There is a lack of knowledge of Espeletia ecophysiology, maybe due to its unusual anatomical modifications and the specific climatic conditions of these ecosystems. Therefore, it is important to determine the relationships between the anatomical modifications of *Espeletia*, its physiological functioning, and its contribution to the ecohydrologic functioning of páramos. Consequently, we studied the physiology of frailejones in two Colombian páramos, focused on the identification of conductive tissues inside the stems, calculated the age, and measured sapflow, using the heat ratio method. Results show that *Espeletia* spp. have a central pith that increases with height, as the size of secondary xylem decreases. Frailejones respond quickly to the changing conditions of weather factors controlling transpiration such as solar radiation, temperature, and fog presence. However, although environmental factors favor transpiration, the sapflow tends to decrease—a particular behavior of the *Espeletia* transpiration processes—since this occurs chaotically over time, including sapflow at night. The transformation of sapflow velocity to depth of water in a basin shows that the water lost through their transpiration is very low, which contributes to the high runoff ratio of páramo ecosystems. For the first time, we determine by radiocarbon the real ages of three *E. hartwegiana*, and their mean growth rates to range between 3.8 and 6.9 cm year^{-1}.

Keywords Growth and age of Espeletia · Night-time transpiration · Radiocarbon · Sapflow · Tropical high mountain ecosystems

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M. F. Cárdenas (✉)
Universidad Nacional de Colombia, Calle 56 N°78A-59 (801), Medellín, Colombia
e-mail: mfcarden@unal.edu.co

C. Tobón
Universidad Nacional de Colombia, Calle 59 A N 63-20, Block 14-327, Medellín, Colombia

B. N. Rock
University of New Hampshire, 20 Pinecrest Lane, Durham, NH 03824, USA

J. I. del Valle
Universidad Nacional de Colombia, Calle 59 A N 63-20, Block 14-328, P.C 568, Medellín, Colombia

Introduction

Páramos are ecosystems in the higher peaks of the Andes, between the tree line and the glaciers, and are present from Venezuela to northern Peru, distributed as biogeographical islands (Hofstede et al. 2003). Due to altitudinal elevation where they occur, the predominant climate is characterized by low temperatures with wide daily range of temperature (Ramsay and Oxley 1997; Sklenář 2006) and soils with large water availability. This is the main reason for the hydric stability and the interaction between hydric and thermic factors, as the main elements determining the growth and metabolic activity of plants in these ecosystems (Azocar and Rada 1993). These ecosystems are characterized as an open shrubby vegetation inside a grasslands matrix, with high levels of vegetation endemism attributed to their fragmented distribution in the landscape (Young et al. 2011).

The most outstanding ecohydrologic features of the páramo ecosystems are their high water regulation and a high water yield, defined as the proportion of rainfall (R) that becomes runoff (D) (D/R), of about 63%, compared to those of tropical dry forest (19% on average), the tropical rain forest (42% on average), and the cloud forests (57%) (Tobón 2009). Characteristics such as low temperatures, high relative air humidity, and well-developed organic soils, with high moisture content are the main factors controlling their ecohydrologic functioning. The incoming rainfall that becomes water runoff depends also on the soil infiltration capacity and soil hydraulic conductivity, which are usually very high in páramo basins (Tobón et al. 2004). Additional factors contributing to this large water yield and regulation of the páramos are low evapotranspiration, due to the presence of fog and low clouds, a low leaf area index, of about 1.3 (Azocar and Rada 1993; Cavieres et al. 2000; García-Varela and Rada 2003; Rada et al. 1998), and low temperatures. Moreover, some physiological adaptations found in tropical high mountain plants include high nightly respiration (Azocar and Rada 1993), high photosynthetic capacity (Goldstein et al. 1994), and short duration changes in the open and closing of stomata, caused by variations in irradiance, and the momentary intensities of transpiration and conductance [Lösch and Schulze (1995), cited by Mora-Osejo (2001)].

Species of the genus *Espeletia*, known as frailejones, are one of the most conspicuous forms in the páramos of the northern Andes. The frailejones exhibit a giant caulirosulan habit, one of the typical adaptive forms in this kind of environments (Azócar and Rada 2007; Cuatrecasas 1968). Other morphologic characteristics of these plants are the dead leaves that remain attached to the plants after leaf senescence, as a strategy of this plant to insulate the stem, to prevent freezing and to retain nutrients. In addition, the central pith accumulates large amount of water, thus it can provide water to the transpiring leaves and the foliar pubescence under specific demanding conditions (García-Varela and Rada 2003; Nobel and Goldstein 1992; Rada et al. 1985; Rojas-Zamora et al. 2013). Moreover, frailejones have unusual anatomical modifications, consisting of primary thickening meristems at the shoot apex and sunken stomatal crypts found in the leaves (Rock 1972; Roth 1973).

The water stored in the pith can maintain the average intensity of transpiration for about 2.5 continuous hours, but this may vary according to the species (Goldstein et al. 1994). This explains the fast recovery of transpiration rates after a reduction or total suspension of transpiration under unfavorable environmental conditions (Larcher 1995). The distribution of the pith and the xylem along the stem of frailejones is not homogenous (Fig. 1a): the pith is narrow in the base of the plant and becomes broader to the top; while the xylem becomes wider toward the base, which is the older part of the plant, as a consequence of its secondary growth via the vascular cambium (Rock 1972; Trautner 1962). A recent study (Rock, personal communication) has shown that the caulirosulan *Espeletia* exhibit a Primary Thickening Meristem (PTM) similar to those described in monocots by DeMason (1983), thus accounting for the massive amount of pith beneath the stem tip, as shown in Fig. 1b.

The pubescence or trichomes on the leaves of *Espeletia* spp. increases its temperature by 5 °C (Meinzer and Goldstein 1985) and protects the photosynthetic mesophyll of the plant from damage by excessive radiation and UV radiation during sunny days reflecting the shorter UV wavelengths of the incident radiation (Lange et al. 1981). The trichomes of the leaves also have undulations that reduce transpiration (Roth 1973). In addition, transpiration may also be reduced by the presence of areolate cavities on the lower surfaces of *Espeletia* leaves, resulting in stomatal crypts located under mesophyll units (areoles) as shown in Fig. 2 (Rock 1972).

