Influence of rainfall interception by endemic plants versus short cycle crops on water infiltration in high altitude ecosystems of Ecuador

J. L. Janeau, S. Grellier and P. Podwojewski

ABSTRACT

Owing to their high water retention, the volcanic ash-soils of the Northern Andean highlands (páramos) can be considered as natural 'water storage tanks' for drinking water and for irrigation. Vegetation plays an important role in transferring rain to the soil and in controlling the soil water content. To assess this role, we quantified the stemflow process under rainfall simulations for seven of the main plants along an altitude gradient on the Pichincha volcano in Ecuador. The volume of water transferred into the soil was higher at the lower rainfall intensity than at the higher intensity. The results were compared to the stemflow measured with potato and maize crops growing in the lower altitude range. The results showed that the relative volume of stemflow increased with altitude from 8% in the crop area to 58% in the upper part of the catena. Low values of stemflow were associated with potatoes and maize annual short-cycle crops while high values were associated with the natural vegetation. For cultivated crops rainwater interception by stemflow delayed the soil surface crusting and runoff process. This study shows that rainwater interception by vegetation is of great importance for soil water recharge in these Andisols.

Key words | Ecuador, infiltration, páramo, rainfall simulation, stemflow, water reservoir

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INTRODUCTION

The hydrological role of mountains as water sources and storage reservoirs is crucial for human populations (Messerli & Ives 1997). Viviroli *et al.* (2011) showed that land use and vegetal cover in mountainous areas have a direct impact on the quantity of the water stored in the soil. A part of the rain intercepted by the vegetation enters the soil through stemflow processes, which describes the portion of precipitation that is intercepted by the canopy and transferred to the soil by flowing down the stems. As mentioned in the reviews of Crockford & Richardson (2000), Levia & Frost (2003), Muzylo *et al.* (2009), and more recently Wang *et al.* (2011), stemflow processes have previously been studied in a range of different ecosystems from arid areas to rain forests and at different scales. However at present, no data exist for high altitude ecosystems.

In the Northern and Central Andes (Colombia, Ecuador), highland vegetal ecosystems such as the páramo are considered as the water tanks of the Andean valleys (Buytaert *et al.* 2006a, 2011; Crespo *et al.* 2011). The high water retention capacity of volcanic ash-soil ($>500\ \mathrm{g\ kg^{-1}}$ at $-1{,}500$ kPa), associated with a specific and complete soil vegetal cover (Poulenard *et al.* 2002; Roa-Garcia *et al.* 2011) confer upon these ecosystems an important role in water availability and regulation for the population of the Northern and Central Andes (Luteyn 1992; Buytaert & De Bievre 2012). Rainwater is stored in soils during the rainy seasons and progressively released during the dry seasons (Hofstede 1995; Pourrut 1995). However, the hydrological function of the different patterns of vegetation and soils in these highlands, especially in volcanic areas, is for the most part unknown. One important function of this vegetation is to catch low energy rain, drizzle, and fog moisture on leaves. This process concentrates small amounts of water and transmits it directly to the roots

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through stemflow, thereby reducing dripping and evaporation at leaf surface (Quinn & Laflen 1983; Crockford & Richardson 2000; Foot & Morgan 2005).

In northern Ecuador, vegetation and soil types vary with altitude (Jørgensen & Ulloa 1994). Although previous studies on the hydrodynamics of soil permeability exist (Poulenard *et al.* 2001; Buytaert *et al.* 2005), the role of vegetation in controlling water resources in these systems is still unknown.

The páramo contains between 3,000 and 4,000 species of vascular plants, of which ca. 60% are endemic (Jørgensen *et al.* 1992; Luteyn 1999; Young *et al.* 2002). The vegetation of the páramo can be divided into three belts (Cuatrecasas 1968; Sklenar & Jørgensen 1999; Buytaert *et al.* 2002):

- The super-páramo with shrub and cushion-form plants at high altitudes ranging between 4,200 and 4,800 meters above sea level (m.a.s.l).
- The grass páramo or 'pajonal' (3,800–4,200 m) has an open type vegetation dominated by bunchgrasses (tussocks).
- The sub-páramo (3,200–3,800 m) is a transitional zone of shrubs and grassland between the upper part of the páramo and the Andean forest. Smallholders looking for new land have recently started to clear this natural ecosystem to plant potatoes or maize at lower altitudes.

