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Altitudinal analysis of carbon stocks in the Antisana *páramo*, Ecuadorian Andes

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Abstract

Aims

The importance of quantifying carbon stocks in terrestrial ecosystems is crucial for determining climate change dynamics. However, the present regional assessments of carbon stocks in tropical grasslands are extrapolated to unsampled areas with a high degree of uncertainty and without considering the carbon and nitrogen composition of vegetation and soil along altitudinal ranges. This study aims to assess carbon and nitrogen concentrations in soil and vegetation, aboveground carbon stocks distribution and soil organic carbon stocks along an altitudinal range in the *páramo* region in the Ecuadorian Andes.

Methods

The vegetation inventory was conducted using 15×15 m sampling plots distributed in three altitudinal ranges. Based on the patterns exhibited by the dominant vegetation growth forms, biomass and soil were sampled to quantify the corresponding carbon and nitrogen concentrations. Subsequently, the aboveground live biomass along the *páramo* altitudinal range was estimated using allometric equations. Finally, soil and vegetation carbon stocks were estimated for the entire basin.

Important Findings

Altitudinal analysis supported a potential distribution of carbon and nitrogen concentrations in soil, litter and live tissues, where higher concentrations were found in the low altitudinal range mainly for tussocks and acaulescent rosettes. Cellulose in litter showed higher concentrations at low altitudinal ranges for acaulescent rosettes and cushions only. For the same growth forms, lignin patterns in litter were higher in high altitudinal ranges. Soil texture provided complementary information: high percentage of silt was highly correlated to high soil nitrogen and carbon concentration. Tussocks were found to be responsive to altitude with their, highest aboveground carbon stocks occurring at the low altitudinal range, but cushions and acaulescent rosettes responded differently. The established relationships among soil, vegetation and altitude shown in this study must be taken into account to estimate both aboveground and soil organic carbon stocks in *páramo* regions—such estimates will be considerably inaccurate if these relationships are ignored.

Keywords: Andes, carbon, growth forms, nitrogen, *páramo* grassland

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INTRODUCTION

Approximately 25% of the world's terrestrial ecosystems are grasslands distributed from arid to humid regions (Ojima *et al.* 1993). Grasslands are biomes that contain large belowground carbon stocks in roots and soil organic matter (Verschot *et al.* 2006), related to interannual climatic variability and differences in land management practices (Connant *et al.* 2001). The IPCC 2013 Guidelines (IPCC 2013) highlight the importance of quantifying above- and belowground carbon stocks and emissions from grasslands due to burning and land-use change. However, such recommendations do not include the

influence of local factors such as altitude, vegetation and soil texture on carbon stocks, which are necessary in order to understand the complex biogeochemical interactions between soil and plant community (Osanai *et al.* 2012). For example, small clay particles favor water-holding capacity and nutrient contents of the soil (Jobbagy and Jackson 2000) and enhance carbon sequestration by stabilizing soil organic carbon (Paul 1984).

The largest montane grasslands in the Neotropics occur in high-altitude ecosystems known as *páramos*. These are mostly distributed in the northern Andes (Hofstede *et al.* 2003; Myers *et al.* 2000) and represent 9.4% of the global grassland area (White *et al.* 2000). The *páramos* contain many microhabitats, hold enormous biodiversity and supply important ecosystem services such as water regulation, water provision and carbon storage (Buytaert *et al.* 2006; Myers *et al.* 2000). Despite their importance, they are subjected to a high rate of degradation due to grazing, burning and land conversion (Hofstede *et al.* 1995; Verweij and Budde 1992).

Many studies have emphasized the environmental controls on the dynamic pool of carbon in high-latitude (tundra) and high-altitude (*páramo*) grasslands as a crucial component of the global terrestrial carbon budget, but the effects of vegetation and soil on carbon dynamics in these ecosystems remain unresolved (Alvarez and Lavado 1998; Anthelme and Dangles 2012; Körner 2007; Parton *et al.* 1987; Paruelo *et al.* 1997; Paul 1984; Tonneijck *et al.* 2010). In particular, soil carbon storage in *páramos* can be large because they occur on volcanic soils (Andosols) (Tonneijck *et al.* 2010); indeed, it is probably much greater than that contained in vegetation (Kadovic *et al.* 2012).

A common practice to estimate carbon stocks in *páramos* usually includes only the most common or dominant vegetation: the tussocks from the family Poaceae. However, it is unknown if this methodological approach is accurate enough to estimate the carbon stocks in this ecosystem, given the plethora of species and growth forms that *páramos* contain. Additionally, there is not much information on how the soil–vegetation interaction affects the carbon stocks along altitudinal ranges, which in turn should influence carbon estimates at the landscape level. The present study attempts to overcome these limitations by (i) describing the vegetation and soil characteristics of a *páramo* grassland, (ii) using this information to selectively sample carbon and nitrogen concentrations in the living biomass of the most dominant plant growth forms and (iii) determining carbon and nitrogen concentrations in the topsoil underneath the plants sampled.

MATERIALS AND METHODS

Study site

The study site was Los Crespos-Humboldt (LCH) basin, located on the southwestern slope of the Antisana volcano in the Andes of Ecuador (0°30′S, 78°11′W) (Fig. 1). The basin is part of the Antisana Ecological Reserve (628.1 km^2), one of

the main water sources for La Mica Reservoir, which supplies water to the city of Quito, Ecuador's capital. The LCH basin (15.2 km^2, 4010–5300 m a.s.l.) is covered by glacier (15%), moraine (17%) and *páramo* grassland (68%). Precipitation varies from 900 to 1200 mm/year and the average temperature from 4.8 to 7°C.

