Grass allometry and estimation of above-ground biomass in tropical alpine tussock grasslands

IMMACULADA OLIVERAS,[1]* MAARTEN VAN DER EYNDEN,[2,3] YADVINDER MALHI,[1] NELSON CAHUANA,[4] CARLOS MENOR,[5] FLOR ZAMORA[4†] AND TORBJØRN HAUGAASEN[2]

[1]*Environmental Change Institute, School of Geography and the Environment, University of Oxford, South Parks Road, Oxford OX13QY, UK (Email: imma.oliveras@ouce.ox.ac.uk);* [2]*Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, Ås, and* [3]*The Government of Norway's International Climate and Forest Initiative, Norwegian Ministry of the Environment, Oslo, Norway;* [4]*Universidad Santo Antonio Abad del Cusco, Cusco, Peru; and* [5]*Departamento de Geología y Geoquímica, Facultad de Ciencias, Universidad Autónoma de Madrid, Madrid, Spain*

Abstract The puna/páramo grasslands span across the highest altitudes of the tropical Andes, and their ecosystem dynamics are still poorly understood. In this study we examined the above-ground biomass and developed species specific and multispecies power-law allometric equations for four tussock grass species in Peruvian high altitude grasslands, considering maximum height (h_{max}), elliptical crown area and elliptical basal area. Although these predictors are commonly used among allometric literature, they have not previously been used for estimating puna grassland biomass. Total above-ground biomass was estimated to be of 6.7 ± 0.2 Mg ha^{-1} (3.35 ± 0.1 Mg C ha^{-1}). All allometric relationships fitted to similar power-law models, with basal area and crown area as the most influential predictors, although the fit improved when tussock maximum height was included in the model. Multispecies allometries gave better fits than the other species-specific equations, but the best equation should be used depending on the species composition of the target grassland. These allometric equations provide an useful approach for measuring above-ground biomass and productivity in high-altitude Andean grasslands, where destructive sampling can be challenging and difficult because of the remoteness of the area. These equations can be also applicable for establishing above-ground reference levels before the adoption of carbon compensation mechanisms or grassland management policies, as well as for measuring the impact of land use changes in Andean ecosystems.

Key words: above-ground productivity, Andes, *Calamagrostis* spp., carbon stock, puna.

INTRODUCTION

Estimation of carbon stocks in tropical ecosystems and emissions of greenhouse gases from tropical deforestation and forest degradation have received increasing attention in recent years (e.g. Maniatis & Mollicone 2010; Asner 2011). Progress in developing a forest carbon compensation mechanism for tropical countries under the United Nations Framework Convention on Climate Change (UNFCCC), commonly referred to as Reduced Emissions from Deforestation and Forest Degradation – REDD+ (e.g. UNFCCC 2010), has sparked further research on establishing reliable methods for carbon estimation in tropical ecosystems (Phillips *et al.* 1998; Malhi & Phillips 2004; Saatchi *et al.* 2007; Asner 2009). Tropical forests have received the most attention (e.g. Saatchi *et al.* 2011;

Asner *et al.* 2012), but other tropical non-forest ecosystems can also contain substantial amounts of carbon (e.g. Scurlock & Hall 1998; Scurlock *et al.* 2002; Gibbon *et al.* 2010).

The Andean Neo-tropical tussock grasslands (termed as puna or páramo depending on their species composition) span the entire tropical Andes, and represent the main ecosystem at altitudes above approximately 3500 m a.s.l. However, despite their extensive distribution, we lack integrative descriptions of their physiognomy and functioning (Baldassini *et al.* 2012). The Andean high-altitude grasslands have been exposed to human activity for millennia (White & Maldonado 1991), but anthropogenic pressures have significantly increased over the last decades (Luteyn 1992, in Ramsay & Oxley 1996), mainly from grazing and burning (Bustamante & Bittencourt 2007). Apart from the direct impact on the ecosystem diversity and degradation, grazing and burning have also direct implications for carbon stocks. In an overview of twelve different Andean grassland biomass studies

doi:10.1111/aec.12098

(including puna/páramo) provided by Hofstede *et al.* (1995), above-ground biomass estimations ranged from 205 g m^{-2} to 2829–3553 g m^{-2}, depending on the degree of grazing or burning and pools sampled, which translates into 1.0 to 14.1–17.8 Mg C ha^{-1}. Ramsay & Oxley (2001) estimated standing biomass of 794 g m^{-2} and 837 g m^{-2} at two Ecuadorian páramo grassland sites, which translates to 4.0–4.2 Mg C ha^{-1}, and Gibbon *et al.* (2010) estimated 6.5 Mg C ha^{-1} in their grazed Peruvian puna sites. Although the different methodologies used in the various studies make comparisons difficult, it is recognized that high-altitude grasslands can play an important role in climate change mitigation and may be a suitable area for carbon compensation mechanisms because of their extensive distribution and ability to sequester carbon (Conant 2010).