Detailed studies on the vegetation of each altitudinal stratum in the Andean highlands can be found in van der Hammen (1968), Veneklaas & Van Ek (1990), and Sklenar & Jørgensen (1999). Poulenard *et al.* (2001) hypothesized that in the Pichincha volcano the vegetal cover of the three páramo strata induced high soil water infiltration rates higher than 60 mm h^{-1}, providing a strong protection against erosion. The vegetal cover was also responsible for very high moisture in the soil during the whole year thereby controlling the infiltration rate (Poulenard *et al.* 2001, 2002). We tested this hypothesis and present the results of a stemflow study using an original method (rainfall simulation associated with an experimental collector) in the proper- and sub-páramo natural areas. Neither of the experimental sites were subject to grazing or fire. The rainfall simulations were repeated under two types of rain which are representative of the study area. The experiment tested the stemflow of herbaceous tussocks and six individual shrub plant species in their natural environment and compared the results with the two most cultivated plants in the Andes: potato and maize in tilled fields located at lower altitude in the sub-páramo ecosystem.

The objectives of the study were: (i) to quantify the amount of rainwater that was intercepted and captured by these plants and transferred to the soil through stemflow; and (ii) to connect the stemflow values of each studied plant to its ecological context.

MATERIALS AND METHODS

Study site

The study was conducted in the Rumihurcu watershed (0°24′59″N–78°35′56″W), located along the eastern slope of the Pinchincha volcano that dominates at 4,784 m.a.s.l. of altitude the city of Quito, Ecuador (Figure 1). The climate of the páramo is a high altitude tropical climate (Perrin *et al.* 2001). It is cold with an average temperature of 9 °C at 3,600 m. Mean daily temperature is constant through the year but daily amplitude is very high with night temperatures that can be close to 0 °C. The temperature regime is cryic

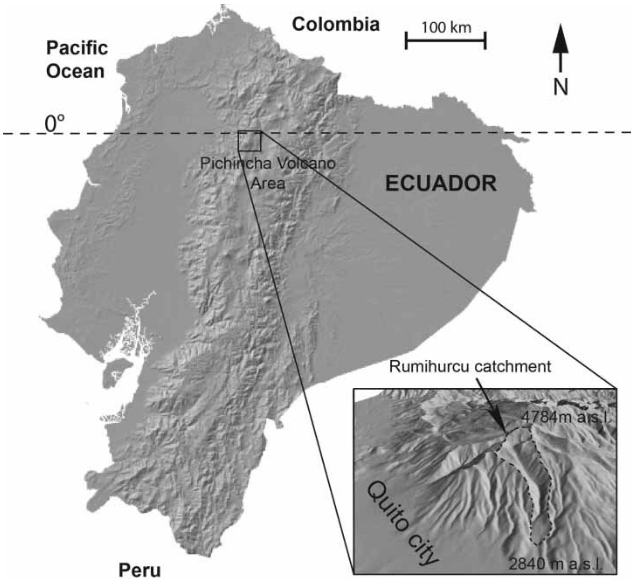

Figure 1 | Location of the study area, Rumihurcu catchment, Pinchincha Volcano, Ecuador.

isofrigid above 4,000 m and isomesic below 4,000 m (Soil Survey Staff 1999).

According to all rainfall data recorded in the area of Quito over the last 100 years and collected by Instituto Nacional de Meteorología e Hidrología (INAMHI), annual precipitation over the catchment varied from about 1,100 mm to more than 1,700 mm with low seasonal variation (Bouvier *et al.* 1999). Rainfall increases with altitude within the inter-Andean valleys (Bouvier *et al.* 1999) and rainfall intensities are very low, exceptionally exceeding 40 mm per day. Frequent fogs, drizzle, and hailstorms contribute to the total precipitation amount.

The experiment was done along a representative catena comprising two areas of the páramo ecosystem (Troll 1968; Sklenar & Jørgensen 1999) from upstream to downstream with four land uses (Table 1):

- The high altitude grassland (3,800–4,200 m.a.s.l.) has an open type vegetation dominated by bunchgrasses (tussocks). Poaceaes like *Calamagrostis* sp., *Festuca* sp., *Stipa* sp., and dwarf bamboos form the pajonal which covers 70% of the soil surface (Ramsay & Oxley 1997).
- The shrub-grassland (3,200–3,800 m.a.s.l.) is a transitional zone between the lower part of the páramo and the Andean forest. The coverage of small trees and scrubs (matorral) is greater than in the páramo.
- Medium altitude grasslands (3,200–3,800 m.a.s.l.) are composed of grassland and some cultivated fields that appear as patches in the lowest part of the sub-páramo.
- Crop areas (3,200–3,800 m.a.s.l.) where smallholders looking for new virgin land have recently started to clear the natural sub-páramo ecosystem to cultivate short-cycle plant crops such as potatoes in high altitude areas and maize at lower altitude up to a maximum of 3,200 m (Huttel *et al.* 1999).