Sampling design

Sampling was conducted during November and December 2012. The sampling strategy was based on a digital elevation model and a topographic map 1:25 000 (IGM 1990) of the LCH basin. Sampling followed a stratified random design (Daniel 2012) that improved the representativeness of the altitudinal range and reduced sampling errors. A total of 27 permanent sampling plots, each measuring 15 × 15 m were divided into 2 × 2 m subplots (except for the subplots at the corners). The plots were randomly established in the low, mid and high areas of the basin (Fig. 1). These three sampling areas, here called catchments, roughly correspond to three altitudinal ranges: low catchment (*n* = 10 plots, 4000–4200 m a.s.l.), mid catchment (*n* = 10, 4200–4400 m a.s.l.) and high catchment (*n* = 7, 4400–4600 m a.s.l.) (Fig. 1).

The plots were established facing north using a compass (SILVA professional S15T DCL) and the corners were marked with PVC tubes. The slope, altitude and geographic coordinates of each plot were measured using a clinometer (CL1002), an altimeter (Multi Function Altimeter with Digital Compass) and a GPS (Magellan eXplorist 100), respectively.

The floristic inventory was conducted in those plots that did not fall in an area with evident signs of burning or permanent grazing. The sampling method of Mena (1984) was applied to count all individuals per species, and the Braun-Blanquet (1964) method was used to estimate the area covered by all vascular and nonvascular plant species in each 2 × 2-m subplot. For a given area, this method classifies the area covered by a species in seven percentage categories (%): <1, 1–5, 5–15, 15–25, 25–50, 50–75 and ≥75. Plants were further sorted into growth forms according to the classification for Ecuadorian *páramos* proposed by Ramsay and Oxley (1997): stem rosette, basal rosette, tussock, acaulescent rosette, cushion, upright shrub, prostrate shrub, erect herb, prostrate herb and creeping herb. The cover was determined as the area occupied by the base of the plant. We measured the two horizontal dimensions and applied the formula of an ellipse to calculate the grassland basal area (*GBA*) for all vegetation growth forms. Botanical vouchers were collected for vascular plants only, as deemed necessary for taxonomical identification (Cleef 1981; Cuatrecasas 1968; Rangel *et al.* 1983; Ronquillo 2010); vouchers were identified at the National Herbarium of Ecuador (QCNE) and the Catholic University's Herbarium (QCA), both in Quito.

Finally, for each of the main growth forms in each plot, we sampled leaves, leaf litter and roots following standard protocols (Law *et al.* 2008). In each plot, one topsoil sample (0–0.3 m depth) was collected in each cardinal point, 3 m
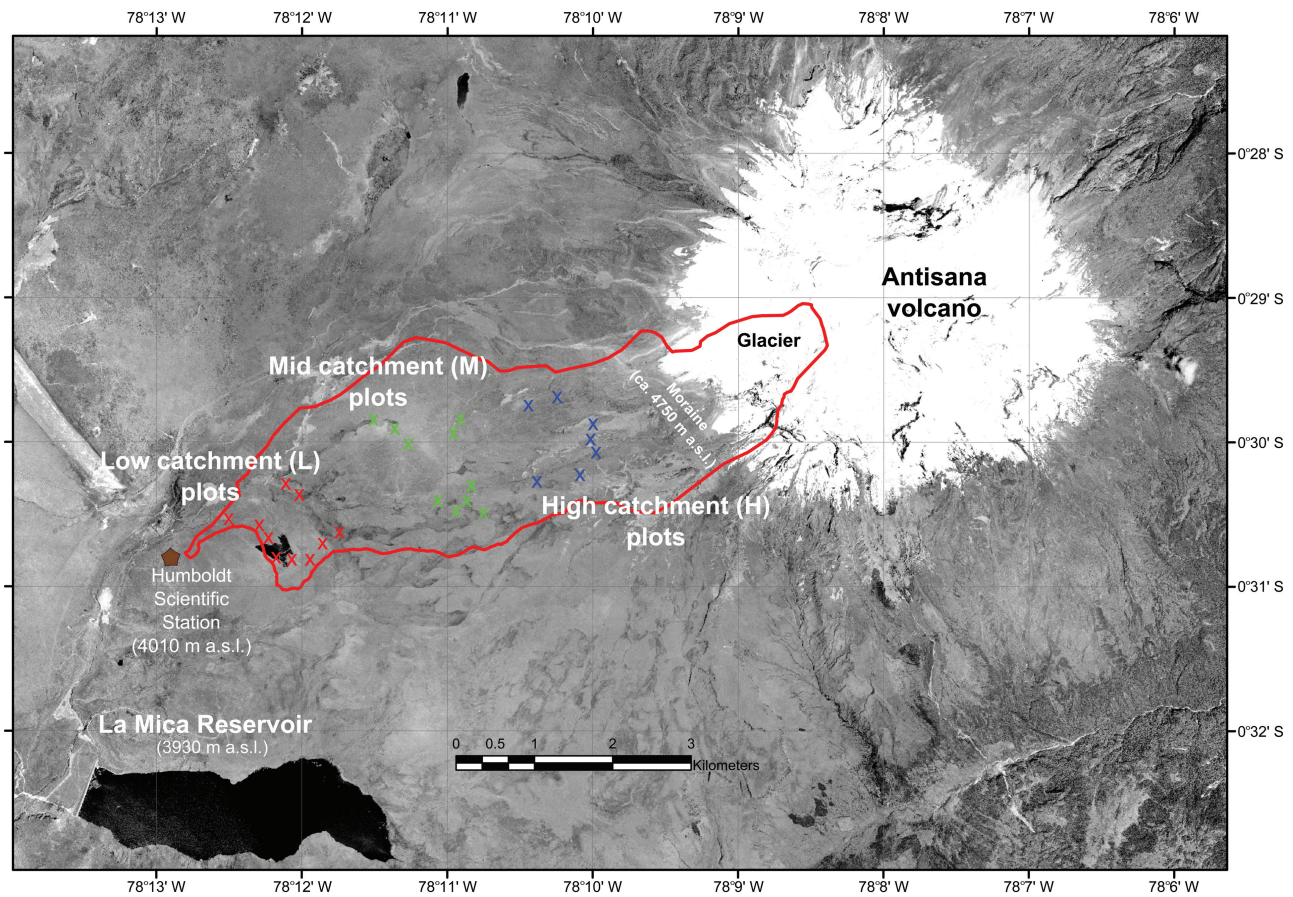
Figure 1: The 'Los Crespos-Humboldt' basin on the slope of the Antisana volcano in Ecuador. Sampling plots (*n* = 27) are shown as crosses (red = low catchment plots, green = mid catchment plots, blue = high catchment plots). Source: ASTER Satellite Image, 15 m resolution.