Quantification of above-ground biomass and above-ground productivity can be achieved by three broad methods: (i) through intensive biomass destructive sampling; (ii) through allometric equations (Brown 1997; Navar *et al.* 2004; Chave *et al.* 2005; Feldspauch *et al.* 2011), and (iii) through remote sensing techniques (e.g. Saatchi *et al.* 2007; Asner 2009). Destructive methods may be a feasible method in open grasslands, but the remoteness of some areas and limited resource availability for transportation and processing the samples often make them very costly and logistically challenging. Remote sensing methods require targeted field-based measurements for calibration and validation. Allometric equations require an initial extensive destructive biomass sampling, but they can later be used as a consistent and non-destructive method for estimating above-ground biomass and productivity. Currently there are reliable allometric equations for different types of tropical forests (e.g. Chave *et al.* 2005; Feldspauch *et al.* 2011). However, few equations have been developed for non-forest tropical and subtropical ecosystems (Johnson *et al.* 1998; Navar *et al.* 2004). One of the first steps towards an integrative assessment of above-ground productivity in non-forest tropical and subtropical ecosystems would be the development of reliable allometric equations for major ecosystems, which could be adopted as a systematic method for measuring, reporting and verifying carbon compensation schemes. With this regard, multispecies models allow for wider applicability than species-specific models, but their suitability is easily more limited because of the inherent variability introduced in the models when considering different species together.

The tropical montane cloud forest – puna transition zone is experiencing increased deforestation and degradation from fire and grazing pressure (Bustamante & Bittencourt 2007), but comprehensive studies on the carbon stocks and productivity of these grasslands and the impacts of disturbance on them are scarce. This study focuses on the puna grasslands of the south-eastern Andes of Peru, which are under increasing pressure from fire (Oliveras *et al.* 2013) and grazing. The study was conducted on relatively undisturbed puna grassland in the buffer area of Manu National Park: the area had not been burned in 6 years and there was no grazing activity. The aims of this study were to (1) estimate above-ground biomass and biomass carbon content in a puna ecosystem, (2) develop allometric equations for dominant grasses and (3) explore the suitability of allometric equations as a reliable method for estimating above-ground productivity in tropical montane tussock grasslands.

METHODS

Study site

The study was carried out in the south-eastern Peruvian Andes, at approximately 3300 m a.s.l. in the south-western buffer area of Manu National Park (13°18′S, 71°58′W) (Fig. 1). At this altitude, a typical puna vegetation type is observed, dominated mainly by tussock-forming grasses. Dominant species include *Calamagrostis* spp., and *Festuca dolichophylla* J. Presl. (Gibbon *et al.* 2010). Average annual rainfall ranges from 1900 to 2500 mm, with a wet season spanning from October to April (Gibbon *et al.* 2010). Mean annual temperature is approximately 11°C at 3600 m a.s.l. (Gibbon *et al.* 2010). Puna soils are largely composed of an organic-rich A-layer, stony B/C-layers, and no Oh-layer (Gibbon *et al.* 2010; Zimmermann *et al.* 2010).

