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Cabrera Pantoja, M.J.

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Non-destructive allometric estimates of
aboveground and belowground biomass of
high mountain vegetation in the Andes

Cabrera, M

Samboni-Guerrero, V

Duivenvoorden, J.F

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2.1 - INTRODUCTION

Biomass is the main indicator of carbon allocation at different levels of community organization and therefore essential to estimate the global carbon balance (Flombaum and Sala 2007). In ecosystem studies plant biomass is an important predictor of primary productivity and plant response to disturbances and climate change (terHorst and Munguia 2008, Nafus et al. 2009). Monitoring programs to study the effects of human impact or climate change on plant communities, such as those developed for the Andes of South America (Cuesta et al. 2012, 2017, Báez et al. 2014), demand reliable and non-destructive estimation methods to estimate aboveground and belowground biomass in permanent plots. In these studies multispecies biomass estimation methods are a prerequisite to efficiently deal with species-rich plant communities (Oliveras et al. 2014 b, Chave et al. 2005). However, biomass estimates of high mountain vegetation are usually obtained applying destructive harvesting methods (Smith and Klinger 1985, Beekman and Verweij 1987, Tol and Cleef 1992, Hofstede et al. 1995, Ramsay and Oxley 2001, Montilla et al. 2002, Liu et al. 2014, Nie et al. 2016). Allometric equations have been widely used to estimate the biomass of plant communities in a non-destructive way, but mostly in the context of lowland forest studies (Zianis and Mencuccini 2004, Kerkhoff and Enquist 2006).

The biomass of the vegetation of the high mountains of the northern Andes, also called páramo (Luteyn 1992), is a key factor controlling the supply of drinking water and the retention of carbon, which are crucial environmental services for the human population (Molina et al. 2007, Harden et al. 2013, Ochoa-Tocachi et al. 2016). Páramo grasslands in Ecuador and Colombia are generally characterized by a low nutrient availability, low temperatures and a wet climate (Luteyn 1992). In these páramo environments, the productivity and decomposition occur in low rates, and plant growth is constrained (Körner 2003, Hofstede et al. 2014). Plant species in the páramo show a great variety in growth forms to cope with these harsh environmental conditions (Hedberg and Hedberg 1979, Ramsay and Oxley 1997). This variation in growth forms reflect different mechanisms of carbon assimilation that ultimately influence size-mass relationships used in allometric regression techniques of biomass estimation (Dorrepaa 2007, Cáceres et al. 2014). With this in mind, the aims of our study were 1) to develop and evaluate non-destructive multispecies allometric models for aboveground, belowground and total biomass of páramo plants arranged according to their growth form, and 2) to show the applicability of these models by estimating the biomass of páramo vegetation sampled in a series of small plots.

2.2 - METHODS

Study sites

The study sites were located at Cumbal (0°56' N and 077°50' W), Ovejas-Tauso (1°09' N and 77°20' W) and Paja Blanca (0°59' N and 077°37' W), at elevations between 3400 m and 3700 m above sea level (asl). These areas represent high Andean ecosystems in Nariño, southern Colombia (Appendix 2-1). The areas have a yearly rainfall between 900 mm and 2000 mm and the monthly rainfall is relatively low from July to September (Solarte-Cruz et al. 2007). Above 3200 m the areas are covered by páramo vegetation (Luteyn 1992). Frequently found vascular plant species belong to *Blechnum*, *Calamagrostis*, *Carex*, *Disterigma*, *Espeletia*, *Festuca*, *Jamesonia*, *Miconia*, *Oreobolus* and *Paspalum*. The areas are sparsely inhabited by farmer families, who mainly use their land for agriculture (potato), charcoal production (Delgado et al. 2007), or extensive grazing by cattle.

Field data

In 2013 and 2014, we established a total of 61 plots of 1 m² in páramo vegetation that had been undisturbed by human activities for at least ten years, as witnessed by the lack of signs of soil removal, agriculture or burning. Plot locations were randomly selected, but we excluded sites with inaccessible terrain conditions (for example, steep slopes or ravines) and peat bogs. In each plot, we counted the number of individuals of each vascular plant species. Clonally growing plants were defined as a plant clump of continuous cover that was spatially separated from neighbouring clumps of the same species (Johnson et al. 1988). Unidentified plant species were collected for taxonomical identification at the herbarium of the Universidad de Nariño. Nomenclature followed Tropicos (2016). We classified the species into seven growth forms, each of which occurs wide-spread in páramo vegetation (Cleef 1978, Hedberg and Hedberg 1979, Pedraza-Peñalosa et al. 2003): basal rosettes, caulirosettes, cushion, herbs, sedges/grasses (non-tussock forms), shrubs, and tussocks. For each species in a plot we measured the plant height and basal diameter of all individuals. Plant height was measured as the length from the soil surface to the apical leaf using a tape measure (± 0.1 cm). Basal diameter was measured within 0.5 cm from the soil surface, using a calliper (± 0.01 cm) for basal rosettes, cushion, herbs and sedges/grasses, and a diameter tape (± 0.1 cm) for tussocks and caulirosettes. Plants used for the allometric regression models ('allometric set') At each plot we established a list of the most abundant genera that collectively represented more than 80% of all vascular plants in the plot. From these genera, we selected three plants that occurred outside the plot but within a distance of 3 m from the plot boundary. After measuring the height and the basal diameter of each of these plants, we harvested their aboveground and