Water is important to the physiology of plants because it participates in all physiological processes. Plants, and in particular, *Espeletia* spp. require large quantities of water in nonwoody tissues such as the stem pith, leaves, and roots, where it can comprises

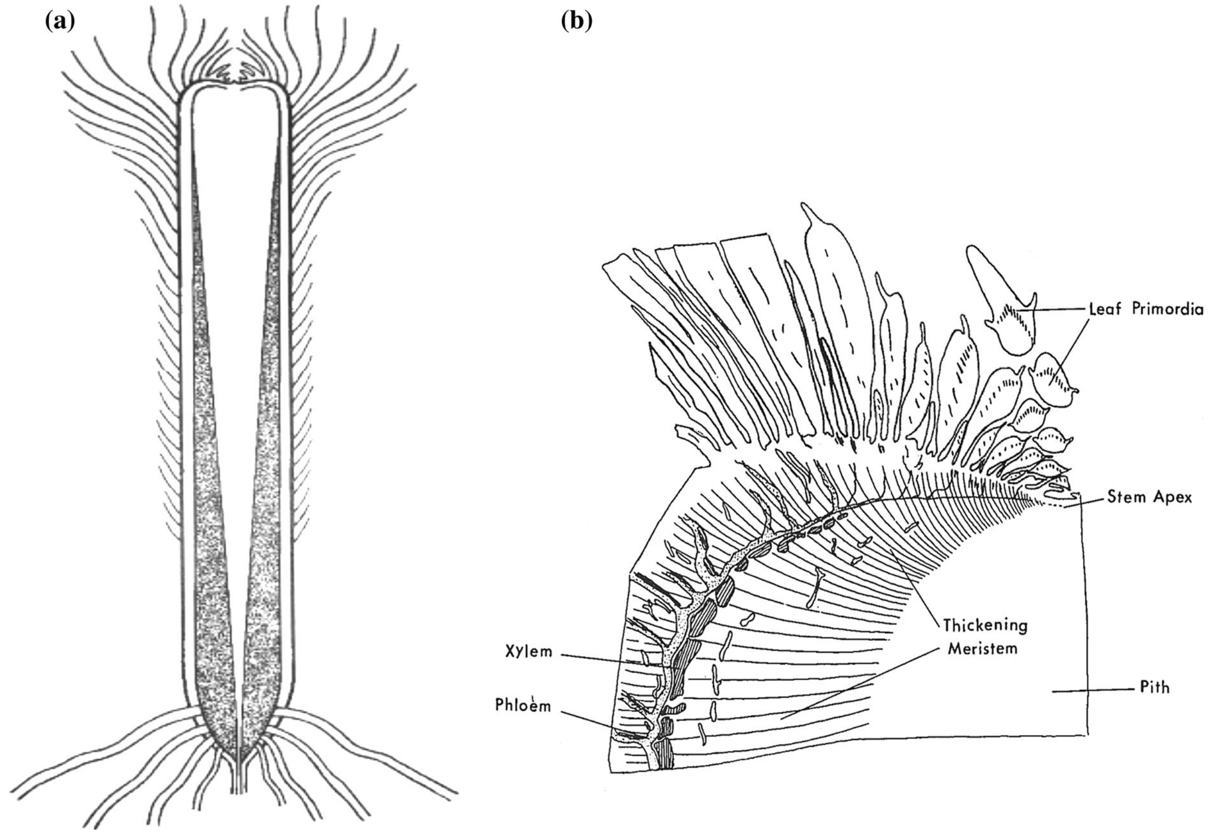

Fig. 1 **a** Longitudinal section of *Espeletia hartwegiana*, according to Weber (1963). Taken from Mora-Osejo (2001); **b** Sketch through the longitudinal stem tip of *E. schultzii,* showing the Thickening Meristem and formation of the massive pith, characterizing the megaphytic growth form typical of the genus

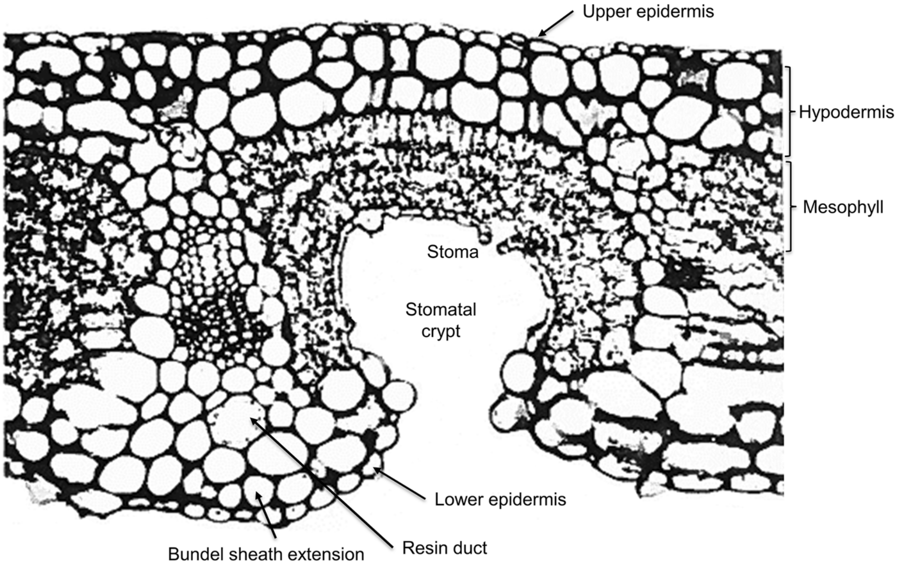

Fig. 2 A cross section of a typical mature *Espeletia* leaf, showing the upper epidermis, a multilayered hypodermis, mesophyll, a resin duct in a bundle sheath extension, a stomatal crypt, and an open stoma. ×100. (Rock 1972)

between 70 and 95% of the biomass (Lambers et al. 2008). Transpiration is an inevitable consequence of photosynthesis, but it also has important effects on the leaf's energy balance, since as water evaporates from mesophyll cell surfaces, it cools the leaf. Without this mechanism, the temperature of leaves could rise to lethal levels (Lambers et al. 2008). In most species of *Espeletia*, including the megaphytic species, the top of the leaves consists of a single layer of upper epidermis and one or more layers of hypodermal cells which function as water storage as shown in Fig. 2 (Rock 1972).