Data collection

We established eight transects of 30 m length and 2 m width in a puna area of the Wayqecha Biological Reserve in July 2010. Each transect consisted of eight 4 m^2 plots evenly distributed along the transect. At each transect, eight plots of 2×2 m were delineated, each separated by two metres. At each plot, we identified all plants to the genus or species level. For each tussock we measured the longest basal diameter (d_1), the basal diameter perpendicular to d_1 (d_2), the height as encountered in the field (h), the maximum height (stretched by hand; h_{max}), the longest tussock crown diameter (d_{c1}) and the diameter perpendicular to d_{c1} (d_{c2}). The crown- and basal diameters were used to estimate elliptical crown areas (CA) and basal areas (BA), following Johnson *et al.* (1998). The highest vegetative tiller was defined as plant height, excluding reproductive tillers that may surpass vegetative tillers (whose biomass is negligible, Guevara *et al.* 2002). All plants were hand clipped at ground level. Following Ramsay and Oxley (2001), fixed dead material (i.e. dead leaves still attached to the tussocks, Waren *et al.* 1994) was harvested, but ground litter was not. Most dead material remained attached to the tussocks and the ground litter content was little compared with the attached dead material. All plants were fresh weighed, bagged and subsequently oven dried at 70°C to
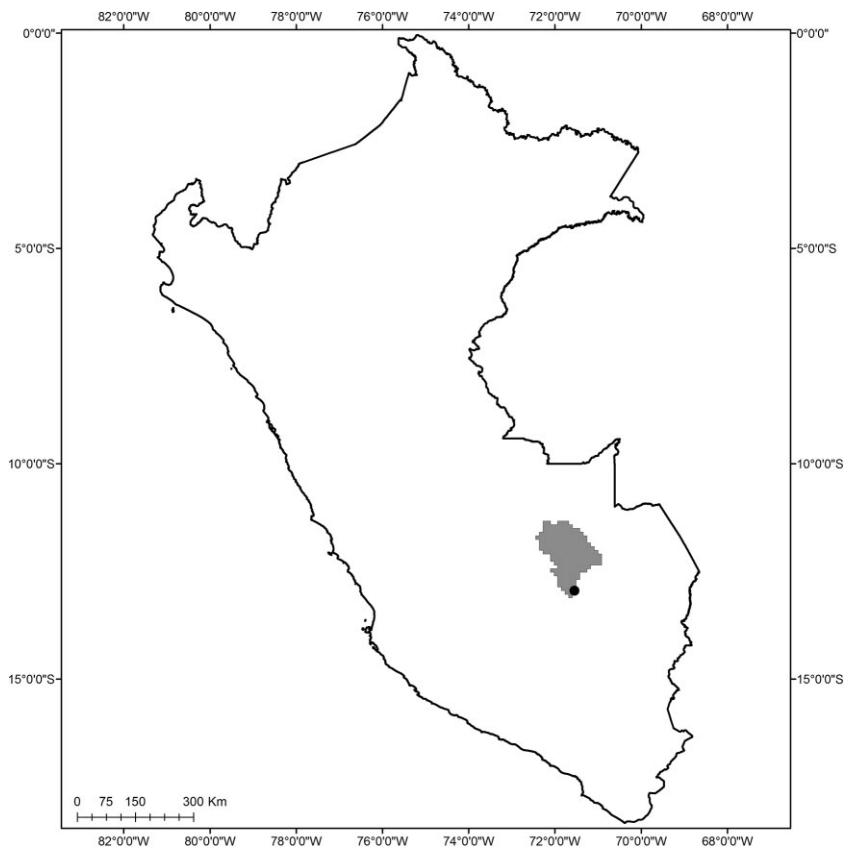
Fig. 1. Location of the study area (black dot), next to the southern Andean corner of Manu National Park (in grey), Peru (outline).

constant weight, and weighed to the nearest 0.1 g. Dried vegetative biomass was assumed to contain 50% carbon, following the same criteria as previous studies in the same area (Gibbon *et al.* 2010).

Regression models

We developed species-specific allometric equations for the four dominant tussock grasses: *Calamagrostis* spp. ($n = 1334$), *Festuca dolichophylla* ($n = 223$), *Scirpus rigidus* ($n = 638$) and *Juncus balticus* ($n = 177$). These have growth forms (i.e. tussocks) that make them suitable for developing allometric equations and constituted the majority (84.9%) of the total biomass at the study site. In addition, multispecies equations were developed, combining data from the four aforementioned species. The remaining species were rosette or cushion plants, and were therefore excluded from the analysis.

We tested 12 models (Table 1) based on linear relationships ($y = ax + b$ or $Y = ax_1 + bx_2 + cx_3$ for multiple explanatory variables) and non-linear regressions according to the power function ($y = ax^b$ or $y = ax_1^b \cdot x_2^c$ for multiple explanatory variables). One of the most common approaches to fit power-law relationships is by log-transforming both sides of the equation, yielding to a linear relationship, $\log(y) = \log(a) + b \cdot \log(y)$. However, stochasticity manifests

Table 1. Regression models tested to estimate above-ground biomass (AGB)

Model	Equation
I	$AGB = a + b(BA)$
II	$AGB = a(BA)^b$
III	$AGB = a + b(h_{max})$
IV	$AGB = ah_{max}{}^b$
V	$AGB = a + b(CA)$
VI	$AGB = a\,(CA)^b$
VII	$AGB = a + b(CA) + c(h_{max})$
VIII	$AGB = a(CA)^b \cdot (h_{max})^c$
IX	$AGB = a + b(BA) + c(CA)$
X	$AGB = a(BA)^b \cdot (CA)^c$
XI	$AGB = a + b(BA) + c(h_{max}) + d(CA)$
XII	$AGB = a(BA)^b \cdot (h_{max})^c \cdot (CA)^d$

BA = basal area (cm^2), CA = canopy area (cm^2), h_{max} = plant maximum height (cm).

differently in power-law and in log-transformed models (Gingerich 2000; Kerkhoff & Enquist 2009; Xiao *et al.* 2011). We therefore explored the error structure and distribution of power-law models of untransformed data (non-linear relationships, NLR) and log-transformed linear regressions (LR) following Xiao *et al.* (2011) using the *smart*

library of R (Warton *et al.* 2006). Data were not corrected for logarithmic bias (Baskerville 1972). The response variable was plant above-ground biomass (g), and explanatory variables were basal area (cm^2), crown area (cm^2), and maximum height (cm). We chose maximum height because it was a better predictor than height encountered in the field in all models (data not shown).