belowground biomass. We defined biomass as plant tissue belong to living organs following Körner (2003). Biomass did not include necromass, which we defined as tissue from organs that showed 100% decay but that were still attached to the plant. Furthermore, the aboveground biomass in our study included leaves, stem or culm, but reproductive organs were excluded. To collect the roots, we carefully excavated each plant following the direction of the root system, by manually digging into the soil until a depth of 1 m. For some plants, it was necessary to extract an entire volume of soil in order to keep secondary and third roots attached (Sierra-Escobar and Mora-Osejo 1994). In the laboratory we separated the aboveground necromass from the aboveground biomass. We washed the roots on a sieve to remove any soil material. We did not distinguish between living roots or dead roots; so all roots were treated as belowground biomass. Finally, we weighed all biomass samples using an analytical balance (Ohaus PA214; ± 0.0001 g), after having dried them at 70°C until constant weight.

Allometric regression models

We hypothesized the existence of allometric scaling relationships between plant biomass and each of four single predictor variables: basal diameter, plant height, the virtual rectangular area described by the product of plant height and basal diameter, and the virtual cylindrical volume described by the product of plant height and basal area, with basal area defined as $\pi * (\text{basal diameter})^2 / 4$ (Johnson et al. 1988). Using the information from the allometric set, we tested these allometric relationships applying simple power-law functions ($Y = aX^b$). We fitted these functions using log-linear ordinary least square regression analysis, i.e., applying linear least square regression after log transforming both sides of the equation ($\ln Y = \ln(a) + b \ln(X)$). We assumed a log-normally distributed, multiplicative error structure of our allometric data sets (Xiao et al. 2011). We ran these models considering plants from each growth form apart. For each allometric model, we reported the percentage relative standard error (PRSE) of the model parameters ($\text{PRSE} = 100 \times (\text{SE} / |\text{parameter}|)$), the residual standard error (RSE), the adjusted r^2 (r_{adj}^2), the AIC_c (second-order variant of AIC adjusted to correct for small-sample bias; Burnham and Anderson 2010), and the AIC_c weight (Burnham and Anderson 2010). PRSE values above 20 indicate that parameter estimates become less reliable (McCune and Grace 2002, Sileshi 2014). Model selection was based on AIC_c weights (Burnham and Anderson 2010, Sileshi 2014), calculated using R package MuMIn (version 1.15.6. <https://CRAN.R-project.org/package=MuMIn>). Selected models were validated on the basis of residual plots, outliers and influential points (Zuur et al. 2009).

Biomass prediction of individual plants

Applying the selected models we predicted the aboveground, belowground and total biomass of individual plants. These plant biomass predictions (B_{fit}) were back transformed into arithmetic units using the exponential function as follows:

$$B_{final} = \exp(B_{fit}).CF$$

with CF as a correction factor (Baskerville 1972, Chave et al. 2005) calculated as:

$$CF = \exp((RSE^2)/2)$$

in which RSE was the residual standard error of the selected allometric model.

Prediction errors

To examine bias in the biomass estimation (i.e., any systematic under- or overestimation compared to the true biomass), we regressed the log-transformed observed biomass versus the biomass predictions (B_{fit}) of the plants in the allometric set (Piñeiro et al. 2008). We further used the observed and predicted biomass (B_{final}) from individual plants or groups of plants of the allometric set to calculate absolute percentage errors (Sileshi 2014), as follows: Absolute percentage error = $100 * \text{abs}(\text{observed biomass} - \text{predicted biomass}) / \text{observed biomass}$. The absolute percentage errors were calculated by means of cross-validation (James et al. 2013), i.e., by holding out a subset of k randomly picked plants from the allometric set, estimating the regression equation coefficients with the remaining plants using the selected model, and applying those regression results to predict the biomass of the hold-out set. Prediction errors based on cross-validation tend to have an upward bias if the group size (k) becomes large (Fushiki 2011). For this reason we also reported the absolute percentage errors calculated without cross-validation, i.e., using predicted biomass values estimated with regression results obtained from all plants of the allometric set. These errors have a downward bias (Fushike 2011). Finally, we estimated the 95% upper and lower prediction intervals around the biomass prediction of single plants observed in the plots (i.e., not belonging to the allometric set), according the method supplied by Sokal and Rohlf (1995) (Appendix 2-4E).