For each area we selected the tallest upright shrub species as these have a large potential to harvest rain (Ramsay & Oxley 1997). With the exception of maize, all of the plants used for this experiment had reached maturity and their aerial cover on the soil surface was estimated using the 'point quadrat' method (detailed below). In high altitude grasslands, the páramo system covered 42.1% of the studied catchment area. We measured the stemflow values of three species: one tuft (tussock) of *Stipa ichu* Ruiz & Pav. Kunth. (Poaceae), and two upright shrubs: *Lupinus pubescens* Benth. (Fabaceae) (Figure 2) and *Valeriana microphylla* Kunth. (Valerianaceae). In the shrub-grassland (matorral) system representative of 27.1% of the catchment, we selected two upright shrubs: *Baccharis polyantha* Kunth. (Asteraceae) and *Liabum nonoense* Hieron. (Asteraceae). In the medium altitude grassland (natural prairies), which occupied 6.1%

Table 1 | Ecosystem surface area and the main plant species studied in each ecosystem in the Rumihurcu catchment

Ecosystem[a]	Land use	Altitude (m.a.s.l.)	Altitude of the experiment (m.a.s.l.)	% area in the catchment	Plant species studied	Soil cover (% m^{-2})
Proper-páramo	High altitude grassland	4,200–3,800	3,960	42.1	*Stipa ichu*	59.7
					Valeriana microphylla	27
					Lupinus pubescens	31
Sub-páramo	Shrub cover: *Matorral*	3,800–3,200	3,800	27.8	*Baccharis polyantha*	15.7
					Liabum nonoense	30.5
	Medium altitude grassland	3,800–3,200	3,800	6.1	*Miconia quitensis*	17.5
					Hypericum laricifolium	6.7
	Crops	3,800–3,200	3,395	10.4	*Solanum tuberosum*	14
			3,240		*Zea mays*	33.2

[a] 7.7% of Rumihurcu lower altitude catchment (2,800 m.a.s.l.) is occupied by suburban areas and pathways (considered as very low infiltration surfaces) and 5.9% by plantation of *Eucalyptus* sp.

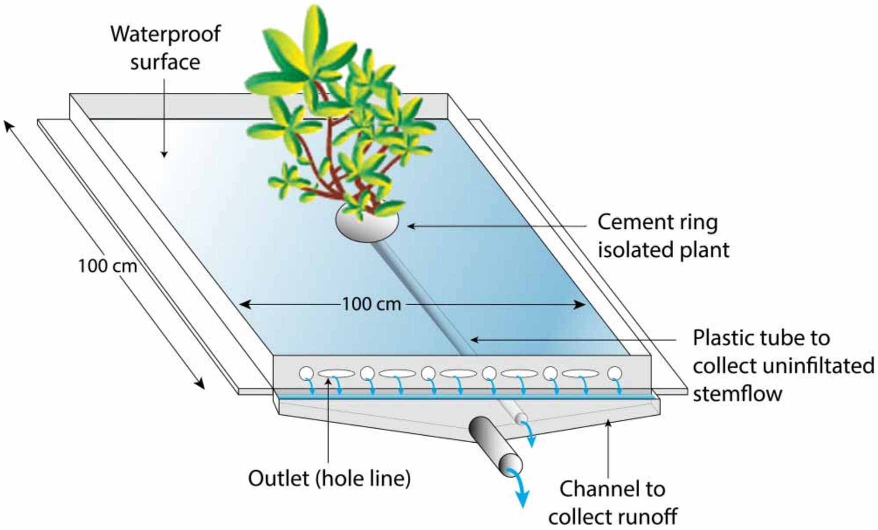

Figure 2 | Metal frame and runoff tube collectors for each 1 m^2 plot used for the rainfall simulations.

of the catchment, we studied *Miconia quitensis* Benth. (Melastomataceae) and *Hypericum laricifolium* Juss. (Hypericaceae). Finally, in the crop system, covering 10% of the catchment, maize (*Zea mays* L., Poaceae) and potato (*Solanum tuberosum* L., Solanaceae) plants were selected.

The soils are non-allophanic, vitric Andisols (Shoji *et al.* 1993; W.R.B. 2014) or Thaptic Hapludand (Soil Survey Staff 1999). The surface A horizon (0–20 cm) is a sandy loam which has an organic carbon content >120 g kg^{-1}. It has a low bulk density of 0.8 g cm^{-3}, a high total porosity; the volume of pores is estimated to be 0.65 cm^3 cm^{-3} of the soil bulk volume and the water content in the surface horizon is higher than 500 g kg^{-1} at −1,500 kPa (Poulenard *et al.* 2001). The soils developed from Holocenic volcanic andesitic ashes are more than 300 years old (Robin *et al.* 2008). The soil characteristics between 3,200 and 4,200 m.a.s.l. are relatively homogenous along the catena.