Although there seems to be some understanding about the physiology of *Espeletia*, most of these studies have focused on describing morphologic issues, but few studies explain the relationship between the particular anatomy features of frailejones and their physiological functioning. In this research, we hypothesized that those features are the result of coevolution of these plants under limiting environmental conditions, particularly with respect to the low soil water availability and low air temperatures. Accordingly, we expected to find low transpiration rates in frailejones and high water-use efficiency. Given the importance of understand the functioning of *Espeletia*, and the magnitude of water flow inside the plant resulting from transpiration, our research addresses two main questions. (i) How do anatomical modifications of *Espeletia* affect its physiological functioning? (ii) To what extent does this functioning contribute to the overall hydrology of páramo ecosystems? To answer these questions, we have pursued a comprehensive study of the physiognomy, physiology, and the ecohydrologic relationships between *Espeletia* and the particular meteorologic conditions of the páramos, and its contribution of overall hydrologic functioning of páramo ecosystems.

Methodology

Study sites

The research was carried out in two páramos of Colombia: Romerales (04°40′52.8N, 75°24′52.1W) and páramo of Belmira (06°39′44.6N, 75°40′27.0W), both located on the Central Andean Range in Colombia. The specific climate conditions of these ecosystems are presented in Table 1. The species of studied frailejón were *E. hartwegiana* in Romerales, and *E. occidentalis* in Belmira.

In both páramos, we installed meteorologic stations (Davis® and Campbell Sci® weather station), to measure precipitation, temperature, relative humidity, solar irradiance, wind speed, and direction at 15 min intervals. We also installed soil stations to measure soil moisture and temperature (Decagon®) at four depths in the soil profile in Belmira: 5, 15, 25 and 35 cm, since soils are shallow. These measurements were carried out for 2 years (2014–2016).

Growth of *Espeletia* spp.: allometric relationships, ages, and mean growth rates.

The inner distribution of tissues in frailejón stems is important; not knowing this relationship may lead to errors in the sapflow measurement, since there is a risk of inserting needles in a different area of the xylem. Therefore, for a better understanding of the inner distribution of xylem of frailejones based on the observations of Weber (1963), cited by Mora-Osejo (2001), we used the principle of allometric growth, in which the relative growth of a part of one organism is proportional to the relative growth of the whole organism or any of its parts (Gayon 2000); meaning $\left(\frac{1}{y}\right)\frac{\partial y}{\partial t} = k\left(\frac{1}{x}\right)\frac{\partial x}{\partial t}$, which results in the allometric function $y = cx^K$, where y is the biologic variable to be estimated, as a function of the variable x with a scaling k, and with the constant c (integration constant) which is characteristic of the given organism (Huxley 1932; Thompson 1917).

We sampled and measured the pith diameter and the widths of xylem at different heights at intervals of 10 cm approximately, on six individuals in each páramo, using an increment borer of 5 mm diameter. In the páramo of Romerales, we made 43 measurements, between the base of the plants and 200 cm, while in Belmira we made 42 measurements between 0 and 125 cm of plant height. The data were adjusted to the allometric equation by regression to estimate parameters c and k. To meet the statistical assumptions of heteroscedasticity, with no autocorrelation and normality, the expression $y = cx^K$ was linearized. The resulting equation $\ln(y) = \ln(c) + k * \ln(x)$, satisfy the above statistical assumptions. Nevertheless, when the original model is recovered using antilogarithms, a bias is induced. To correct this bias, we used the mean square error (MSE) suggested by Zapata et al. (2001).

Table 1 Average climatic conditions measured on the study sites

Páramo	Altitudinal range (masl)	Temperature (°C)	Relative air humidity (%)	Solar irradiance (W m^{-2})	Wind speed (m s^{-1})	Annual precipitation (mm)
Belmira	3050–3200	10	92	328	3	1478
Romerales	3600–4200	5	91	257	4	970

After this correction, the new equation is $\ln(y) = \ln(c) + 0.5 * \mathrm{CME} + k * \ln(x)$.

To determine the age of *Espeletia*, and based on the available budget, we sampled three individuals of different heights, assuming that they have different ages, according to their heights [65 (R1), 105 (R2), and 210 cm (R3)]. Samples (of about 40 mg) were taken from the inner part of the stem base of selected plants, by means of an increment borer, taking special care to sample only the oldest wood, next to the pith. However, with the taller plant (R3), we had an ambiguous result, so we used a second adjacent sample (R3') to determine the real age (del Valle et al. 2014). Samples were analyzed in the International Chemical Analysis Inc. laboratory at Miami (Florida, USA), through the AMS radiocarbon analysis, by which the age of each individual was determined, using the software CaliBomb and the postnuclear bomb peak radiocarbon content curve in North Hemisphere Zone 2 (NHZ2) (Reimer et al. 2004).

Temperatures of the plants and leaves

We made measurements of leaves temperature in nine individuals in each páramo, classified into three height categories: tall (over 120 cm), medium (61–120 cm), and low (0–60 cm). In each individual, we measured the temperatures on three leaves, at both sides of the leaves, separated in three groups according to its position in the rosette: one apical, one adult, and one senescent leaf. Measurements were made continuously for 2 days, using type T thermocouples, connected to a CR100 data logger to record data every 15 min. Since the weather conditions in páramos are highly variable, during the measurement days, we had plenty of sunshine, fog, and low clouds' presence and drizzle, which are common on these ecosystems; considering that our interest is to model leaf temperature as a function of meteorologic variables, the data were good enough to get a satisfactory fit.

In order to relate the measured values of leaf temperature with meteorologic variables measured in a nearby weather station, we used a linear model with two indicator variables: height of the plant and position of the leaves in the rosette. With the dataset and using principal component analysis, we ran a linear regression using the IBM_SPSS® statistical software, testing the criteria of normality, no collinearity, additivity, and homogeneity of variance, with a significance level of $p > 0.05$.

The main purpose of these measurements and modeling was to compare temperatures and vapor saturation pressures between frailejón leaves and the surrounding air, at different times of the day and night; hence, we also estimated this variable using the Clausius–Clapeyron equation.