The best statistical model was selected by comparing the squared coefficient of regression (r^2), the residual standard error (RSE) of residuals, and the Akaike's information criterion (AIC) for all models. While higher values of r^2 show better fit, least squares approximation minimizes RSE. Similarly, the model with the lowest AIC indicates the best model, that is, the one which offers the best fit whilst allowing for the number of parameters (Akaike 1974).

Models were developed and calibrated with 80% of the data (*Calamagrostis* spp., $n = 1085$; *Festuca dolichophylla*, $n = 183$; *Scirpus rigidus*, $n = 508$; and *Juncus balticus*, $n = 140$). The remaining 20% of data were used to validate the models by applying prediction using the best fitted models (*Calamagrostis* spp., $n = 249$; *Festuca dolichophylla*, $n = 40$; *Scirpus rigidus*, $n = 130$; and *Juncus balticus*, $n = 37$). All statistical analyses were carried out using the R software 2.13.2 (R Development Core Team 2012).

RESULTS

Above-ground biomass and carbon stock

The above-ground vegetation was estimated to contain on average 6.7 ± 0.2 (standard error) Mg ha^{-1}dry biomass, which translates into 3.35 ± 0.1 Mg C ha^{-1}. *Calamagrostis* spp., *Scirpus rigidus*, *Festuca dolichophylla*, and *Juncus balticus* contributed 68.4%, 7.8%, 7.7%, and 1.0% to the total biomass, respectively. The four focal species thus comprise

84.9% of the total above-ground biomass. The sites had a high species richness, with a total number of 21 herbaceous species, 12 shrub species (being *Senecio rhizomatosus*, and *Ageratina cuzcoensis* the most common) and 5 fern species (belonging to *Licopodium* and *Blecnum* genera).

Allometric equations

Power-law relationships (models II, IV, VI, VIII, X and XII, Table 1) were explored by applying the logarithmic transformation of data and fitting a linear relationship, as the analysis of the error distributions supported the assumption of multiplicative log-normal error better than non-linear regression error (Appendix S1). Linear regressions did not show good fits for any species-specific (Appendices S2–S5) or multispecies models (Table 2). Models improved when the power function was used, either with a single or with multiple estimators (Table 2 and Appendices S2–S5). The analysis showed that models based on basal area and crown area were good estimators of plant above-ground biomass in both species-specific (Appendices S2–S5) and in multispecies regressions (Table 2), but adding maximum height to the models always improved them. However, maximum height itself was a poor predictor of above-ground biomass.

The power-law relationship based on basal area and crown area (model X) and the power-law relationship based on basal area, maximum height and crown area (model XII), gave the best fits for all species and for the multispecies analysis (Table 2, Appendices S2–S5) and we therefore tested the consistency of these models by comparing 20% of the measured above-ground biomass data (that had been not used to derive

Table 2. Regression models for four puna grass species combined (*Calamagrostis* sp., *Scirpus rigidus*, *Festuca dolichophylla* and *Juncus balticus*)

Regression	Coefficient				r^2	RSE	AIC
	a	b	c	d			
I	−7.518	0.011			0.708	65.87	21 948
II	0.061	0.756			0.734	0.334	1 262
III	−105.9	3.000			0.249	105.6	23 797
IV	−3.045	2.554			0.517	0.452	2 448
V	−43.94	0.082			0.678	69.16	22 139
VI	−2.532	1.316			0.686	0.364	1 607
VII	−38.29	0.084	−0.132		0.678	69.15	22 139
VIII	−3.245	1.021	0.921		0.718	0.345	1 394
IX	−35.51	0.007	0.043		0.783	56.75	21 365
X	5.5e-3	0.478	0.675		0.817	0.278	548
XI	−29.62	0.006	−0.138	0.045	0.784	56.72	21 364
XII	1.0e-3	0.480	0.935	0.373	0.851	0.251	150