Plot biomass

We calculated plot biomass by summation of the plant biomass estimates (B_{final}) of all plants recorded in a plot. We bootstrapped the plant biomass estimates in each plot to calculate a 95% non-parametric confidence interval around the plot biomass (applying the R package “bootstrap”). For this, we used bias-corrected and accelerated (BCa) confidence limits (Efron and Tibshirani 1993). These confidence intervals were divided by the plot biomass to obtain their relative width. We qualitatively compared

our plot biomass values with results from multi-species biomass estimations of high mountain vegetation elsewhere. In addition, we evaluated how the number of plant biomass predictions that were obtained by extrapolation, affected the relative width of the bootstrapped confidence intervals around the plot biomass estimates. We did this because we expected that in new studies, in which our regression equations are used, some plant measurements may fall outside the range observed in our allometric set. We also expected that in new studies the vegetation composition may differ substantially from our allometric set. Therefore, we explored how the relative width of the confidence intervals around the plot biomass values depended on the Bray-Curtis dissimilarities (Legendre and Legendre 1998) between each plot and the allometric set, quantified on the basis of plant counts regarding growth forms or genera. For correlation analysis we used the Spearman rank (r_s) coefficient. All statistical analyses were done in R software 3.2.4 (<https://www.R-project.org/>).

2.3 - RESULTS

Measurements of plants from the allometric set

The allometric set consisted of 476 plants, distributed over 31 genera (Appendix 2-2). In this set, tussocks were most abundant (144 plants) and basal rosettes least (14 plants) (Table 2-1). On average, tussock plants showed the highest plant height ($37.7 \pm \text{SD} = 14.4$ cm), and caulirosettes the highest basal diameter (2.9 ± 1.4 cm) and total biomass values (30.8 ± 24.0 g) (Table 2-1).

Model selection

For the aboveground, belowground and total biomass of basal rosettes and tussocks, the allometric regression models with the highest relative likelihood (as expressed by the AICc weights; Burnham and Anderson 2010) were those with the product of basal diameter and plant height (i.e., the rectangle) as descriptor (Appendix 2-3). The biomass of cushion plants was best modelled using their basal diameter. Regarding the other growth forms, several descriptors yielded relatively high AICc weights. The biomass was well modelled using rectangle or volume regarding caulirosettes; height and rectangle in case of herbs; diameter (clearly for aboveground and total biomass) and rectangle (for belowground biomass) for sedges/grasses; and volume and rectangle regarding shrubs. For several growth forms, the PRSE values of models that were ultimately selected for biomass prediction were well above 20 (Table 2-2; Appendix 2-3).

Table 2-1: Plant height, basal diameter and biomass of N plants in the allometric set. Values indicate: mean \pm SD (minimum, maximum)

Growth form	N	Plant height (cm)	Basal diameter (cm)	Belowground biomass (g)	Total biomass (g)
Basal rosettes	14	5.8 \pm 3.9 (0.4, 14.4)	1.0 \pm 1.2 (0.1, 4.6)	1.0 \pm 1.0 (0.01, 3.1)	1.2 \pm 1.1 (0.02, 3.1)
Caulirosettes	63	30.1 \pm 12.5 (10.6, 66.1)	2.9 \pm 1.4 (0.4, 6.2)	21.8 \pm 22.1 (0.51, 113.8)	30.8 \pm 24.0 (1.59, 122.5)
Cushions	40	3.9 \pm 1.1 (2.2, 8.8)	1.4 \pm 0.8 (0.3, 3.2)	0.8 \pm 1.7 (0.03, 9.9)	1.3 \pm 1.8 (0.09, 10.6)
Herbs	57	17.0 \pm 10.0 (3.5, 51.6)	0.2 \pm 0.1 (0, 0.6)	0.4 \pm 0.6 (0.01, 3.1)	0.7 \pm 0.7 (0.08, 3.4)
Sedges/grasses (non-tussock)	63	24.0 \pm 11.5 (6.6, 51.6)	1.0 \pm 0.5 (0.3, 2.5)	0.5 \pm 0.5 (0.05, 3.0)	1.5 \pm 1.3 (0.25, 6.4)
Shrubs	95	16.5 \pm 10.3 (1.5, 56.5)	0.3 \pm 0.2 (0, 1.4)	0.5 \pm 0.8 (0.001, 5.1)	4.5 \pm 5.0 (0.11, 32.7)
Tussocks	144	37.7 \pm 14.4 (9.2, 77.4)	0.6 \pm 0.4 (0.1, 2.8)	4.1 \pm 4.7 (0.03, 27.9)	5.9 \pm 8.2 (0.16, 52.0)

Table 2-2: Allometric models selected to predict plant biomass. Shown are the parameters and variables of the model $Biomass = e^{ln(a) \cdot Predictor^b}$, in which D = basal diameter; H = plant height; BA = basal area; N = number of plants in the allometric set; meanx = average of predictor values; sumx² = sum of squares of predictor values; meanx and sumx² are supplied to calculate prediction intervals of single plants not belonging to the allometric set (see Appendix 2-4E).