Sapflow measurements

Transpiration rates in *E. occidentalis* and *E. hartwegiana* were measured applying the Heat Ratio Method (HRM) (Burgess et al. 2001), with adaptations to the specific morphologic conditions of *Espeletia* in relation to the standard measure of sapflow in woody species. Based on the results from the prior study of the physiological characteristics of these plants, sensor's length was reduced to 1.2 cm. We installed one sapflow station in each páramo. Every station had eight sensors located in four plants (two sensors in each plant), connected to a CR1000 data logger (Campbell Sci®). Although the conventional method recommends measurements at different depths of transverse axis of xylem, in order to determine the differential speeds of sap inside it, in this study, we measured the average flow, since the xylem is too narrow to allow inserting more than one thermocouple inside it.

Sapflow measurements were made for over six months in each site, but data were discontinuous since environmental conditions of low temperature and high humidity affected the batteries and cables.

Nevertheless, we confirmed that observed behavior of sapflow in frailejones was consistent during the wet and dry seasons (2016). Results shown here are of some sunny days, when the vegetation is more active, and the transpiration and sapflow rates are higher. To verify the sap velocities, during those days, we collected all data in every measurement,—140 temperature data, one every second, instead of averages.

Results

Allometric internal relations

The total diameter of stem and the width of bark have an insignificant relationship with height. On the contrary, the diameter of pith and the width of xylem show a clear dependence with height of stem in both species studied (Fig. 3a, b). Table 2 shows the equations.

Ages and mean growth rates of *E. hartwegiana*

The samples for dating were taken in February 5, 2016 (considered as 2015.5). Table 3 shows the ages of *E. hartwegiana* individuals, including the R3' sample, dated to determine the real germination year of the taller plant. The smaller and younger individual has a growth rate in height of 5.9 cm year^{-1}, while the intermediate and the tallest individuals have similar ages but very different growth rates in height (varying between 3.8 and 6.9 cm year^{-1}, respectively). Meanwhile, the stem diameter at the base seems to grow unrelated to height at the rate between 0.24 and 0.49 cm year^{-1}.

Temperatures of the air, leaves, and soils

There is no significant difference between mean temperatures measured in the bundle and undersides of leaves. According to the data, the temperature on the underside of leaves is a function of air temperature,

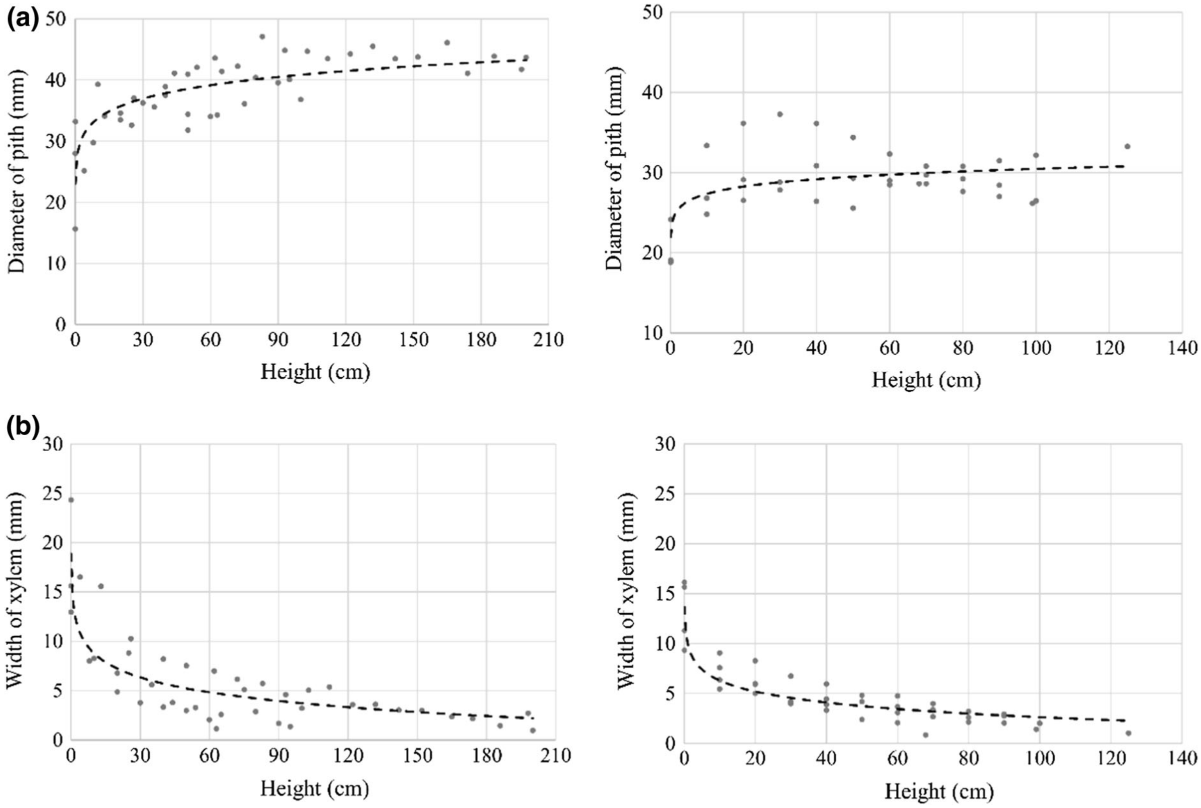

Fig. 3 Relationship between frailejones: **a** height (cm) and the diameter of pith (mm); **b** height and the width of xylem (mm) in *E. hartwegiana* (left) and *E. occidentalis* (right)

Table 2 Allometric models of height (cm) with diameter of pith (mm) and with the width of xylem to *E. hartwegiana* and *E. occidentalis*

Relationship	Species	Model	R^2
Height (cm)—diameter of pith (mm)	*E. hartwegiana*	$y = 28.127\times^{0.083}$	0.521
	E. occidentalis	$y = 24.701\times^{0.047}$	0.336
Height (cm)—width of xylem (mm)	*E. hartwegiana*	$y = 14.694\times^{-0.29}$	0.596
	E. occidentalis	$y = 9.96\times^{-0.259}$	0.740

Table 3 Ages determined by ^{14}C of three *E. hartwegiana* and their mean growth rates

Sample	R1	R2	R3	R3′
Height to the base of the rosette (cm)	65	105	210	210
Diameter in the base of stem (cm)	5.37	6.74	9.14	9.14
F14C ± SD	1.0731 ± 0.0025	1.1903 ± 0.0035	1.211 ± 0.0035	1.1872 ± 0.0035
Estimated year of wood formation, calibrated (^{14}C)	2004.05	1987.12	1985.02	1987.3
Age (years)	11	28	30	28
Mean rate of growth in height *h*/age (cm year^{-1})	5.9	3.8	6.9	
Mean rate of growth in diameter *d*/age (cm year^{-1})	0.49	0.24	0.30	

relative humidity of atmosphere, wind speed, solar radiation, and the indicator variable apical leaves (IV_L: 0.1). The other indicator variables (middle leaves and height of plant) were not significant to the model. Based on observations and field data, we established that apical leaves are 20% of total leaves.