The best-fit parameters are reported for each model, squared coefficient of regression (r^2), residual standard error (RSE), AIC = Akaike's Information Criterion, degrees of freedom = 1956.
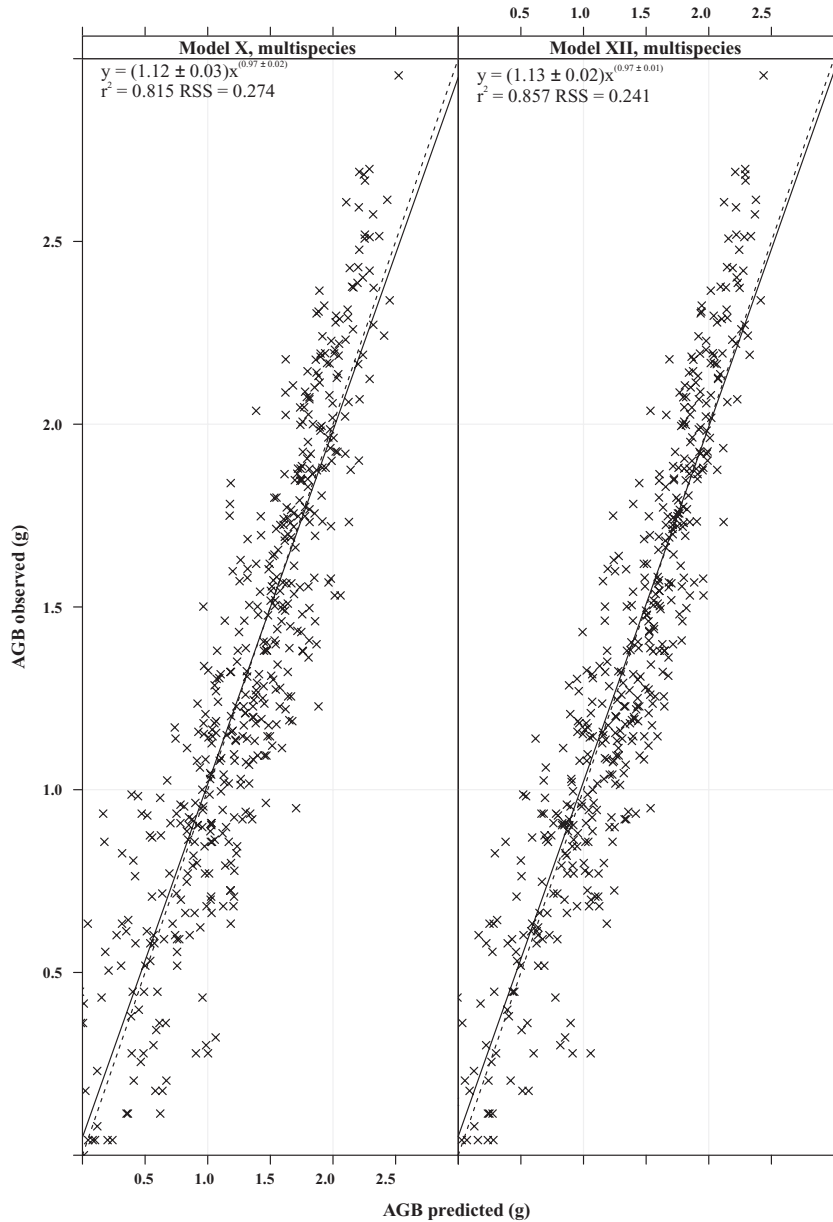
Fig. 2. Multispecies regressions between predicted above-ground biomass (AGB predicted) with Models X and XII and the above-ground biomass collected in the field (AGB observed). Each cross corresponds to an individual tussock. Coefficient values are expressed with the standard error (± SE). The black line corresponds to the model regression, and the dashed line corresponds to the 1:1. RSS corresponded to residual standard error.

the models) with the estimated above-ground biomass by the models. Model XII gave a slightly better fit than model X for all species, probably because of the inclusion of maximum height (Fig. 2, Appendices S6,S7).

The multispecies analysis confirmed models X and XII as the best models (Table 2), and the validation identified model XII as the best one for the multispecies equation (Fig. 2). Comparing this analysis to the species-specific models, the multispecies models X and XII (Table 2) had higher regression coefficients and higher RSE and AIC than models X

and XII for *Scirpus rigidus* (Model X: $r^2 = 0.806$, RSE = 0.222, AIC = −82.1; Model XII: $r^2 = −0.842$, RSE = 0.200, AIC = −186, Appendix S3), *Festuca dolichophylla* (Model X: $r^2 = 0.784$, RSE = 0.234, AIC = −7.4; Model XII: $r^2 = 0.816$, RSE = 0.218, AIC = −33, Appendix S4) and *Juncus balticus* (Model X: $r^2 = 0.766$, RSE = 0.242, AIC = −4.57; Model XII: $r^2 = 0.778$, RSE = 0.238, AIC = 0.70, Appendix S5). Models X and XII for *Calamagrostis* spp. had a higher coefficient of regression and lower RSE and AIC (Model X: $r^2 = 0.841$, RSE = 0.246, AIC = 37.8;

Model XII: $r^2 = 0.855$, RSE = 0.235, AIC = −59.7, Appendix S2) than the multispecies models X and XII (Table 2), being consistent with validation data (Fig. 2, Appendices S6,S7).