Growth form	N	Aboveground biomass					Belowground biomass						
		Predictor	ln(a)	b	RSE	meanx	sumx ²	Predictor	ln(a)	b	RSE	meanx	sumx ²
Basal rosettes	14	D . H	3.59	0.76	1.1	0.88	35	D . H	1.88	1.04	0.89	0.88	35.1
Cauli-rosettes	63	D . H	0.23	0.38	0.81	4.22	49.1	D . H	0.24	0.54	1.1	4.22	49.1
Cushions	40	D	1.38	1.38	0.74	0.18	15.8	D	1.39	1.25	0.9	0.18	15.8
Herbs	57	H	4.25	0.95	0.95	2.67	20.5	H	4.35	0.95	1.17	2.67	20.5
Sedges/grasses	63	D	0.31	1.29	0.81	0.18	16.9	D . H	1.87	0.31	0.85	2.88	30.7
Shrubs	95	BA . H	0.94	0.21	1.02	0.4	300	D . H	2.23	0.5	1.41	1.23	109
Tussocks	144	D . H	3.62	1.15	0.71	2.94	91.4	D . H	2.16	1.01	0.98	2.94	91.4

Growth form	N	Total Biomass					
		Predictor	ln(a)	b	RSE	meanx	sumx ²
Basal rosettes	14	D . H	1.52	0.93	0.83	0.88	35
Cauli-rosettes	63	BA . H	1.55	0.32	0.7	4.87	141
Cushions	40	D	0.58	1.33	0.73	0.18	15.8
Herbs	57	D . H	1.31	0.53	0.75	0.92	63.1
Sedges/grasses	63	D	0.25	0.85	0.66	0.18	16.9
Shrubs	95	BA . H	1.12	0.22	0.96	0.4	300
Tussocks	144	D . H	1.85	1.04	0.74	2.94	91.4

Biomass predictions of plants from the allometric set

The intercept and slope of the regressions of observed versus predicted biomass (Figure 2-1) did not differ significantly from 0 and 1, respectively, indicating that the fitted biomass values were in principle reliable (Sileshi 2014). Biomass predictions of single plants from the allometric set yielded absolute percentage errors that were generally well above 100% (Figure 2-2).

Summing the predicted biomass over several plants, however, reduced the error. Applying similar group sizes, the errors for belowground biomass were about two to three times larger than those obtained for aboveground and total biomass. For plant groups composed of several growth forms, applying for each growth form a number of plants that corresponded to the mean growth form density (rounded off to zero) across all plots, we obtained cross-validated absolute percentage errors of $14 \pm 10.0\%$ (mean \pm SD for 100 randomizations) for aboveground biomass, $27 \pm 23.0\%$ for belowground biomass, and $12 \pm 10.2\%$ for total biomass. Without cross-validation these errors were $11 \pm 10.3\%$, $24 \pm 18.0\%$, and $10 \pm 9.0\%$, respectively.

Plant observations in the plots

On average, a 1-m² plot contained 86 (\pm SD = 50.7) plants (Appendix 2-4). Shrubs and tussock plants were most frequently observed (in 60 and 59 plots, respectively), followed by caulirosettes (51 plots), herbs (46), cushions (41), sedges/grasses (41) and basal rosettes (34). In all plots together, we recorded 5521 plants distributed over 64 genera, which was twice the number of genera found in the allometric set. However, most of the more abundantly occurring genera in the plots were also part of the allometric set. For example, of the 24 genera that were registered with 50 plants or more in all plots combined, 21 were included in the allometric set. The Bray-Curtis dissimilarity between a plot and the allometric set was 0.71 ± 0.14 ; 0.37, 0.97 (mean \pm SD; minimum, maximum) for growth forms, and 0.78 ± 0.11 ; 0.47, 0.97 for genera. Individual plots contained 3.6 ± 4.3 (mean \pm SD) plants with heights above the maximum plant height seen in the allometric set, and 8.4 ± 13.5 plants with heights below the minimum height in that set (Appendix 2-4). For basal diameter, these values were 10.7 ± 11.7 and 9.1 ± 12.0 , respectively.