Figure 4 shows the soil temperature at four depths (Fig. 4a), the temperatures of the air and the frailejón leaves (Fig. 4b), and the soil moisture at four depths (Fig. 4c) in páramo of Belmira, for the period between March 23 and April 14, 2016.

Soil temperature has diurnal fluctuations similar to air temperature in the superficial portion, but the fluctuations are smaller at greater soil depths (Fig. 4a). Air temperature has the biggest daily fluctuation, after the leaves underside, with a mean amplitude of 8 °C (Table 4), but its behavior is similar to that measured inside the frailejones (Fig. 4b).

The records of soil moisture show that even in dry periods, the deeper layers remain close to saturation, while the superficial ones, with bigger temporal variations, never had volumetric moisture contents below 0.5 (m^3 m^{-3}) during the period studied (Fig. 4c). Likewise, the minimum temperature in soil, at any depth, stayed over 12 °C (Fig. 4a).

In addition, measurements of temperature below and inside the mid vein of mature leaves and inside the marcescent leaves of the same plant show that temperature fluctuations in marcescent leaves are lower than those inside the plant stem (Fig. 5).

The temperatures and vapor saturation pressures of leaves and the surrounding air show no significant differences between them. At night, the temperature of the leaves remains a little higher than air temperature.

Transpiration of *E. occidentalis* and *E. hartwegiana*

Sapflow measurements in frailejones show that transpiration of these plants is a discontinuous process during the day. Among the factors controlling transpiration or sapflow in frailejones, are temperature and solar irradiance, so these plants respond quickly to these environmental factors, taking into account the rapidly changing conditions of these factors in studied páramos, mostly related to the presence of fog or low clouds. Actually, a linear model evaluating the statistical assumptions mentioned previously with a significance level of $p > 0.05$, shows that temperature, solar irradiance, and the relative humidity explain

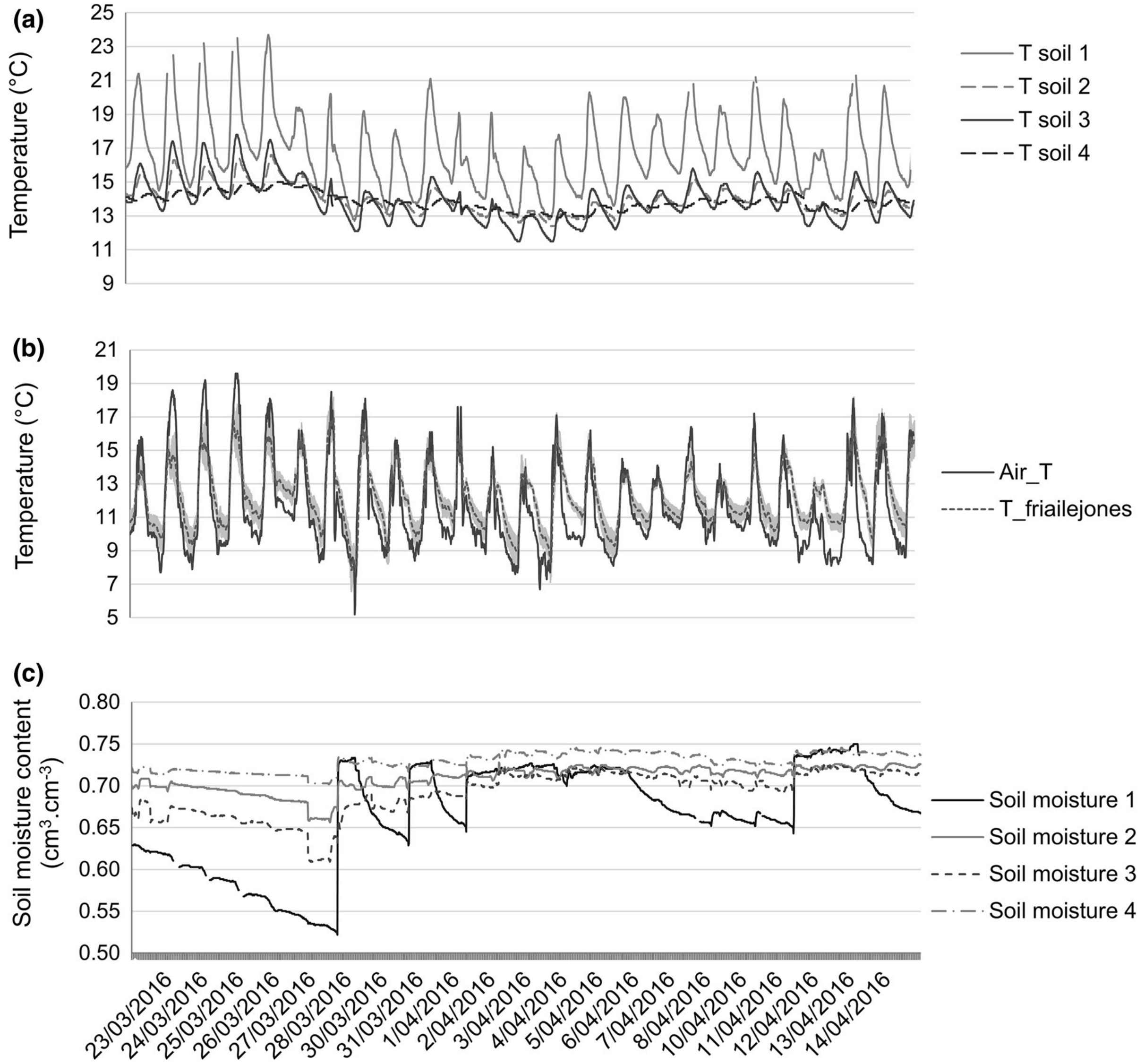

Fig. 4 Soil temperature (°C) at different depths (**a**), temperatures (°C) of air and inside the frailejones (**b**), and soil moisture contents at different depths (**c**), measured during March–April 2016