These soils exhibit water repellency properties after moderate drying (Poulenard *et al.* 2004) with the destruction of the macrostructure and the development of a water-repellent microstructure (Podwojewski *et al.* 2002). Drying processes are accelerated when soils are bare because the black color of Andisols favors the absorbance of the high solar radiation that occurs at high altitude. Therefore, the hydrodynamic behavior of these soils can be strongly modified by overgrazing, fire, and cultivation (Savage *et al.* 1972; Hofstede 1995; Poulenard *et al.* 2001; Buytaert *et al.* 2005).

Experimental procedure: rainfall simulation and point quadrat

We used a rainfall simulator (Janeau *et al.* 1999) that provides artificial rain with the same characteristics as natural rain in terms of amount, drop sizes, kinetic energy, and intensity over a 1 m^2 area reference. The simulated rainfall intensities applied in the experiment were selected considering natural rainfall intensities collected by INHAMI for approximately 100 years in the area of Quito (Bouvier *et al.* 1999) and confirmed from a four-year time series in the studied watershed (Perrin *et al.* 2001).

Two rain events of constant intensity were applied for 60 min on the 1 m^2 plot containing the plant. The rainfall simulation occurred during a relatively dry season and so the simulation was not perturbed by natural rainfall and the vegetation was completely dried prior to rainfall simulation. The first rain event had an intensity of 27 mm h^{-1} (168 J m^{-2}) and the second rain 70 mm h^{-1} (499 J m^{-2}). The second rain event was applied 24 h after the first one to allow complete dripping of intercepted rain on leaves and stem. The rain intensity of 27 mm h^{-1} corresponds to the maximum of rain intensity that is generally observed in the grass páramo at 4,000 m of altitude. This intensity also corresponds to the highest amount of long lasting rains occurring in the sub-páramo at 3,300–2,800 m of altitude (Bouvier *et al.* 1999). The higher rain intensity (70 mm h^{-1}) corresponds to the highest intensity recorded in the sub-páramo at low altitude (3,300–2,800 m). This intensity was not observed at higher altitude during the period studied by Bouvier *et al.* (1999) and recorded by INAMHI in that area (1891–1984). However, it could be considered as an extreme value for an exceptional event. Our main interest was to estimate the time and volume of rainwater necessary to give a constant level of stemflow, therefore we extended the rainfall simulation with the same intensity or a total duration of 1 h.

The soil around the indigenous plant collar is usually highly permeable because of the high numbers of macro-aggregates generated by faunal activity (Mauchamp & Janeau 1993). We observed little splash effect that limits the formation of soil crust (Mauchamp & Janeau 1993). Around each studied plant, a 1 m^2 steel frame was inserted to a depth of 10 cm in the soil. We wished to collect the water arriving at the soil surface that dripped off plant leaves (throughfall) or directly at the soil surface, therefore the interior surface of the 1 m^2 was covered with impermeable cement, forming an inclined surface. The central area around the plant base was isolated with a small cement ring, and water was collected through a plastic tube from that area (Figure 2). The plastic tube was installed to collect the stemflow that did not infiltrate into the soil. Runoff water going out of the frame was collected during 1 min periods at 2 min intervals as soon as the constant runoff rate was reached. To evaluate the amount of water arriving at the soil surface via stemflow, we calculated the difference between the simulated rainfall and the runoff water collected at the outlet of the channel collector, considering that evaporation was negligible during the rainfall simulation.

To estimate the interception surface of each plant (percentage of vegetal cover on the soil), we used the point quadrat system (pin frame). This method has been used by numerous authors and is well described by Sorrells & Glenn (1991). A point quadrat consists of a frame of long (1.3 m) 'knitting needles' which are placed every 5 cm along *X* and *Y* coordinates in the horizontal plane. The frame is set up over the vegetation and the needles are lowered down until the point of a needle touches a plant. Its height and location are then recorded.