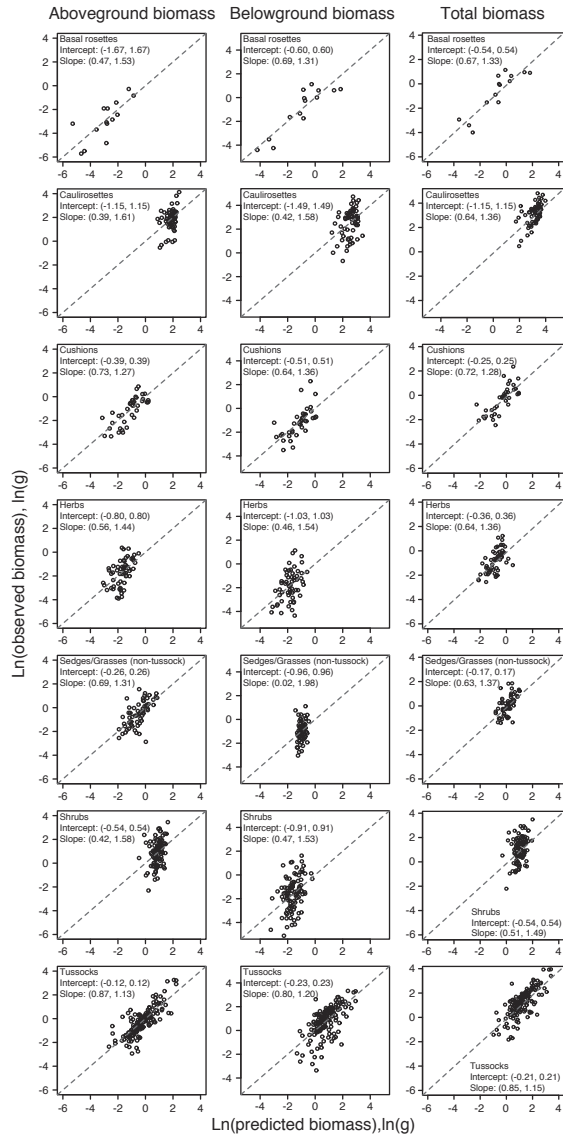


Figure 2-1: Relationships between observed and predicted biomass of plants from the allometric set. The dashed lines represent the line $y = x$. In the left corner of each diagram the 95% confidence intervals of the intercept and slope of the linear regression of the log-transformed observed plant biomass against the log-transformed predicted plant biomass.