apart from the edge, using a 70-mm soil corer (EIJKELKAMP, model GM085). Samples were collected into clearly labeled dark polyethylene bags and later refrigerated.

Laboratory analyses

Carbon and nitrogen analyses

Leaves, litter and roots were dried at 60°C for 48 h. Soil was dried at room temperature. All dry plant and soil samples were grinded in a mill (Retsch Mixer Mill MM200) at a vibrational frequency of 300 min^{-1} for 4 min to obtain a homogeneous sample and then dried again at 60°C overnight. These samples, placed on a tarred tin capsule, were weighed to the nearest hundredth of a gram using a digital lab scale balance (Mettler Toledo AE100). Carbon and nitrogen concentrations in plant and soil samples were measured by an EA1108 CHN-O Element Analyzer (Fisons Instrument) using the Dumas Combustion Method (Dumas 1826; cited by Buckee 1994).

Lignin and cellulose in plants

To measure lignin and cellulose in roots and litter, dry samples were grinded, sieved through a 1-mm mesh and then placed in a F57 filter bag. Lignin and cellulose concentrations were determined using acid detergent fiber methods (ADF 1990) via ANKOM Technology - 01/02 and - 07/02. Lignin (%) and cellulose (%) were calculated as:

$$\text{Lignin} \left(\%\right) = \frac{W_4 - (W_1 C_2)}{W_2} 100 \tag{1}$$

$$\text{Cellulose} \left(\%\right) = \frac{W_3 - (W_1 C_1)}{W_2} 100 - Lignin(\%) \tag{2}$$

where W_1 is the bag tare weight; W_2 is the sample dry weight; W_3 is the weight after the extraction process; W_4 is the weight of organic matter (loss of weight of bag ignited at 525°C for 3 h, plus fiber residue); C_1 is the blank bag correction (final oven dried weight/original blank bag weight) and C_2 is the ash corrected blank bag (loss of weight on ignition of bag/original blank bag weight).

Data treatment and analyses

Altitudinal effects on growth forms and plant/soil chemical composition

Tukey multiple comparisons tests (Tukey 1991) were used to compare carbon and nitrogen pools among different altitudinal ranges. Cellulose and lignin concentrations along the

altitudinal range were also analyzed. In addition, for each growth form, Pearson correlation coefficients were calculated to test for significant relationships among species diversity, soil texture composition and nitrogen and carbon concentrations. Pairwise P values were corrected for multiple inferences using Holm's method (Holm 1979).

To represent the landscape variation of carbon and nitrogen concentrations in different vegetation growth forms along the altitudinal range, a multidimensional scaling (MDS) ordination method was utilized. Such matrix was based on a Euclidean dissimilarity matrix (Anderson 2006; Legendre and Legendre 1998) computed from carbon and nitrogen concentrations (%) in the topsoil (0–0.3 m depth). The dissimilarity matrix was also subject to testing for altitudinal range effects using permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001). All statistical analyses were done with R 2.12.0 (R Development Core Team 2005), using the *vegan* package (Oksanen *et al.* 2011) and the *plotrix* package (Lemon 2006).

Aboveground biomass and carbon stocks

Biomass for tussocks, acaulescent rosettes and cushions—the main growth forms occurring in the study area—were calculated by building allometric equations. These equations relate *GBA* (m^2), represented by the area of an ellipse (Ganskopp and Rose 1992), and aboveground biomass (*B*, kg), represented as the dry weight (Gomez-Diaz *et al.* 2011). To build the allometric equation for each growth form, weighted linear regression models on log-transformed data were used. This model was nonlinear and adjusted for the variation among classes of *GBA*. *GBA* and *B* were related by the following regression equation:

$$B = b \, (GBA)^k \tag{3}$$

where *b* and *k* are parameters estimated statistically. Analyses were conducted in R (R Development Core Team 2005).

In order to calculate the aboveground carbon stocks (kg C/m^2), we first estimate the aboveground biomass per square meter and then multiply for the average percentage of carbon in leaves for each growth form at each altitudinal range.

To extrapolate the aboveground carbon stocks for the entire basin, we (i) related the dominant growth form of each sampling plot with its NDVI (normalized difference vegetation index), (ii) used this relationship to determine the rest of the pixels in the basin and (iii) calculated the percentage of coverage of each growth form in the different altitudinal ranges (Table 1). The NDVI was calculated from an ASTER (Advanced Spaceborne Thermal Emission and Reflection Radiometer) image (this relationship was feasible because the pixel size was the same as the sampling plot: 15 × 15 m). NDVI was validated with field measurements of radiance (W/sr/m^2) taken with a spectroradiometer (ASD FieldSpec 4 HiRes) in all sampling plots.