RESULTS AND DISCUSSION

For both rain intensities, we determined the volume of stemflow (VS) expressed in percent of the total rain and the intensity of constant stemflow (ICS) (Table 2). The correlation between VS and ICS was positive (27 mm h^{-1}: $r = 0.99$, $p < 0.001$; 70 mm h^{-1}: $r = 0.96$, $p < 0.001$). We also expressed the excess of stemflow (in %) after 10 min rain related to the constant stemflow for a 60 min rain. The rainwater collected by stemflow infiltrated completely in all simulations confirming the very high hydraulic conductivity of the soil (Podwojewski & Poulenard 2006). For the different plants studied along the Pichincha volcano

Table 2 | Characteristics of stemflow for each plant species studied as function of rain intensity (27 and 70 mm h^{-1}). The two last columns represent, after 10 min, the part of stemflow in excess related to constant stemflow

Plant species studied	**VS_{10} (%)**		**VS_{60} (%)**		**ICS_{60} (mm h^{-1})**		**VS_{10}/CS_{10} (%)**	
Rainfall intensity	27 mm h^{-1}	70 mm h^{-1}	27 mm h^{-1}	70 mm h^{-1}	27 mm h^{-1}	70 mm h^{-1}	27 mm h^{-1}	70 mm h^{-1}
Stipa ichu	74.7	52.9	58.8	22.7	15.5	13.8	23.1	62.7
Valeriana microphylla	69.1	58.5	52.5	12.8	14.0	2.3	25.0	94.4
Lupinus pubescens	60.0	43.2	55.8	35.9	14.7	26.4	9.3	12.7
Baccharis polyantha	57.3	42.1	45.2	41.8	11.9	28.4	23.1	3.6
Liabum nonoense	56.9	36.3	55.7	34.6	14.8	23.9	3.6	6.1
Miconia quitensis	29.9	36.6	32.3	37.4	8.2	25.3	−2.0	1.2
Hypericum laricifolium	36.9	35.2	36.5	8.0	9.7	4.5	2.6	81.8
Solanum tuberosum	42.9	18.4	30.1	14.6	7.6	12.2	34.4	5.4
Zea mays	20.8	24.7	19.3	18.3	5.4	14.6	4.3	15.5

VS_{10}, part of stemflow (VS) for 10 min rain; VS_{60}, part of stemflow (VS) for 60 min rain; ICS_{60}, ICS for 60 min rain; VS_{10}/CS_{10}, ratio of stemflow related to constant stemflow after 10 min rain.

catena we noticed an increase of the relative VS with altitude (Figure 3) for the nine species studied with a 27 mm h^{-1} rainfall intensity and for 1 h of measurement. For low rain intensities, the cultivated plants *Z. mays* and *S. tuberosum* and the two upright shrubs *M. quitensi*, *H. laricifolium*, located in the lower part of the catena have the lowest stemflow potential (Figure 4(a)). The cumulated stemflow for 1 h rain with 27 mm h^{-1} intensity was maximal for *S. itchu*, *V. microphylla*, *B. polyantha*, *L. pubescens*, *L. nonense* which are located in the upper part of the catena (Figure 4(b)). At 70 mm h^{-1} of rainfall intensity, the water collected by the plants was still high but no significant correlation was found along the catena. Under high rain intensity, the kinetic energy and the larger drop size received by the plant, especially in the páramo area, affected the capacity of this specific vegetation to conduct the rain water to the soil.

The páramo (high altitude grassland)

In the páramo (high altitude grassland), the aerial biovolume of *S. ichu* intercepted 58.8% of total rain at an intensity of 27 mm h^{-1}. This decreased to 22.7% at a rain intensity of 70 mm h^{-1} due to the flexibility of the leaves which fall down under high drop impact. The data show that *S. ichu* exhibits high rain interception and important stemflow at low rain intensity, probably due to the high density and the shape of the thin leaves. These results are similar to those obtained on Liliaceous tussocks by De Ploey (1982). The fasciculate root system of this Poaceae induces high infiltration and the ICS was similar at both rain intensities (Table 2) due to the high soil cover of the plant (59.9%). Some other measurements of rainfall interception on *Stipa tenacissima* under natural rain at very low intensity have been previously published (Domingo *et al.* 1998). These authors observed, albeit with a different methodology, high rain interception rates as observed in the work presented here.

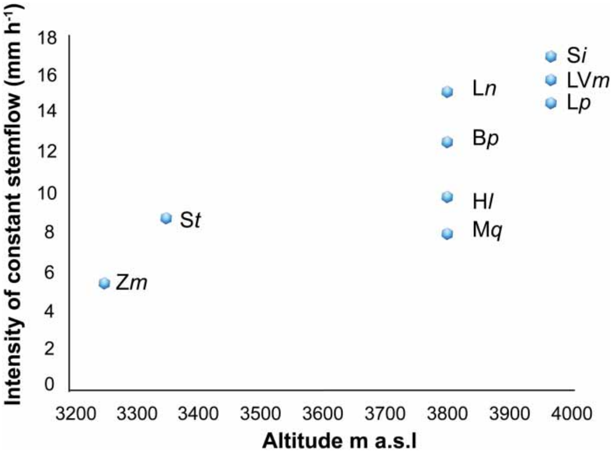

Figure 3 | Intensity of constant of stemflow and altitude for the nine studied species with 27 mm h^{-1} rainfall intensity: *Stipa ichu (St), Lupinus pubescens (Lp), Valeriana microphylla (Vm), Bracchiaris polyantha (Bp), Lupinus nonense (Ln), Miconia quitensis (Mq), Hipericum laricifolium (Hl), Z. mays (Zm),* and *Solanum tuberosum (St).*