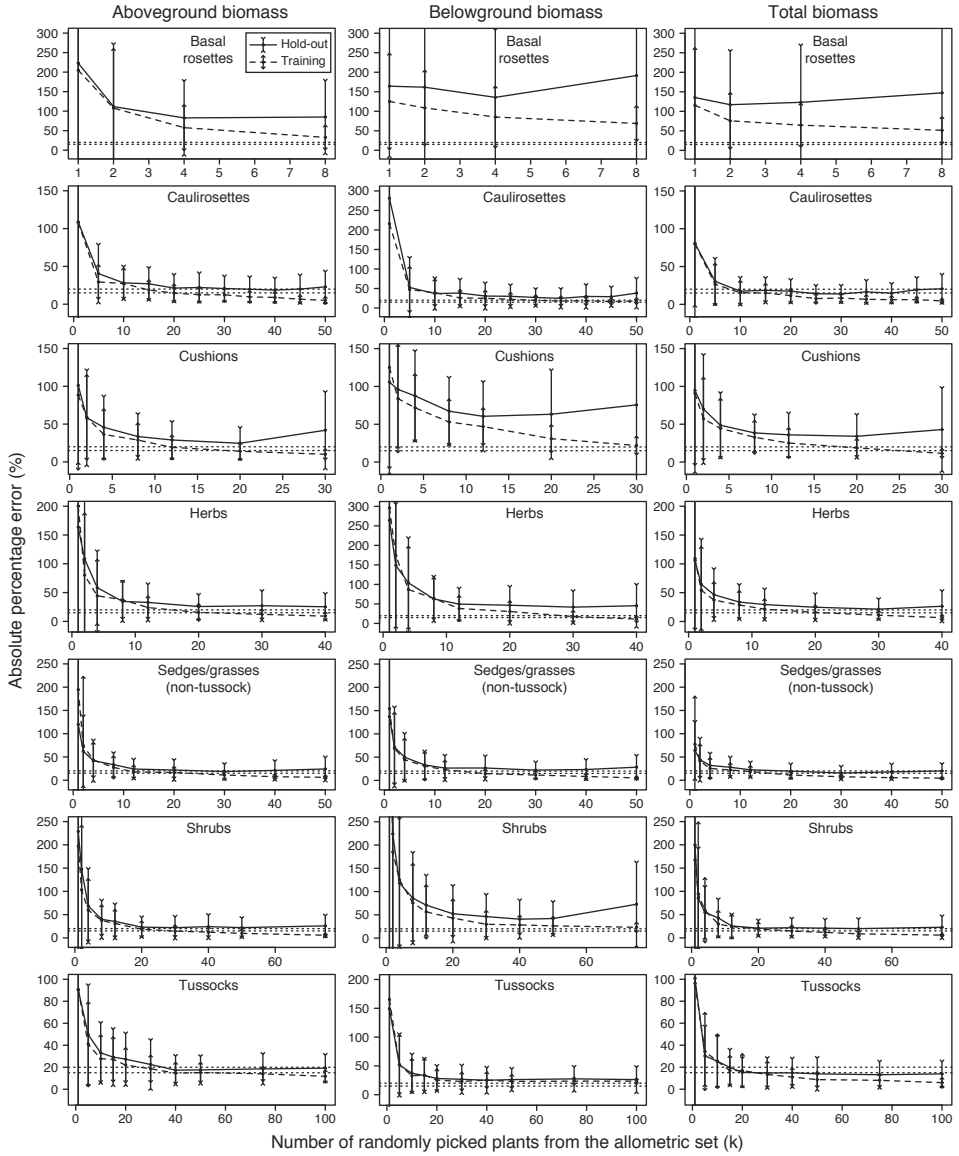


Figure 2-2: Absolute percentage error (%) of the predicted biomass summed over k randomly picked plants from the allometric set. Shown are the mean \pm SD (vertical bars) of 100 randomizations. Notice that some SD bars are too long to fit in the graph. Solid lines connect mean errors found in the hold-out set using cross-validation (James et al. 2013). Dashed lines connect mean errors found in the so-called training set, obtained without cross-validation. Axis scales may change between the graphs. To promote visual comparisons, dotted lines show error levels of 15% (lower line) and 20% (upper line).

Plot biomass

Plot biomass values ranged between 21 and 785 g m⁻² for aboveground biomass, 4 and 1878 g m⁻² for belowground biomass, and 25 and 2530 g m⁻² for total biomass. Averaging the plot biomass values yielded a mean of 329 (± SD = 190) g m⁻² for aboveground biomass, 743 (± 486) g m⁻² for belowground biomass and 1011 (± 627) g m⁻² for total biomass. The mean relative width of the 95% bootstrapped confidence intervals around the plot biomass estimates (Figure 2-3). was 72 (± SD =

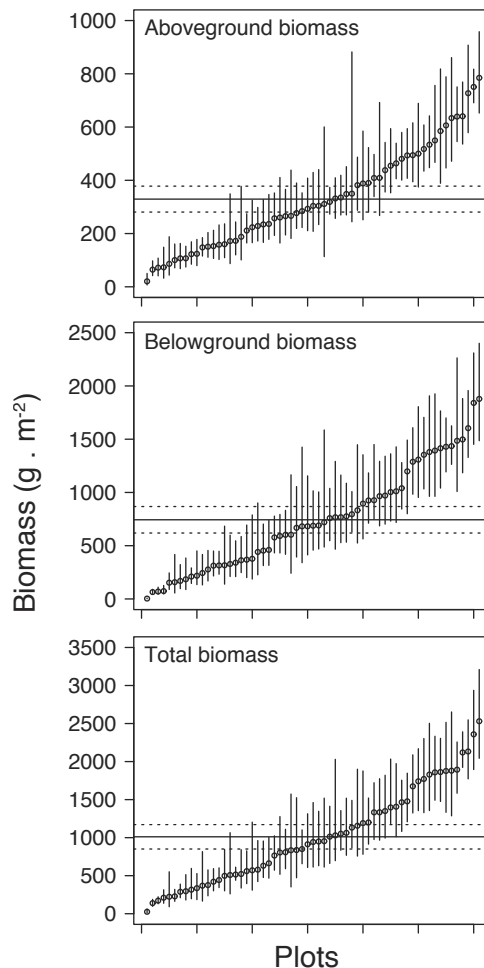


Figure 2-3: Biomass of vascular plants in 61 1-m² plots, presented in order of increasing plot biomass. Vertical lines represent the bootstrapped 95% confidence intervals. The continuous horizontal line in each plot is the across-plot mean, which is surrounded by its 95% confidence limits (dotted lines).

40)% for aboveground biomass, 90 (\pm 43)% for belowground biomass, and 80 (\pm 41)% for total biomass. These relative widths were not correlated, or were negatively correlated, with the number of plants that showed a height of basal diameter exceeding the range of the allometric set (Appendix 2-4). However, they did show a fairly strong and positive association with the Bray-Curtis dissimilarities regarding growth forms (rs values between 0.35 and 0.52; Appendix 2-4). Thus, stronger differences between plots and the allometric set regarding growth form or genus composition reduced the precision of the plot biomass estimates.