Soil organic carbon stocks

The total soil organic carbon stocks (*TCS$_d$*) per square meter (kg C/m^2) in a soil sample of depth *d* (m) was estimated using an equation from a case study in the northern Ecuadorian *páramos* (Tonneijck *et al.* 2010):

$$TCS_d = \sum_{i=1}^{k} {}^b\rho_{s,i} \; C_i D_i (1 - S_i) \tag{4}$$

where *k* is the number of soil layers up to depth *d* (here, *k* = 1 because we only considered a single 0–0.3 m layer), ${}^b\rho_{s,i}$ is the dry bulk density (*b*) of soil (*s*) layer *i* (kg/m^3), C_i is the carbon concentration (fraction) in layer *i* (kg/kg), D_i is the thickness of layer *i* (m) and S_i is the fraction of soil fragments ≥2 mm in layer *i* (kg/kg), a term that can be neglected in the case of *páramo* soil (Tonneijck *et al.* 2010). To estimate soil dry bulk density (${}^b\rho_{s,i}$), we used its relationship to carbon fraction in layer *i* (C_i) as showed by Tonneijck *et al.* (2010):

$$ {}^b\rho_{s,i} = 0.9247 e^{-5.497 C_i} \tag{5}$$

The estimation of the total soil organic carbon stocks for the entire basin only considered the dominant growth form of each pixel.

Table 1: Dominant growth form coverage (%) in the LCH basin according to a supervised classification of an ASTER image (15 × 15 m pixels)

Pixel classification	% of growth form coverage in different altitudinal ranges (catchments)		
	Low	Mid	High
Tussocks	59.7	56.6	45.4
Acaulescent rosettes	28.8	36.9	20.6
Cushions	7.0	3.2	1.1
Other (including minor growth forms, bare soil or rock)	4.5	3.3	32.9

RESULTS

Altitudinal analysis of carbon and nitrogen pools

Soil and litter

Soil carbon concentrations (% C) were significantly higher at the low catchment which is dominated by tussocks and acaulescent rosettes (Fig. 2). A similar pattern was observed with soil nitrogen concentrations (% N). Cellulose in litter showed higher concentrations at the low catchment for acaulescent rosettes and cushions only. In contrast, for these same growth forms, lignin in litter showed the highest concentration at the high catchment. Tussocks did not show any clear altitudinal pattern of litter cellulose and litter lignin concentrations. For soil under tussocks and acaulescent rosettes, the averaged ratio between soil carbon and soil nitrogen was 16:1, but for the soil under cushions this ratio can go up to 19:1 in the high catchment (Table 2).

Live tissues (leaves and roots)

Percentage of C in leaves and roots did not show any particular trend, with exception of leaf % C of acaulescent
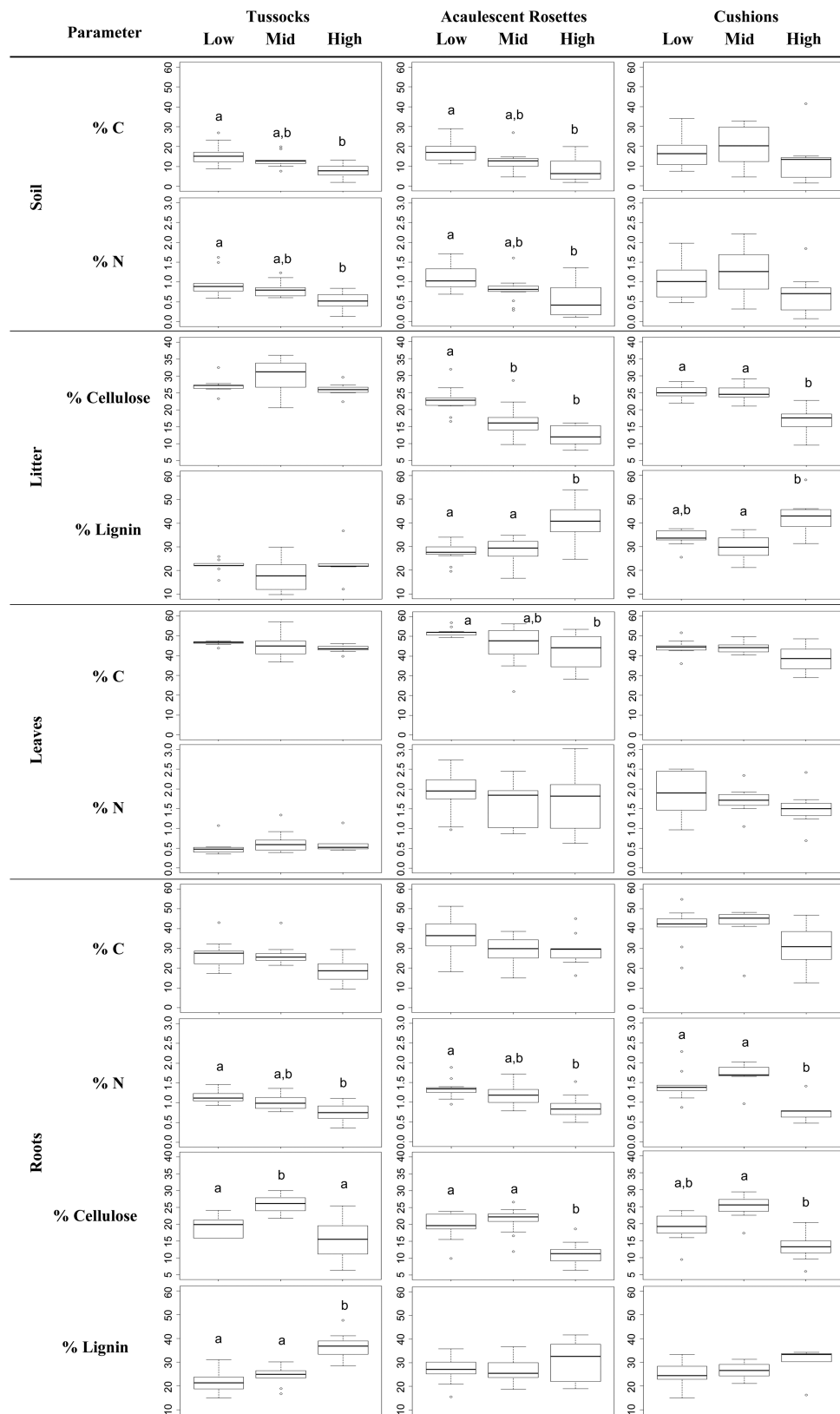
Figure 2: Carbon, nitrogen, cellulose and lignin concentrations of the main growth forms of *páramo* vegetation in the LCH basin, analyzed per altitudinal catchments (low, mid and high). Lowercase superscripted letters indicate significant differences among altitudinal ranges (*P* ≤ 0.05), according to Tukey's test.