Table 4 Maximum, minimum, and mean temperature amplitudes of the diurnal fluctuation measured at different soil depths, inside the frailejones, on the undersides of frailejones leaves, inside the marcescent leaves, and in the air in the páramo of Belmira

Temperature in °C	Air	Leaves underside	Marcescent leaves	Frailejón inside	Soil at 5 cm	Soil at 15 cm	Soil at 35 cm
Mean diurnal fluctuation	7.9	11.5	2.9	5.1	5.7	1.2	0.52
Maximum	19.6	22.0	13.7	17.0	23.7	16.6	15.00
Minimum	5.20	10.5	10.8	7.9	12.7	12.4	12.80

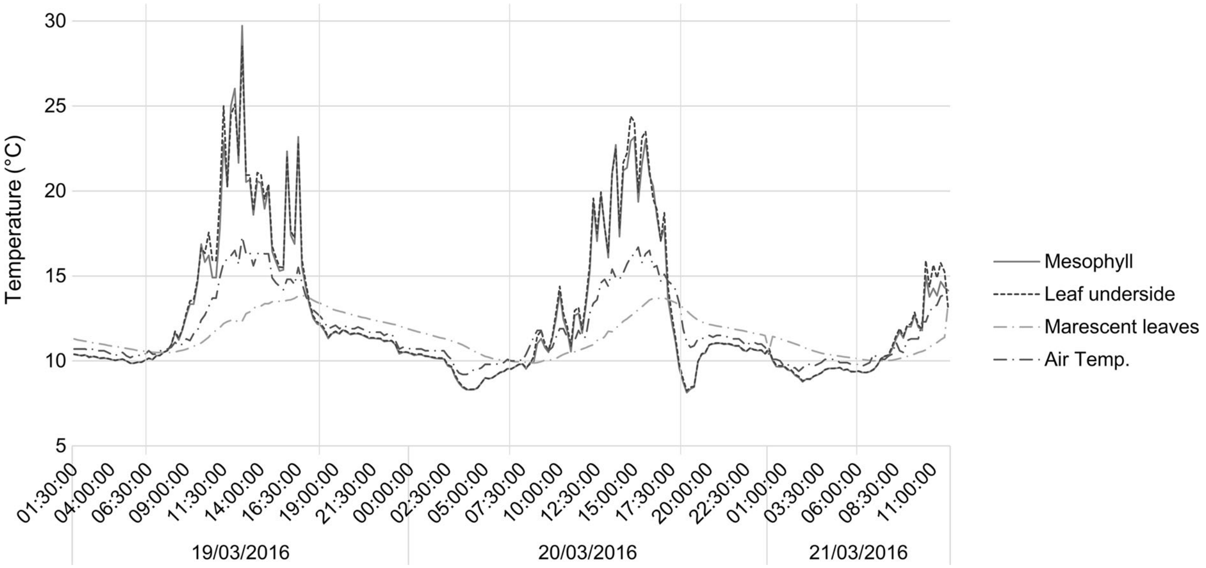

Fig. 5 Air temperature and the temperatures underside the leaves, in the mesophyll, and in the marcescent leaves of frailejones, measured during 2.5 sunny days in March 2016. The vertical lines indicate the time of sunrise (6:30) and sunset (18:00)

76% of sap velocity variation measured at 1.2 cm depth in the plant, $R^2 = 0.765$.

For sunny days, even though the environmental stimulus is the same, sapflow, i.e., transpiration, tends to decrease, and sometimes it reaches zero. On the other hand, results showed that these plants also move water during the night (Fig. 6).

According to the findings, during a sunny day (24 h), a mature individual of *Espeletia* transpires around 1 L of water. Extrapolating the sapflow velocity into water sheet for the entire watershed, it is estimated that the outputs of water through transpiration of *Espeletia* in a dry, sunny season, represent about 21% of outputs via basin discharge, in an ecosystem with 60% water yield.

Discussion

The anatomical adaptations of *Espeletia* to adverse environmental conditions of the páramos, where this genus evolved, occurred not only in its external structure but also internally: the pith thickens increases toward the top of the plant, due to primary thickening meristem. The two species of *Espeletia* studied show a clear allometric relationship between pith diameter and xylem width with plant height, as proposed by Weber (1963), cited by Mora-Osejo (2001). Frailejones possess primary thickening meristems (PTMs, see Fig. 1) similar to those found in megaphytic monocots (DeMason 1983). These thickening meristems occur just beneath the stem apical meristem, accounting for the massive pith tissue, located adjacent to the mature leaves of the rosette, where water is in large demand. Moreover, under adverse weather conditions, this supply of water remains for several hours until the water uptake from the soil is restored, thus preventing wilting. Although, in plants of the same species and height, measurements could have some differences, related to environmental factors or external causes, affecting the fit of models; these results are very important for estimating the sapflow, since this equation allows one to estimate the width of the conductive tissue where the sensors are installed, without the need of boring the plant.