2.4 - DISCUSSION

Our study is the first to use allometric regression modelling to estimate aboveground, belowground and total biomass of multispecies vegetation samples in high mountain vegetation (Table 2-3). The across-plot averages for aboveground and belowground biomass recorded in our field area were within the range of biomass estimates obtained hitherto in the tropical Andes (Table 2-3) or in tropical and temperate biomes elsewhere (Appendix 2-5). These results suggest that our allometric modelling approach has a potential application to estimate the biomass of high mountain vegetation in the tropical Andes and elsewhere.

Compared to the standard practice of destructive biomass estimations in high mountain environments, our method has several advantages. 1) Non-destructive biomass estimation methods greatly facilitate studies of biomass change in vegetation through time. These studies are highly needed for ecosystem monitoring programs, such as those developed in the Andes of South America that focus on páramo restoration (Cabrera and Ramirez 2014, MADS 2015) or páramo responses to global change (Báez et al. 2014, Cuesta et al. 2017). 2) Our biomass values were based on the entire spectrum of vascular species in the plots, and therefore yield an optimal approximation of biomass production of páramo vegetation (Körner 2003). Allometric modelling approaches have been used in the tropical Andes, but only for biomass estimates of particular growth forms, such as tussocks (Verweij et al. 2003, Minaya et al. 2016), caulirosettes (Torres et al. 2012), basal rosettes (Minaya et al. 2016), shrubs (Torres et al. 2012) or cushion forms (Minaya et al. 2016). 3) We separated plants according to growth form in order to optimize the biomass estimation. Growth forms exist because plants apply different mechanisms of carbon assimilation (Dorrepaal 2007, Cáceres et al. 2014). Hence, plants from particular growth forms likely share similar size-mass relationships, for which reason we assume that allometric modelling performs better if growth forms are treated separately. 4) We only used plant height and basal diameter as basic predictors. Measuring these variables can be applied easily to all plants regardless of their growth form, which promotes the replicability of our

field method. Our results thus contribute to achieving the highly needed standardization of non-destructive biomass estimation of high mountain vegetation (Oliveras et al. 2014b). Plant height and basal diameter have been used before to estimate biomass for tussocks (Guevara et al. 2002, Oliveras et al. 2014 a) and shrubs (Ali et al. 2015). We refrained from using canopy diameter as suggested by others (Guevara et al. 2002, Oliveras et al. 2014 a, b). Basal diameter can be measured more precisely than canopy diameter, especially for páramo growth forms such as prostrated shrubs and caulirosettes. 5) Our study showed that potentially useful estimates of belowground biomass can be obtained on the basis of aboveground predictors (Niklas 2005). Environmental conditions typically occurring in páramo like low temperatures, high radiation and strong wind, favour relatively strong carbon investment in belowground organs (Körner 2003, Patty et al. 2010). Because the belowground biomass in páramo vegetation is relatively high, it is important to include this information in ecosystem studies (Niklas 2005, Ma et al. 2008). Belowground biomass estimates are highly needed to understand and predict the dynamics of regional and global carbon cycles (Scurlock and Hall 1998, Ma et al. 2008).

However, our method also comes with important limitations. Allometric biomass estimation methods require meticulously measuring predictor values of individual plants, which is far more time-consuming than destructively harvesting plot biomass, especially in non-forest vegetation. Using 1-m² plots (a plot size commonly used in monitoring programmes of high mountain vegetation (e.g., Cuesta et al. 2017), our field method seemed feasible. If larger plot sizes are applied, the aboveground biomass might perhaps be more efficiently assessed by means of proxies like plant cover (e.g., Cáceres et al. 2014).

Compared to destructive methods, the most important limitation of allometric methods is the uncertainties that inevitably come with the estimates and, moreover, the complexity involved to quantify these errors. Our allometric approach yielded large uncertainties around biomass estimates of groups with 20 plants or less (Fig. 2-2, Appendix 2-4). Errors around biomass estimates of single plants are largely the consequence of added effects of uncertainties related to plant measurements, model selection and model allometry (Chave et al. 2004). Fortunately, the errors of biomass estimates aggregated for groups of plants tended to cancel out. Indeed, for groups that mirrored the plots regarding plant density and growth form composition, we obtained cross-validated absolute percentage errors below 15% for aboveground and total biomass. We illustrate the importance of obtaining a trustworthy estimate of the error with an example (based on Sokal and Rohlf 1995). Assuming an experimental treatment on páramo vegetation using small open-top chambers to artificially increase the temperature (mimicking global warming) applying small, manageable plots that contain 100 plants. To be able to detect an expected treatment effect of 20% biomass