Table 2: Comparison of carbon and nitrogen ratios of the main growth forms of *páramo* vegetation in the LCH basin, analyzed per altitudinal ranges or catchments (low, mid and high)

Parameter	Tussocks			Acaulescent rosettes			Cushions		
	Low	Mid	High	Low	Mid	High	Low	Mid	High
C:N in soil	16:1	16:1	16:1	16:1	16:1	16:1	16:1	14:1	19:1
C:N in leaves	93:1	64:1	72:1	25:1	28:1	24:1	22:1	26:1	26:1
C:N in roots	23:1	27:1	23:1	28:1	25:1	32:1	28:1	25:1	39:1

rosettes, which showed the highest values at the low catchment (Fig. 2). Percentage of N in roots was always lower at the high catchment. Cellulose in roots in general followed this same tendency but not in tussocks. Conversely, lignin in roots tended to have higher concentrations at the high catchment, although this was only significant for tussocks (Fig. 2).

The averaged C:N ratio in tussock leaves varied from 64:1 in the mid catchment to 93:1 in the low catchment (Table 2). The C:N ratios for acaulescent rosette and cushion leaves were similar and varied around 25:1 regardless of altitudinal range. For all growth forms, the C:N ratio of roots varied around 26:1 in the low and mid catchments, while for the high catchment, the ratio increased to 32:1 for acaulescent rosettes and 39:1 for cushions (Table 2).

Relationships to soil texture

Soil texture variables (e.g. % silt and % sand) were highly correlated with altitude ($r_{\text{altitude – }\% \text{ silt}} = -0.89$, $P_{\text{adj}} < 0.001$; $r_{\text{altitude – }\% \text{ sand}} = 0.88$, $P_{\text{adj}} < 0.001$).

In addition, in acaulescent rosettes but not in tussocks, soil % C and soil % N showed a high correlation with % silt, % sand and altitude (Table 3). High soil % C and high % N occurred at low altitudes, where relatively small soil particles were found. Cellulose concentration in litter for acaulescent rosettes and cushions increased with increasing % silt in soils but decreased as sandy soils became more dominant at higher altitudes. This pattern was completely opposite to what was observed with lignin concentration in litter.

In live tissues, root % N for all three growth forms increased with decreasing % sand, which increased at higher altitudes (Table 3). The % cellulose in roots was not related to soil texture nor altitude, except for acaulescent rosettes, in which it decreased with increasing altitude. The % lignin in roots for tussocks increased with increasing % sand and altitude.

Aboveground biomass and carbon stocks

The following allometric equations for aboveground biomass (*B*, kg) estimates of the main growth forms of vegetation, based on *GBA* (m²), were developed:

$$\text{For tussocks}(n = 46): B = 3.89 \times 10^{-1} \times GBA^{0.158145} \quad (6)$$

$$\text{For acaulescent rosettes}(n = 74): B = 4.51 \times 10^{-2} \times GBA^{0.28599} \quad (7)$$

$$\text{For cushions } (n = 29): B = 7.56 \times 10^{-3} \times GBA^{0.703931} \quad (8)$$

The aboveground biomass was higher at the low catchment for tussocks (3.7 kg/m²) and cushions (1.2 kg/m²).

Table 3: Pearson correlation matrix between those parameters that showed statistical significance in Fig. 2 and variables of altitude and soil texture

	Growth form	Parameter	% Silt	% Clay	% Sand	Altitude
Soil	TU	% C	0.58	−0.29	−0.59	−0.55
		% N	0.55	−0.26	−0.58	−0.54
	AR	% C	0.59*	−0.45	−0.57*	−0.58*
		% N	0.60**	−0.44	−0.59*	−0.59**
Litter	AR	% Cellulose	0.55*	−0.42	−0.54*	−0.71***
		% Lignin	−0.66**	0.41	0.67***	0.62**
	CU	% Cellulose	0.76**	−0.32	−0.79***	−0.78***
		% Lignin	−0.77**	0.28	0.81***	0.64
Leaf	AR	% C	0.55*	−0.51	−0.51	−0.51
Root	TU	% N	0.64	−0.25	−0.68*	−0.70*
		% Cellulose	0.49	−0.11	−0.55	−0.36
		% Lignin	−0.76**	0.33	0.80***	0.86***
	AR	% N	0.63**	−0.46	−0.62**	−0.64**
		% Cellulose	0.62**	−0.38	−0.64**	−0.57*
	CU	% N	0.75**	−0.49	−0.74**	−0.64
		% Cellulose	0.54	−0.29	−0.55	−0.44

Abbreviations: AR = acaulescent rosettes; CU = cushions; TU = tussocks.
*$0.01 \leq P \leq 0.05$, **$0.001 \leq P \leq 0.01$, ***$P \leq 0.001$.