Valeriana microphylla caught 52.5% of the rain at low rainfall intensity; however, this value decreased to 12.8% under high intensity due to the fragility of the anatomic structure of this plant (Eriksen 1989). The ICS value also decreased in the same proportion. At high rain intensities, water drops on to the soil surface rather than running off the leaves and along the stem of *V. microphylla*.

For *Lupinus pubescens* (Chocho), the stemflow values were high for both rainfall intensities (55.8–34.6%). The stem and leaves of this plant contain high numbers of lignescent parenchyma (Petrova 2002) (Figure S1, available in the online version of this paper) and they are resistant to the drop splash; this probably explains the relatively large proportion of water arriving at the base of the plant.

In this ecosystem, rainfall varies with altitude and slope exposition; it is considered as high (>1,700 mm $year^{-1}$). Moreover, the root system of the Poaceae (*S. ichu* but also *Calamagrostis* sp. and *Agrostis* sp.) that cover large surfaces probably play an important role in soil hydrodynamics. This, along with high soil infiltration rates, and the specific soil hydric properties (Poulenard *et al.* 2001) probably explain why the area is considered as a water reservoir ('sponge') for the upper part of Ecuadorian Andes (Buytaert *et al.* 2006b). These results suggest that the páramo vegetation has not been influenced by burning, overgrazing (Hofstede 1995; Podwojewski *et al.* 2002; Buytaert *et al.* 2005), and freezing (Sklenar *et al.* 2010), all of which can strongly influence stemflow by increasing the volume of rainwater reaching the soil without generating runoff even under rain events of high intensity and long duration. The stemflow of the majority of plants in the grass páramo is very efficient at low rain