increase at a probability of 5% with a power of 80%, this experiment would need at least 17 treatment and 17 control plots, if the allometrically estimated plot biomass would have uncertainty of 20%. The bootstrapped confidence intervals around the plot means, which were derived from regression results applied to newly measured plants in the plots, also provided uncertainties for sample sizes that match the number of plants we found in 1-m² plots. Due to the exponential allometric models we applied, the upper prediction intervals tended to be larger than the lower intervals (Fig. 2-3). However, assuming that the bootstrapped prediction intervals were normally distributed around the estimated plot biomass and applying a t-value of two, the average widths of the 95% bootstrapped confidence intervals around the plot biomass estimates (which were between 72%, 90% and 80% for aboveground, belowground and total plot biomass, respectively), would roughly correspond to standard errors around the mean plot biomass of 18, 23 and 20%. Across the 61 plots, the landscape-scale uncertainty of the mean plot biomass values showed a coefficient of variation of 58, 65 and 62% for aboveground, belowground and total plot biomass, respectively. This variability is probably controlled for partially by effects of the environment (e.g., soil, elevation) and vegetation dynamics or land use history, a topic not further elaborated here. In comparison, Chave et al. (2004) reported a landscape-scale coefficient of variation of 23% in case of biomass estimates of tropical forest plots in Panama. In view of the above, it is evident that it depends on the research question and the associated sampling design of new studies whether or not our allometric equations can be applied meaningfully. In situations where the growth form or genera composition of target vegetation samples is broadly similar to our allometric set (e.g., showing Bray-Curtis dissimilarities matching those of the plots in our study), the application of our regression equations should yield uncertainties resembling the errors we found, provided the target samples contain at least 50 plants for aboveground and total biomass and 100 plants for belowground biomass. Considering the biogeographic affinities among páramo regions, we would expect that such conditions might be fulfilled in páramos located in Nariño, Macizo Colombiano and the Central Cordillera in Colombia (Londoño et al. 2014), or in páramos of northern Ecuador (Moscol and Cleef 2009, Cuesta et al. 2014). If the composition of growth forms or genera of such sufficiently large target samples becomes more different, larger uncertainties can be expected. For studies that need to non-destructively estimate the biomass of target samples containing 50 plants or less, we would recommend to improve the allometry by extending the size of our allometric set (Appendix 2-2) with measurements of biomass and predictor values of local plants, followed by renewed regression analyses and subsequent model selections. Increasing the number of plants in the allometric set likely reduces the influence of outliers on the RSE, which decreases the prediction errors. In such situations, the allometric set might preferably be expanded with

information from growth forms that showed PRSE values above 20 (Appendix 2-3). Chave et al. (2004) recommended constructing allometric equations for biomass estimation of tropical forests on the basis of at least 100 trees. In our current allometric set only tussocks reached that threshold. In all cases, great care must be taken to measure biomass and predictor values of plants with optimal accuracy.

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Table 2-3: Average aboveground and belowground biomass of páramo vegetation in the tropical Andes. If available, the standard deviation is added in parentheses.

Country	Location	Method	Aboveground biomass (g m ⁻²)	Belowground biomass (g m ⁻²)	Elevation (m asl)	Reference
Ecuador	Daldal	Destructive	815 (30)	133 (117)	3750-4000	Ramsay and Oxley (2001)
Ecuador	Mazar Reserve	Destructive	2020 (600)	no data	3453	Bremer et al. (2016)
Colombia	Laguna Verde	Destructive	603 (122)	1212	3600	Lutz et al. (1987)
Colombia	Laguna Verde	Destructive	197 (42)	886.3 (81)	3620	Beekman and Verweij (1987)
Colombia	Cruz Verde	Destructive	107 (26)	2.4 (0.9)	3300-3400	Cardozo and Schnetter (1976)
Colombia	Chingaza	Destructive	1725 (486)	no data	3670	Tol and Cleef (1992)
Colombia	Los Nevados	Destructive	no data	1327 (693)	4000	Rossenaar and Hofstede (1992)
Colombia	Los Nevados	Destructive	673 (77)	no data	4100	Rocha and Mondragon (1994)
Colombia	Los Nevados	Destructive	355 (44)	no data	4100	Hofstede et al. (1995)
Venezuela	Merida	Destructive	180 (126)	245 (117)	3530-4700	Smith and Klinger (1985)
Venezuela	El Banco	Destructive	no data	334 (108)	3800	Barmola and Montilla (1997)
Venezuela	Gavidia	Destructive	577 (131)	173 (96)	3000-3800	Montilla et al. (2002)
Colombia	Nariño	Allometric	329 (190)	743 (486)	3400-3600	This study