Table 4: Total aboveground soil carbon stocks, total soil organic carbon stocks (0–0.3 m) and total aboveground biomass for the main growth forms at different catchment altitudes (low, mid and high) in the LCH basin

	Total aboveground carbon stocks (kg C)				Total soil organic carbon stocks (kg C)				Total aboveground biomass (kg/m^2)			
	Low	Mid	High	Total	Low	Mid	High	Total	Low	Mid	High	Total
Tussocks	3.3×10^6	1.9×10^6	2.2×10^5	5.4×10^6	3.3×10^7	4.2×10^7	1.8×10^7	9.3×10^7	3.7	1.7	0.44	5.8
Acaulescent rosettes	2.7×10^5	5.7×10^5	1.8×10^5	1.0×10^6	1.6×10^7	2.6×10^7	7.6×10^6	5.0×10^7	0.6	0.8	0.6	2.0
Cushions	1.2×10^5	4.6×10^4	1.0×10^3	1.7×10^5	3.7×10^6	2.1×10^6	3.6×10^5	6.2×10^6	1.2	0.8	0.1	2.1
Total	3.7×10^6	2.5×10^6	4.0×10^5	6.6×10^6	5.3×10^7	7.0×10^7	2.6×10^7	1.5×10^8	5.5	3.3	1.1	9.9

Acaulescent rosettes did not show a clear altitudinal pattern for aboveground biomass (Table 4).

Area-based aboveground carbon stock in tussocks (2.86 kg C/m^2) was significantly higher at the low catchment than at higher altitudes (2.43–2.37 kg C/m^2) (Fig. 3). Acaulescent rosettes and cushions contained similar area-based aboveground carbon stocks in the entire basin (1.05–1.33 kg C/m^2). Also, the total aboveground carbon contained in tussocks was 5 times greater than that contained in acaulescent rosettes and 32 times greater than that contained in cushions. The total aboveground carbon stock for all three growth forms in the basin was estimated as 6.6×10^6 kg C (Table 4).

Soil organic carbon stocks

Area-based soil organic carbon stocks (kg C/m^2) were significantly higher in the low and mid catchments for all growth forms (Fig. 3). Total soil carbon stocks in tussocks were 2 times greater than acaulescent rosettes and 15 times greater than cushions for the entire basin. The total soil organic carbon stock in the basin was estimated as 1.5×10^8 kg C (Table 4).

MDS analysis

The MDS revealed a similarity of sites located at the same altitudinal range (color coding) (PERMANOVA: $F = 6.73$, df1 = 2, df2 = 76, $P < 0.001$) (Fig. 4). MDS showed that higher values of % C in roots were restricted to acaulescent rosettes and cushions. The % cover along with the area-based aboveground carbon stocks for tussocks increased in the low catchment. Sandy soils increased along an altitudinal range, whereas the greatest amount of soil organic carbon stocks was available at the low catchment.

DISCUSSION

Altitudinal analysis of carbon and nitrogen pools

Soil and litter

The soil carbon and soil nitrogen concentrations in cushions do not show a clear altitudinal pattern. This might be not only because they are found in many habitats, from rock formations to swampy areas, but also because they obtain water and nutrients from litter decomposition and peaty mass trapped within their own mounded formations (Kleier and Rundel 2004; Sklenár 1998). On the other hand, soil carbon and soil nitrogen concentrations in tussocks and acaulescent rosettes are higher at low catchments. Their homogeneous growth enhances soil microbial activity and nutrient conservation, in contrast with soils at high catchments that are less vegetated and thus have higher nutrient losses (O'Connor *et al.* 1999).

The cellulose and lignin found in litter are crucial for the regulation of litter decomposition both in the early and later stages (Fioretto *et al.* 2005; Rahman *et al.* 2013). They are also important for soil organic matter by providing energy input for soil microflora and fauna (Bernhard-Reversat and Loumeto 2002; Fiala 1979) and even for local atmospheric composition through the emission of CO_2 by microbial activity (Chen 2014; Vanderbilt *et al.* 2008). This physicochemical quality and composition of plant litter have strong effects on ecosystem functioning. Further, high C:N ratios enrich soil organic carbon, which increases the amount of carbon in the soil, therefore playing an important role in the global carbon cycle (Bell and Worrall 2009).

Live tissues (leaves and roots)

The high concentration of carbon in leaves for acaulescent rosettes makes them decompose at a rapid rate. This drives the nutrient turnover and controls the micro-atmospheric composition of the plant at low catchments.

Although the carbon measured in tussock roots was low on average, tussocks have roots around 1.5 m long, where carbon can be stored. These lengthy tussock roots usually help to stabilize slopes, control erosion and increase soil porosity for water absorption. On the contrary, acaulescent rosettes have thick taproots ~0.15 m long, while cushions have roots around 1 m long, depending on the species and soil texture (Attenborough 1995).