Temperature of leaves was measured in order to test the hypothesis that a small warming of the leaf surface is enough to increase the water vapor pressure gradient, after which transpiration occurs (Larcher 1995), as an adaptation mechanism to move water and minerals in plants under humid and cold environments as páramos. However, when we relate the temperatures and water vapor pressures with other meteorologic variables and with the sapflow velocities in

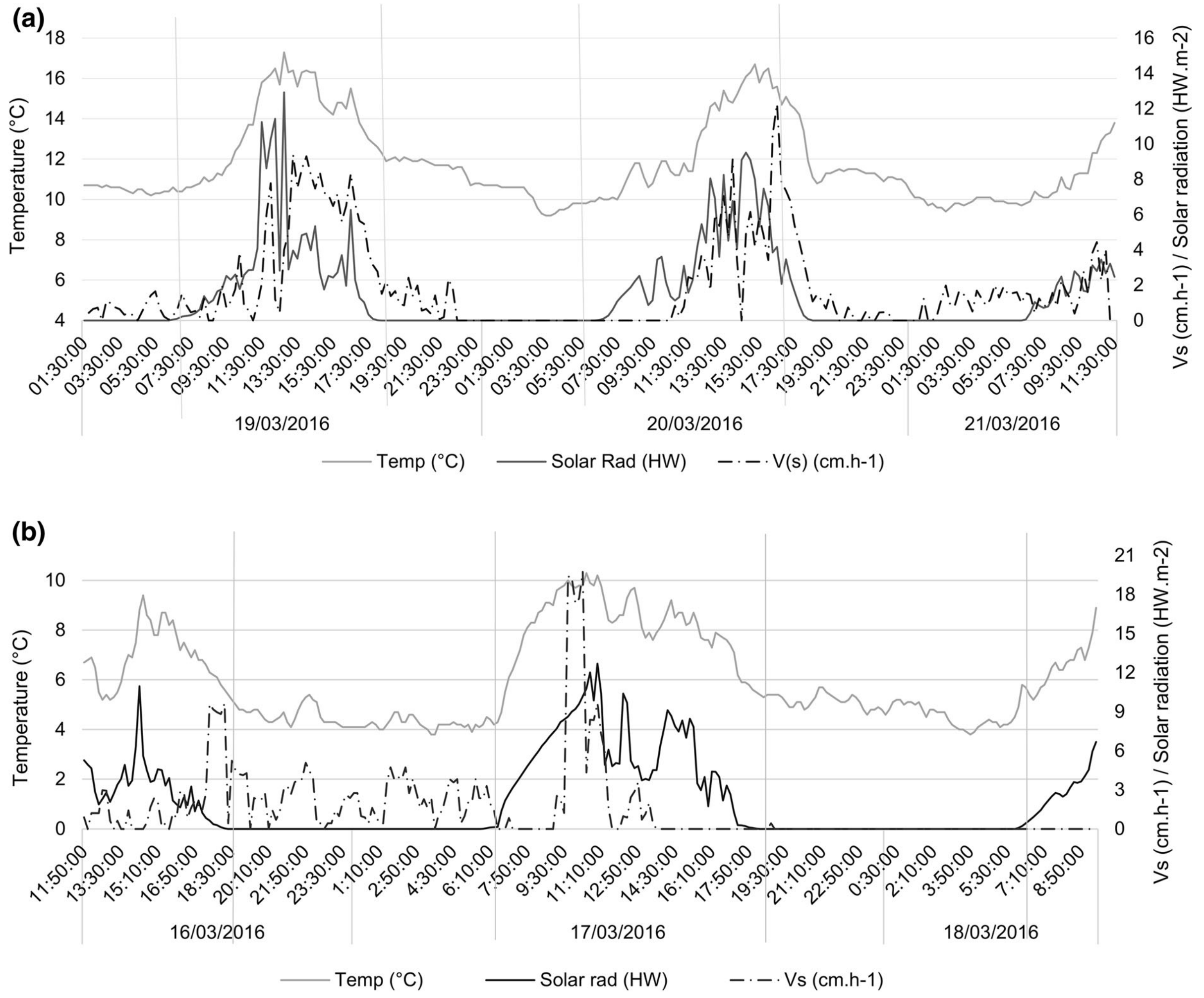

Fig. 6 Relationship between temperature (°C), solar irradiance (HWatts m^{-2}), and sapflow velocity (cm h^{-1}) measured during 2.5 sunny days in the páramo of Belmira (**a**) and 2 days in Romerales (**b**). The vertical lines indicate the times of sunrise (at 6:30 in Belmira, 6:00 in Romerales) and sunset (at 18:00 in both sites)

frailejones, there are no significant correlations, either instantaneous or lagged.

On the other hand, keeping in mind that water moves through plant following a gradient, either of hydric potential, or of water vapor concentration (Lambers et al. 2008), we verify that in the continuous soil–plant atmosphere in the páramo, neither the soil temperature nor the soil moisture content limits the water movement through the plant tissues, since the páramo of Belmira no longer presents temperatures near the freezing point, both in the atmosphere and in the soil; therefore, the plants are no longer subject to water stress generated by the cold and wet conditions preexisting in páramos when this genus developed some of the described adaptive features (Azócar and Rada 2007; Rada et al. 1985; Ramsay 2014; Squeo et al. 1991). However, *Espeletia* retains these functional features, fixed by natural selection during evolution and adaptation to the normal specific climatic conditions of páramos (cold and wet). Therefore, the movement of water through *Espeletia* is mainly determined by local weather conditions. We also verify the effect of thermal insulation of marcescent leaves in frailejones, reported as one of the adaptation mechanisms of these plants to face the low environmental temperatures (Azocar and Rada 1993; García-Varela and Rada 2003; Meinzer and Goldstein 1985; Rada et al. 1985). With regard to leaf temperatures compared to air temperature, our results are similar to those reported by Mora-Osejo (2001) for *E. grandiflora*: similar temperatures at night and the early hours at morning, but show wide differences during the day, due to the high solar irradiance received by leaves. The anatomical modifications exhibited by the succulent leaves typical of frailejones (water-storage cells in the multiple hypodermal layers adjacent to the palisade cells of the mesophyll, distinctive stomatal crypts, and heavy, undulating layers of trichomes; see Fig. 2) may be in response to such variations in high solar irradiance exposure to the leaves.