DISCUSSION

The above-ground vegetation was estimated to contain 3.35 Mg C ha^{-1}. This value is similar to results from Ecuadorian páramo grasslands, where carbon densities of 4.0 and 4.2 Mg C ha^{-1} were found at 3750 and 4000 m a.s.l., respectively (Ramsay & Oxley 2001). However, our results contrast significantly with Gibbon *et al.* (2010) who estimated above-ground carbon density at 6.5 Mg C ha^{-1} for their puna sites. This difference may be explained by the fact that Gibbon *et al.* (2010) also quantified the contribution of litter and moss to the carbon pool. The litter contribution in the study area was, however, negligible because most dead material remained attached to the tussock (up to 70%, Hofstede *et al.* 1995, Appendix S8).

Several other biomass studies have been carried out in a selection of high-altitude tropical and temperate grasslands (Hofstede *et al.* 1995), but differences in sampling techniques make comparisons difficult. More studies with a standardized methodology should be conducted in order to enhance the capability of cross-site comparisons, which will ultimately lead to a better understanding of the spatial distribution of carbon content in high altitude tropical grassland ecosystems. Another source of variation among studies is seasonality and time of biomass sampling. In the current study, we included live and dead above-ground biomass to avoid any seasonal effects, although seasonality in the study area is almost non-existent, because radiation and temperature remain fairly constant throughout the year and relative humidity is still above 85% in the driest months (July–August, Girardin *et al.* 2013).

The current study only reported for above-ground carbon stocks because the goal of the study was to provide estimation of the above-ground biomass as well as sound allometric equations that allow for non-destructive estimations of above-ground biomass. The contribution of below-ground biomass is thought to be very important in open high-altitude grasslands, with similar carbon stocks above-ground and below-ground (Oliveras, unpubl. data, 2012).

Almost 85% of the vegetation was composed of four tussock grassland species, of which *Calamagrostis* spp. accounted for most of the biomass. However, 38 different species of grasses, shrubs and ferns were identified, showing the high diversity of these high-altitude grasslands, as has also been found in other studies in puna and páramo (Luteyn 1999).

This study shows that basal area, maximum height and crown area provide a reliable basis for above-ground biomass estimation in tussock grasslands, using allometric equations. Basal area and crown area were the most influential predictors in our models, but adding maximum height always improved the fit of the models. Other studies in tussock grasslands (Andariese & Covington 1986; Johnson *et al.* 1998; Nafus *et al.* 2009) have also found basal area to be the main explanatory variable. However, results differ with regards to inclusion of other variables. Johnson *et al.* (1998), Andariese and Covington (1986) and Nafus *et al.* (2009) reported small or no improvement when height was added to their models. Guevara *et al.* (2002) reported that adding height improved the model for some species investigated. Nevertheless, equations only based on maximum height were not good predictors of above-ground biomass, nor were equations based on crown area. Basal area was shown to be the main determinant of goodness of fit. This parameter may be time consuming to measure in field, but is still a useful tool to allow for a relatively fast assessment of above-ground biomass, especially in such remote ecosystems.

The *Calamagrostis* spp. allometric equations gave better fits than the multispecies model, but the other species-specific equations had similar estimation results to the multispecies model. Therefore, the equations developed for *Calamagrostis* spp. based on BA and CA (models X and XII) would be the most appropriate in grassland communities where *Calamagrostis* spp. is the dominant tussock grass. However, for species-rich tussock grassland communities, the multispecies models based on basal area and crown area (models X and XII) would give a more solid prediction of above-ground biomass. Nafus *et al.* (2009) also developed multispecies grassland equations in a study conducted in Arizona. Independent of the variables included, the successful combination of different species into one model may have important implications for future estimates of above-ground carbon stocks in tussock grasslands using allometric equations, as it eliminates the need of species identification and destructive sampling. However, it must be underlined that multispecies models are only an advantage in general above-ground biomass, productivity and carbon stock measurements. In ecological studies, it would be of interest to know the species composition of the investigated area, especially in such highly diverse ecosystems. It is also important to note that, although these allometries may be applicable in most tropical Andean grasslands with similar species composition (thus dominated by *Calamagrostis* sp., *Juncus* sp., *Scirpus* sp. and *Festuca* sp. tussocks), validation studies for other areas would be very valuable to test its wider applicability. This is especially important for areas with different environmental factors or different species composition.