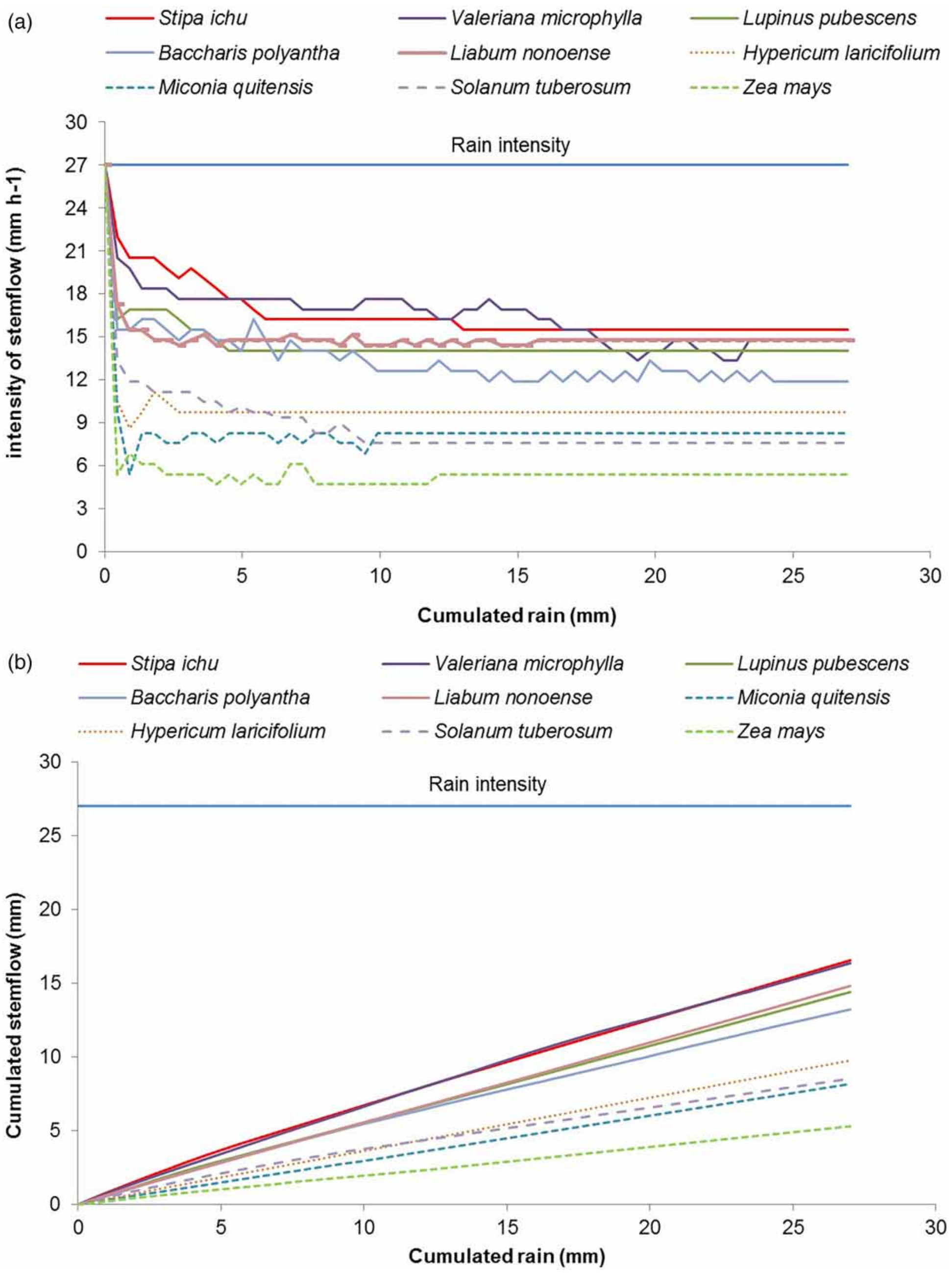

Figure 4 | (a) Intensity of stemflow at 27 mm h^{-1} rain intensity for the nine studied plants with low intensity for *M. quitensi*, *H. laricifolium*, *Z. mays,* and *S. tuberosum* located in the lower part of the catena. (b) Cumulated stemflow for 60 mn rain with 27 mm h^{-1} intensity with maximum values for *S. itchu*, *V. microphylla*, *B. polyantha*, *L. pubescens*, and *L. nonense* located in the upper part of the catena.

intensities and is higher than other plants tested at lower altitude. This indicates that the specific features of the vegetation of this ecosystem mean that plants 'drive' rainwater directly to the soil (Table 2). For high rain intensities, the stemflow of this ecosystem is still very effective for short duration rain events.

The sub-páramo

Shrub area

In the sub-páramo shrub area, we studied the behavior of *Baccharis polyantha* (Chilca) and *Liabum nonoense*

(Chazaso). Similar to other shrubs, *B. polyantha* shrub harvests an important amount of water: 45.2 and 41.8% with high ICS of 11.9 and 28.4 mm h^{-1} for rain intensities of 27 mm h^{-1} and 70 mm h^{-1}, respectively. These results show a natural resistance to the kinetic energy of the drops due to the plant's woody structure described by Pourrut (1995).

L. nonoense has a high water collection power (55.7% under low rainfall and 34.6% under high intensity rainfall). The decrease at high rain intensity can be explained by the relative pliability of the leaves of the Asteraceae family. However, the structure of this Asteraceae is not sensitive to drop weight despite having a high ICS (23.9 mm h^{-1} at high rain intensities).

Grassland area

In the sub-páramo grassland area, we selected two upright shrubs with a height of more than 15 cm: *Miconia quitensis* (Colca) and *Hypericum laricifolium* (Romerillo). The shrub *M. quitensis* collected 32.3 and 37.4% of stemflow with an ICS of 8.2 and 25.3 mm h^{-1}, respectively for the first and second rainfall intensities. These medium-high values of water harvesting for high rainfall intensities are related to the shape and the structure of this plant and to its natural resistance due to ligneous constituents.

H. laricifolium caught 36.5% of rainwater under the lower rain intensity. This value decreased drastically to 8% with higher rainfall intensity. The ICS values were low, 9.7 mm h^{-1} and 4.5 mm h^{-1}, respectively. *H. laricifolium* has thin acicular leaves that do not retain the drops and this factor probably explains the results obtained.

In this grassland located at medium altitude of the Pichincha volcano, only *H. laricifolium* had reduced stemflow collection and ICS due to its morphology. As mentioned by Calder (1996), the size of the rain drops interacts with the morphology of the plant to determine the stemflow volume potentially collected by the plant. The high proportion of excess stemflow during the first 10 min rain of high intensities (82%) should be considered in light of the very low constant stemflow of this plant (only 4.5 mm h^{-1}).

Field crops

In the sub-páramo field crops, the potato plant (*Solanum tuberosum)* intercepted relatively little rainwater and the stemflow parameter values were low (Table 2). The part of the stemflow during the first 10 min for low intensity rains is also relatively high (34%) compared to other plants of the sub-páramo and to maize (4%). However, this value is very low for high intensity rain (5%) (Table 2). The pliable morphology of the potato crop leaves does not allow high water fluxes along the leaves and stem under strong rain intensities. Instead, water drops directly from the leaves to the soil, potentially generating splash effects and crusting (Foot & Morgan 2005). Under low intensities the high pliability of leaves is less important and water accumulation at the plant base was higher.