The cellulose found in roots was very similar among the three growth forms of vegetation, giving the same strength to their leaves and rigidity to the cells and making them difficult to break down. Cellulose gives the physical support required not only to anchor the plant but also to absorb water and minerals. Lignin also strengthens the cell wall and plays an essential role not only for water transport within the plant but also in the carbon cycle because it sequesters atmospheric carbon in living tissues for relatively long periods. Lignin found in tussock roots increased with altitude ($P < 0.001$), while the same trend was observed for acaulescent rosettes and cushions. The high lignin concentration in the species located in the high catchment could explain the survival of certain species to such relatively hostile environment, filled with loose
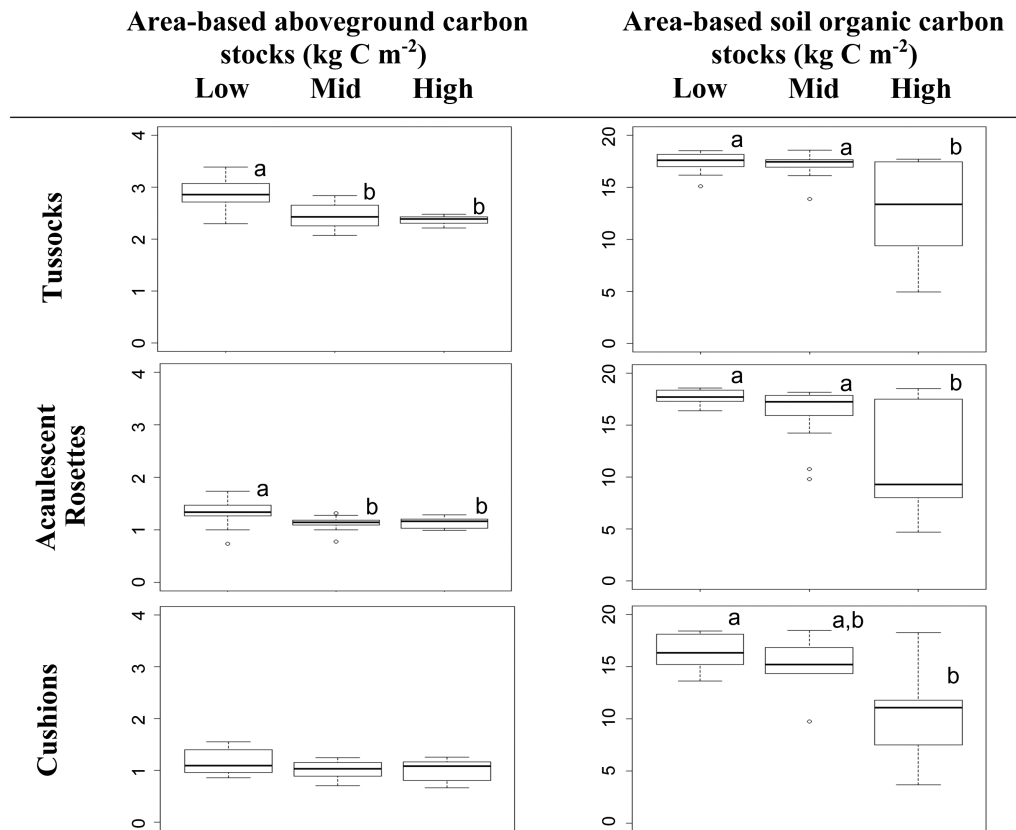
Figure 3: Comparison between the area-based aboveground carbon stocks and area-based soil organic carbon stocks for the main growth forms at different catchment altitudes (low, mid and high) in LCH basin. Lowercase superscripted letters indicate significant differences among altitudinal ranges ($P \leq 0.05$), according to Tukey's test.
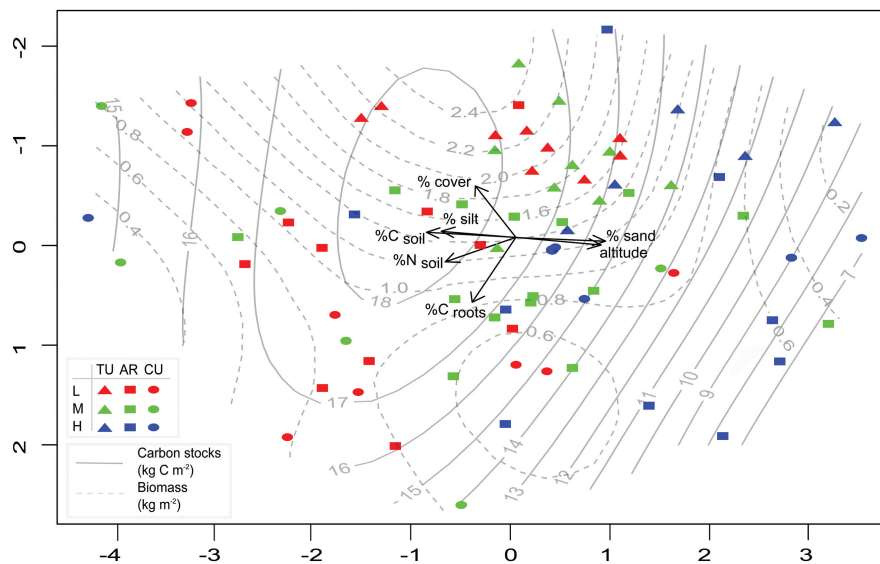

Figure 4: MDS of carbon composition (total stress 14.49%). MDS translates Euclidean dissimilarity computed from normalized carbon stocks into distance among sites and growth forms of vegetation into a two-dimensional plot with equally weighted dimensions. Sites are coded according to growth forms (TU = tussocks, AR = acaulescent rosettes, CU = cushions) and altitudinal ranges (L = low catchment, M = mid catchment, H = high catchment) as colors. Arrows indicate the strength and direction of the gradient of the variables indicated.

stones, sandy soil, low soil water-holding capacity and low nutrient content (Körner 2003; Molau 2004; Rada *et al.* 2001). Additionally, they have to cope with climatic conditions of low oxygen concentration, low rainfall, high solar radiation, strong wind abrasion and night frost (Baruch 1984).