The current study provides a reliable method for non-destructive biomass and productivity estimation in high-altitude tussock grasslands. Most allometric equations have been developed for tropical forests, but grasslands can also store large amounts of carbon and have as much productivity as forest ecosystems (Scurlock & Hall 1998). The applicability of these results may be useful in remote and often challenging puna grasslands of the Tropical Andes, where destructive sampling can be of limited applicability due to logistical constraints. These equations can be also applicable to measure the productivity of grassland systems and for establishing reference levels before the adoption of carbon compensation mechanisms or grassland management policies, as well as for measuring the impact of land use changes in Andean ecosystems.

ACKNOWLEDGEMENTS

REFERENCES

Akaike H. (1974) A new look at the statistical model identification. *IEEE Trans. Automat. Contr.* **19,** 719–23.

Andariese S. W. & Covington W. W. (1986) Biomass estimation for four common grass species in Northern Arizona ponderosa pine. *J. Range Manage.* **39,** 472–3.

Asner G. P. (2009) Tropical forest carbon assessment: integrating satellite and airborne mapping approaches. *Environ. Res. Lett.* **4,** 034009.

Asner G. P. (2011) Painting the world REDD: addressing scientific barriers to monitoring emissions from tropical forests. *Environ. Res. Lett.* **6,** 021002.

Asner G. P., Mascaro J., Muller-Landau H. C. *et al.* (2012) A universal airborne LiDAR approach for tropical forest carbon mapping. *Oecologia* **168,** 1147–60.

Baldassini P., Volante J. N., Califano L. M. & Paruelo J. M. (2012) Regional characterization of the structure and productivity of the vegetation of the Puna using MODIS images. *Ecología Austral* **22,** 22–32.

Baskerville G. (1972) Use of logarithmic regression in the estimation of plant biomass. *Can. J. For. Res.* **2,** 49–53.

Brown S. (1997) Estimating biomass and biomass change of tropical forests: a primer. *FAO For. Pap.* **134** [Cited 24 September 2012.] Available from URL: http://www.fao.org/docrep/w4095e/w4095e00.htm

Bustamante J. A. & Bittencourt M. D. (2007) Ecological zoning of an Andean grasslands (puna) at the Manu Biosphere Reserve, Peru. *Int. J. Environ. Sustain. Dev.* **6,** 357–72.

Chave J., Andalo C., Brown S. *et al.* (2005) Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* **145,** 87–99.

Conant R. T. (2010) *Challenges and Opportunities for Carbon Sequestration in Grassland System – A Technical Report on Grassland Management and Climate Change Mitigation.* Food and Agriculture Organization of the United Nations, Rome.

Feldspauch T. R., Banin L., Phillips O. L. *et al.* (2011) Height-diameter allometry of tropical forest trees. *Biogeosciences* **8,** 1081–106.

Gibbon A., Silman M. R., Malhi Y. *et al.* (2010) Ecosystem carbon storage across the grassland–forest transition in the high Andes of Manu National Park, Peru. *Ecosystems* **13,** 1097–111.

Gingerich P. D. (2000) Arithmetic or geometric normality of biological variation: an empirical test of theory. *J. Theor. Biol.* **204,** 201–21.

Girardin C. A. J., Farfan-Rios W., Garcia K. *et al.* (2013) Spatial patterns of above-ground structure, biomass and composition in a network of six Andean elevation transects. *Plant Ecol. Div.* doi: 10.1080/17550874.2013.820222.

Guevara J. C., Gonnet J. M. & Estevez O. R. (2002) Biomass estimation for native perennial grasses in the plain of Mendoza, Argentina. *J. Arid Environ.* **20,** 613–19.

Hofstede R. G. M., Mondragon Castillo M. X. & Rocha Osorito C. M. (1995) Biomass of grazed, burned, and undisturbed páramo grasslands, Colombia. I. Aboveground Vegetation. *Arct. Alp. Res.* **27,** 1–12.

Johnson P. S., Johnson C. L. & West N. E. (1998) Estimation of phytomass for ungrazed crested wheatgrass plants using allometric equations. *J. Range Manage.* **41,** 421–5.

Kerkhoff A. J. & Enquist B. J. (2009) Multiplicative by nature: why logarithmic transformation is necessary in allometry. *J. Theor. Biol.* **257,** 519–21.

Luteyn J. L. (1992) Páramos: why study them? In: *Páramo: An Andean Ecosystem under Human Influence* (eds Balslev & Luteyn) pp. 1–14. Academic Press, London.

Luteyn J. L. (1999) *Páramos: A Checklist of Plant Diversity, Geographical Distribution and Botanical Literature.* Memoirs of the New York Botanical Garden. New York Botanical Garden, New York.