For maize (*Zea mays)*, the results indicate for both intensities a low stemflow rate of total rain due to the small surface cover by one vegetal on 1 m^2. Frasson & Krajewski (2011) proposed that as a consequence of the anatomic structure of maize, specific areas under the canopy could receive different sizes of drops which can generate crusting and runoff. The ICS values are low under low intensity and increase with rain intensity due to the straight structure of the plant. Similar results were found by Quinn & Laflen (1983), Bui & Box (1992), and van Dijk & Bruijnzeel (2001).

Rainfall simulations made on bare tilled plots (Poulenard *et al.* 2001) found complete infiltration with 27 mm h^{-1} rain during 1 h with the onset of runoff occurring after 30 min at a rain intensity of 60 to 80 mm h^{-1} (Podwojewski & Poulenard 2006). This runoff increased rapidly with rainfall intensity (Podwojewski & Poulenard 2006), probably because the slaking of aggregates was the cause of soil crusting (Poulenard *et al.* 2001), while the runoff on undisturbed plots with natural vegetation cover only began after 1 h at a rain intensity of 100 mm h^{-1}. In these highlands, the irreversible drying of bare Andisol, the development of water repellency, and soil surface crusting were considered as responsible for the increase in runoff and the reduction in the water retention capacities of the páramo ecosystem (Poulenard *et al.* 2001).

However, in our experiment, we found that the infiltration rate was very high; we did not observe any runoff after 1 h of rainfall simulation on either tilled cultivated or natural undisturbed páramo plants. On tilled plots, the protection of bare soils by the vegetation delays runoff. The more the soil cover is important, the more the delay in runoff onset will be important. Therefore, even for cultivated crops, the stemflow process is important for leading rainwater directly to the roots and minimizing the 'splash effect' of raindrops. The cultivation of potato crops is considered to generate more soil erosion than maize cultivation (Fiene & Auerswald 2007). Our results also confirm that potato fields are less protected from the splash effect during heavy rains than is maize. Consequently, potato crops are also more prone to generate runoff and erosion than maize in lower areas with potentially higher rainfall intensities. Potatoes are more adapted than maize to the lower average temperatures occurring at high altitudes (Huttel *et al.* 1999); their higher water interception by stemflow with low intensity rains may also contribute to this adaptation to higher altitudes. The low soil surface covered by maize, especially when the crop is at the juvenile stage, increases the potential of splash crusting and runoff after soil preparation, as mentioned by Poulenard *et al.* (2001).

This experiment demonstrated the poor stemflow properties of cultivated crops and their direct effect on potential crusting and runoff, especially on tilled surfaces, generating rill erosion and contributing to the deregulation of water retention capacity of the volcanic ash soils of the páramo (Figure S2, available in the online version of this paper).

This experiment also revealed an important function of plant species in these ecosystems by collecting the rainwater during low intensity rains thereby enhancing the water harvesting process. At higher altitudes, plants directly transmit the collected water to the root system, protecting the soil macrostructure and preserving the high soil moisture. This mitigates soil water repellency properties and therefore maintains water infiltration rates at high levels enabling groundwater recharge in the Andean mountains.

CONCLUSION

This study showed that in the páramo ecosystem the main vegetal species are adapted to low rainfall intensities and conduct over 50% of rainwater through stemflow directly to the soil. Stemflow is therefore a major process which allows infiltration of rainwater into the soil in the volcanic ash soils of Ecuadorian highlands. In this experiment, conducted in an area untouched by fire, the soil surface had a high porosity which induced high water infiltration. Moreover, the stemflow volume varied with the morphological characteristics of the studied plants. In high altitude grasslands, stemflow was more efficient at low rainfall intensities while in shrubland (matorral) of lower altitude, stemflow was more efficient at high intensities, which occur more frequently in these altitudinal natural areas. Therefore, the conservation of the páramo ecosystem is essential to preserve the exceptional hydric soil properties of these volcanic ash soils. Unfortunately, the most cultivated plants have a weak potential of stemflow. However, the stemflow process delays soil surface crusting and runoff processes in these tilled areas. Regarding stemflow efficiency, potato crops are more adapted than maize to higher altitude.

Finally, given the importance of native vegetation in the upper slopes of the Pichincha volcano, and the weak potential of stemflow of cultivated plants, the results of our study underline the importance of maintaining the páramo native plant cover as an essential soil ecosystemic service provider and as a regulator of the water reservoir for the lowlands where the main cities in Western Andes are located.

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