Given the constraints in the páramos for the growth and development of frailejones, it has been assumed that their growth rates are extremely low, on the order of 1 cm year^{-1} (Azócar and Rada 2007), so the medium or large plants were considered as centenarians. A review of 15 studies on the current growth rates in height of *Espeletia* presents variations ranging from 0.2 to 14.8 cm year^{-1} (Ramsay 2014). So far, the estimation of age in frailejones has been based on two facts: (i) calculating the current periodical growth rates of height (h) between two consecutive measurements ($[h_2 - h_1]/[t_2 - t_1]$), where t_1 and t_2 are the dates of the measurements (ii) and the assumption that taller frailejones are always older than those of lower height. In relation to fact (i), current growth rates are different from mean growth rates (h/age). The uses of these small current growths of taller frailejones, as mean growths, tend to greatly overestimate the ages of frailejones. The ontogenetic growths of height are usually sigmoid-shaped curves, when this curve of a given individual plant approaches its maximum height, current growth tends to zero. The only way to calculate the mean growth of any organism is to find its age. For wild trees and shrubs with secondary growth, there are two methods to determine the age: annual growth rings and radiocarbon. Trautner (1962) found annual growth rings in *E. neriifolia* in a seasonally dry páramo from Venezuela. However, we found no growth rings in our species, perhaps due to the absence of a dry season in the páramos studied. The so-named “bomb effect” on the radiocarbon content of the CO_2 in the atmosphere is a potent biogeochemistry tracer allowing dating with high precision organic materials produced since 1954 to the present (Reimer et al. 2004; del Valle et al. 2014). The use of this method allows us to determine for the first time the ages and mean growth rates of three frailejones (*E. hartwegiana*).

So far, all the estimates of the age of frailejones have been based on the false assumption that taller plants are older, but size (as height and diameter in *Espeletia*) are poor predictors of age in all organisms as shown in Table 3 in which two of the samples have similar age but almost have 100% difference in height, although they were growing in the same páramo and under the same conditions. Despite the low number of *Espeletia* dated, we obtained mean height growth rates between 3.8 and 6.9 cm year^{-1}, which agree with that found in Venezuelan páramos (Sarmiento et al. 2003). Radiocarbon emerges as an accurate, fast, and cost-effective method to determine the age of the species of *Espeletia* without annual growth rings.

According to the environmental conditions of the habitat of frailejones, their low growth rate, we choose the HRM to estimate their transpiration, since it works well when the flow is low or close to zero (Bleby et al. 2004). Transpiration rates measured in the two *Espeletia* species using HRM indicate that sapflow during the day is highly influenced by solar irradiance and temperature, since soil moisture is not a limiting factor. However, it is interesting to see that periods of sapflow are discontinuous, opposite to what happens in trees, whose transpiration is continued while the environmental conditions are at nonlimiting levels. It appears that species of *Espeletia* are adapted to respond very fast to environmental stimuli—which might be related to the high photosynthetic capacity reported by Goldstein et al. (1994)—necessary in tropical high mountain ecosystems where unexpected changes caused by variations in radiation and fog presence lead to short duration of stomata opening, which impacts on the momentary intensities in transpiration and conductance (Lösch and Schulze 1995, cited by Mora-Osejo 2001). However, there seems to be a contradiction between high potential for photosynthetic capacity and the low sapflow and low mean height growth rates found in this study for *Espeletia* spp., especially if we consider that those plants have a high proportion of water in their tissues. Perhaps the measurements by Goldstein et al. (1994) were made when there was high photosynthetic activity, which, however, is not the situation usually experienced by these tropical high mountain ecosystems. On the other hand, frailejones seem to reach a level at which the sapflow is reduced or completely stopped, maybe as a mechanism of protection against the strong irradiance, as suggested by their leaf anatomy. Small quantities of sapflow also occurs discontinuously during the night, which matched the reports of high nightly respiration in these plants (Azocar and Rada 1993).

One of the more common explanations to the loss of water from leaves to atmosphere at night is the water vapor pressure differential (Becker 1998; Benyon 1999; Hogg and Hurdle 1997; Snyder et al. 2003); but in this study, we established that there is no significant difference in water vapor pressures among the leaves of frailejones and the surrounding atmosphere, which makes sense in an ecosystem with high air humidity and soil moisture content. The more likely explanation to this nightly water flow is related to the inner reservoirs in the pith and the leaf hypodermal layers, since they provide water to transpiration during the day, but must be refilled at night, because hydric relationships in trees are determined, in part, by the availability of inner reservoirs for transpiration (Zweifel and Häsler 2001). Moreover, it has been shown for several species that the static flow assumption in plants is not true (Snyder et al. 2003) and that the only possible explanation to the time lags between water loss by leaves transpiration and water uptake by roots is the inner water storage (Goldstein et al. 1998; Schulze et al. 1985; Steppe et al. 2006). In short, the amount of water leaving the páramos through transpiration of frailejones is very low, which helps to maintain the high water yield in these ecosystems: the high photosynthetic efficiency of frailejones influences a rapid response to appropriate environmental stimuli to its physiological functioning, but they also seem to have self-regulatory mechanisms that stop sapflow, even when stimuli, such as solar irradiance and temperature, remain. It does not mean the plants stop their physiological functions; instead, they are functioning continuously, by using their water storages. Consequently, the nightly sapflow observed in *Espeletia*, might indicate the refilling of water in the pith and leaf hypodermal water-storage layers, the main water reservoirs of *Espeletia*.

Although the specific morphologic and physiological adaptations of *Espeletia* spp. were successfully demonstrated in the past, it is possible that temperature increases in tropical high mountains due to climate change (Greenpeace 2009; Buytaert et al. 2014; IDEAM 2017) would promote the climb of species from the cloud forests (Ramirez et al. 2009; Larsen et al. 2012; Llambí et al. 2014), which have fast growth rates and regeneration strategies better adapted, to new environmental conditions (Ramirez et al. 2009; Larsen et al. 2012; Llambí et al. 2014). Under this new scenario, it can be expected that páramo vegetation will ascend as far as the environmental conditions allow them to do so (Greenpeace 2009; Anderson et al. 2012; Larsen et al. 2012); however, if the páramo is located on the top of the mountain, the consequence is that páramo vegetation will tend to disappear (Greenpeace 2009; Gonzáles and Mason 2010; Anderson et al. 2012); such is the case experienced in the páramo of Belmira.

Conclusion

According to our findings, height of frailejones is a poor predictor of the individual's age, but radiocarbon method is useful to determine the ages and growth rates of the species of *Espeletia* without annual growth rings. We also found that *Espeletia* individuals apparently are not under water stress, at least in the páramos at lower altitude, such as Belmira. Sapflow measurements in *Espeletia* showed that episodic water movement and nightly flow might indicate the refilling of water in the pith and leaf hypodermal water-storage layers—the main water reservoirs of the plant—but also that the amount of water leaving the páramos through transpiration of frailejones is very low, which helps to maintain the high water yield in these ecosystems.

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