Malhi Y. & Phillips O. L. (2004) Tropical forests and global atmospheric change: a synthesis. *Phil. Trans. R. Soc. B Biol. Sci.* **359,** 549–55.

Maniatis D. & Mollicone D. (2010) Options for sampling and stratification for national forest inventories to implement REDD+ under the UNFCCC. *Carbon Balance Manage.* **5,** art 9, 14.

Nafus A. M., McClaran M. P., Archer S. R. & Throop H. L. (2009) Multispecies allometric models predict grass biomass in semidesert rangeland. *Rangel. Ecol. Manage.* **62,** 68–72.

Navar J., Mendez E., Najera A., Graciano J., Dale V. & Parresol B. (2004) Biomass equations for shrubs species of Tamaulipan thorn scrub of North-eastern Mexico. *J. Arid Environ.* **59,** 657–74.

Oliveras I., Malhi Y., Salinas N. *et al.* (2013) Changes in forest structure and composition after fire in tropical montane

cloud forests near the Andean treeline. *Plant Ecol. Div.* doi: 10.1080/17550874.2013.816800.

Phillips O. L., Malhi Y., Higuchi N. *et al.* (1998) Changes in the carbon balance of tropical forests: evidence from long-term plots. *Science* **282,** 439–42.

R Development Core Team (2012) *R: A Language and Environment for Statistical Computing.* R Foundation for Statistical Computing, Vienna. ISBN 3-900051-07-0, [Cited 28 August 2012.] Available from URL: http://www.r-project .org

Ramsay P. M. & Oxley E. R. B. (1996) Fire temperatures and post fire plant community dynamics in Ecuadorian grass páramo. *Vegetatio* **124,** 129–44.

Ramsay P. M. & Oxley E. R. B. (2001) An assessment of aboveground net primary productivity in Andean grasslands of central Ecuador. *Mt. Res. Dev.* **21,** 161–7.

Saatchi S., Harris N. L., Brown S. *et al.* (2011) Benchmark map of forest carbon stocks in tropical regions across three continents. *Proc. Natl Acad. Sci. USA* **108,** 9899–904.

Saatchi S., Houghton R. A., Dos Santos Alvalá R. C., Soares J. V. & Yu Y. (2007) Distribution of aboveground live biomass in the Amazon basin. *Global Change Biol.* **13,** 816–37.

Scurlock J. M. O. & Hall D. O. (1998) The global carbon sink: a grassland perspective. *Global Change Biol.* **4,** 229–33.

Scurlock J. M. O., Johnson K. & Olson R. J. (2002) Estimating net primary productivity from grassland biomass dynamics measurements. *Global Change Biol.* **8,** 736–53.

UNFCCC (United Nations Framework Convention on Climate Change) (2010) Outcome of the work of the Ad Hoc Working Group on Long-term Cooperative Action under the Convention: policy approaches and positive incentives on issues relating to reducing emissions from deforestation and forest degradation in developing countries; and the role of conservation, sustainable management of forests and enhancement of forest carbon stocks in developing countries. UNFCCC COP 16, Cancun. [Cited 23 July 2013.] Available from URL: http://unfccc.int/resource/docs/ 2010/cop16/eng/07a01.pdf#page=2

Waren C. H. A., Paps W. A. & Williams R. J. (1994) Long-term vegetation change in relation to cattle grazing in subalpine grassland and heathland on the Bogong High Palins: an analysis of vegetation records from 1945 to 1994. *Aust. J. Bot.* **42,** 607–39.

Warton D. I., Wright I. J., Falster D. S. & Westoby M. (2006) Bivariate line-fitting methods for allometry. *Biol. Rev.* **81,** 259–91.

White S. & Maldonado F. (1991) The use and conservation of natural resources in the Andes of southern Ecuador. *Mt. Res. Dev.* **11,** 37–55.

Xiao X., White E., Hooten M. B. & Durham S. L. (2011) On the use of log-transformation vs. nonlinear regression for analyzing biological power laws. *Ecology* **92,** 1887–94.

Zimmermann M., Meir P., Silman M. R. *et al.* (2010) No differences in soil carbon stocks across the tree line in the Peruvian Andes. *Ecosystems* **13,** 62–74.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Akaike's Information Criterion coefficients on untransformed data.
Appendix S2. Regression models for *Calamagrostis* sp.
Appendix S3. Regression models for *Scirpus rigidus*.
Appendix S4. Regression models for *Festuca dolichophylla*.
Appendix S5. Regression models for *Juncus balticus*.
Appendix S6. Species-specific regressions between predicted above-ground biomass with model X and the above-ground biomass collected in the field.
Appendix S7. Species-specific regressions between predicted above-ground biomass with Model XII and the above-ground biomass collected in the field.
Appendix S8. Photo of one of the Wayqecha transects.