In general, tussocks leaves have slower decomposition rates than acaulescent rosettes and cushions, at low and mid catchments. This can be attributed to their high C:N ratios and, at the high catchment, to high lignin concentration. Acaulescent rosettes and cushions leaves show a constant C:N ratio of 25:1 throughout the altitudinal range, which should promote rapid decomposition by microbial activity.

Relationships to soil texture

Most soils in the Ecuadorian highlands are derived from volcanic material (Hall and Beate 1991); however, soil particle sizes differ among altitudinal ranges. In this study, sandy soils were predominant at higher elevations (>4500 m a.s.l.) (Fig. 4). This soil drains well but also dries out and warms up rapidly, reducing the capability of holding moisture and providing poor conditions to store plant nutrients (Buytaert *et al.* 2005) (Table 3). On the other hand, silty soils, mostly located at lower altitudinal ranges, are poor in aeration and percolation but offer high water-holding capacity, which in this study resulted in enriched soil carbon and nitrogen concentrations (Table 3).

Aboveground biomass and carbon stocks

Tussocks, acaulescent rosettes and cushions were the dominant growth forms in the study area (as they are in the Ecuadorian *páramos* in general; personal observation). This implies a strong relationship between growth form adaptation and environmental variables, such as high-elevation atmosphere, high radiation and drying wind effects (Ramsay and Oxley 1997). Several studies (Hedberg 1992; Ramsay and Oxley 1997) agree that tussocks and acaulescent rosettes are responsible, on average, for >50% vegetation cover from 4000 to 4400 m a.s.l., which in this study corresponds to the low and mid catchments. Vegetation cover diminishes with altitude because of the less favorable climatic conditions, under which only a few plants can survive and adapt such as those that developed pubescence in order to expand its boundary layer (Sklenar and Ramsay 2001; Stern and Guerrero 1997).

Aboveground biomass in tussocks was higher along the low and mid catchments (4000–4400 m a.s.l.) (Fig. 4). At these altitudes, tussocks benefit from the air that is trapped between the leaves and cool down slowly (Ramsay 2001). At higher altitudes, tussock biomass is less abundant but becomes important as shelter to other growth forms, enabling them to increase their size (Ramsay and Oxley 1997). The biomass of acaulescent rosettes and cushions did not show a particular trend with altitude: both grow at the soil surface and remain slightly warmer than night air temperature at night (Hedberg and Hedberg 1979). Hard and soft-mat cushions maintain the internal temperature stable and tend to be conspicuous in flooding zones or where water is retained (Bosman *et al.* 1993; Cleef 1981; Jorgensen and Ulloa 1994).

It appears that aboveground herbaceous biomass for the three growth forms of *páramo* vegetation in the area will not decline below its current abundance and distribution as long as they are not exposed to practices of burning and grazing (Hofstede 1995; Laegaard 1992; Ramsay 1992; Verweij 1995). Most probably, the vegetation will continue to capture more carbon in all plant components.

Soil organic carbon stocks

Higher levels of soil organic carbon stocks are found in the low and mid catchments, which could be associated to higher content of soil silt fraction. Silt and clay stabilize the soil organic carbon by protecting organic matter from microbial decomposers (Paul 1984; Six *et al.* 2002). The association between soil organic carbon stocks and the change in soil texture with depth is still vague and needs further analysis. It is important to realize, for example, that other regional studies of grasslands (Jobbagy and Jackson 2000; Spain *et al.* 1983) also based their results of soil organic carbon concentrations at the top 30 cm of soil. The carbon concentration patterns at higher depths are basically unknown. The increase of carbon stocks in the low and mid catchments (Fig. 4) was expected because of the predominance of the silt fraction in the soil texture at these elevations (Sacramento *et al.* 2014).

Note also that the global averaged values for Andosols in tropical grasslands (Jobbagy and Jackson 2000; Schlesinger 1986) underestimated the values of soil organic carbon stocks compared to studies conducted *in situ* (Eswaran *et al.* 1993; Poulenard *et al.* 2003; Tonneijck *et al.* 2010), including this one.

CONCLUSION

The established relationships among soil, vegetation and altitude shown in this study must be taken into account to estimate both aboveground and soil organic carbon stocks in *páramo* regions. Such estimates will be considerably inaccurate if these relationships are ignored.

1. The high soil nutrient availability in tussocks and acaulescent rosettes at low catchments enhance litter quality and therefore microbial activity. This physicochemical quality and composition of plant litter have strong effects on ecosystem functioning. In addition, the high C:N ratios enriches the soil organic carbon and therefore playing an important role in the global carbon cycle.
2. Tussocks and acaulescent rosettes are responsible for >50% of vegetation cover from 4000 to 4400 m a.s.l. This aboveground biomass in the area will not decline below its current abundance and distribution as long as they are not exposed to practices of burning and grazing.
3. Fine textured soils enhanced the accumulation of soil carbon stocks. This emphasizes the importance of the *páramo* vegetation for carbon sequestration as well as other ecological processes.

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