Shrub biomass estimation in the semiarid Chaco forest: a contribution to the quantification of an underrated carbon stock

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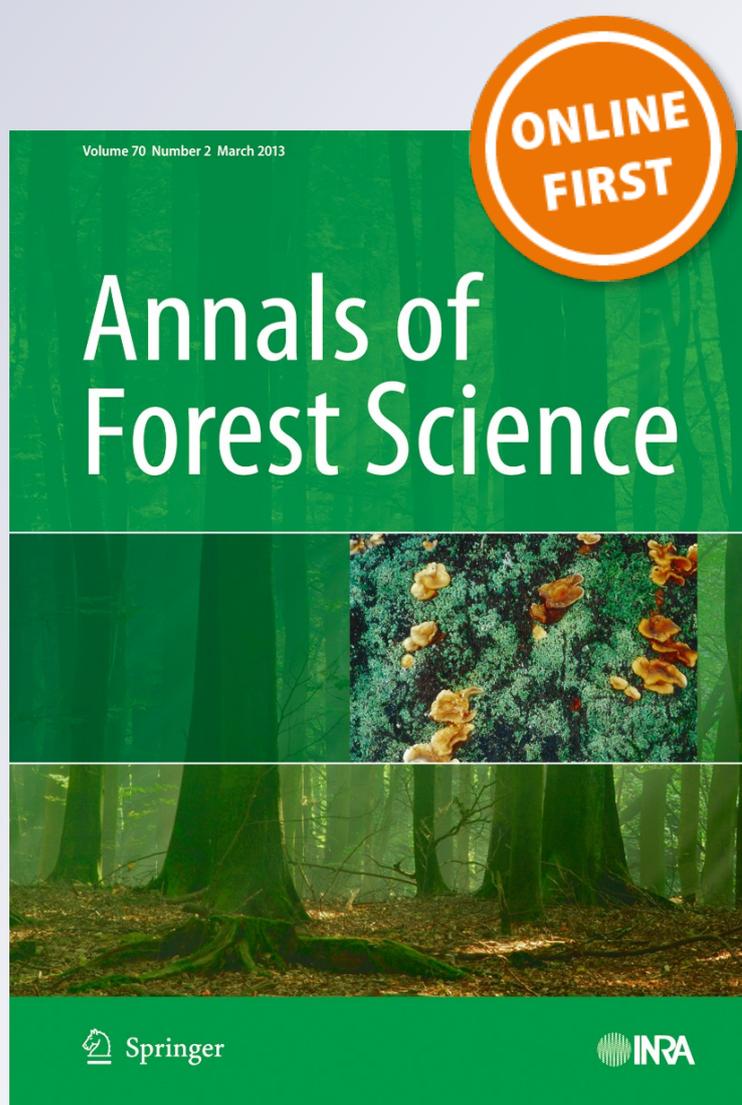**Georgina Conti · Lucas Enrico · Fernando Casanoves · Sandra Díaz**

Abstract
• *Context* The quantification of biomass of woody plants is at the basis of calculations of forest biomass and carbon stocks. Although there are well-developed allometric models for trees, they do not apply well to shrubs, and shrub-specific allometric models are scarce. There is therefore a need for a standardized methodology to quantify biomass and carbon stocks in open forests and woodlands.
• *Aims* To develop species-specific biomass estimation models for common shrubs, as well as a multispecies shrub model, for the subtropical semiarid Chaco forest of central Argentina.
• *Methods* Eight shrub species (*Acacia aroma*, *Acacia gilliesii*, *Aloysia gratissima*, *Capparis atamisquea*, *Celtis ehrenbergiana*, *Larrea divaricata*, *Mimozyganthus*

carinatus, and *Moya spinosa*) were selected, and, on average, 30 individuals per species were harvested. Their total individual dry biomass was related with morphometric variables using regression analysis.
• *Results* Crown area as well as crown-shaped variables proved to be the variables with the best performance for both species-specific and multispecies shrub models. These allometric variables are thus recommended for standardized shrub biomass assessments.
• *Conclusion* By accounting for the shrub component of the vegetation, our models provide a way to improve the quantification of biomass and carbon in semiarid open forest and woodlands.

Contribution of the co-authors Georgina Conti conducted sampling design, field work, and data analysis and wrote the manuscript. Lucas Enrico participated in field work and in writing the manuscript. Fernando Casanoves helped in data analysis and manuscript revision. Sandra Díaz coordinated the research project and participated in writing the manuscript.

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1 Introduction

Plant biomass is a key ecosystem property resulting from the net balance between carbon gains through photosynthesis and losses by respiration, tissue turnover, and natural or human-induced removal (Chapin et al. 2011). The quantification of forest biomass has a long history because of the importance of its derived products to many societies (e.g., timber, fuel). It has received renewed attention in the past decades because forest standing biomass represents about 44 % of the world forest carbon pool (Pan et al. 2011) and therefore plays a fundamental role in climate change mitigation. The United Nations Framework Convention on Climate Change has included plant biomass as an essential climate variable needed to improve the prediction and

mitigation of global climate change and its impact on human societies (GTOS 2010). Renewed interest in improving measurement of biomass comes from the Reduction of Emissions due to Deforestation and Forest Degradation mechanisms (REDD and REDD+), which require the monitoring of changes in carbon fluxes and stocks in the context of deforestation and forest degradation.

Plant biomass is often estimated by harvesting a sample of individuals of a species or growth form and relating their dry mass with morphometric variables through an allometric model (usually referred to as a "dimensional analysis" *sensu* Whittaker and Woodwell 1968). Dimensional analysis to quantify biomass relies on the consistency of an allometric relationship between plant dimensions and the dry mass for a given species or group of species (Jenkins et al. 2004). For tree species, stem-related variables, specifically diameter and height, have proven to accurately predict individual biomass (Chave et al. 2005). The development of general or species-specific tree biomass functions, as well as the standardization of their parameters, has experienced a global surge during the last few years as part of the research on climate change (Brown 1997; Chave et al. 2005; Jenkins et al. 2003; Ketterings et al. 2001; Nelson et al. 1999; Pilli et al. 2006).

In woodlands and open forests, woody development takes different physiognomies, with shorter individuals with high basal ramification resulting in a high crown area. The standard diameter at breast height commonly used in forestry studies, is thus impractical in these systems. On the other hand, measuring only the main stem would result in an underestimation of the actual biomass stored in the forest. In multistemmed species estimations, each stem is usually considered as a separated tree, applying the standard relationship between diameter and height with biomass per stem. However, this can be extremely time consuming for shrub species with more than ten ramifications per plant, as is common in the Chaco (Fig. 1). In addition, variables that express the size of the crown often appear to be more useful for shrub biomass estimations, since they define better the architecture of the shrub (Chojnacky and Milton 2008; Hierro et al. 2000; Hofstad 2005; Murray and Jacobson 1982; Oñatibia et al. 2010; Vilà 1993).

Allometric models for open forests and woodlands are much less common than those for closed forests, likely because the former store less carbon per unit area and also because shrublands and the shrub component of forests and woodlands have less economic value (e.g., as timber) and tend to not be represented in forestry inventories. However, shrubs represent a large biomass and carbon pool usually underestimated in carbon storage assessments, a pattern especially true for the subtropical Chaco region, the most extensive semiarid forest in South America (Conti and Díaz 2013).

Biomass models have been developed for a number of shrub species in different ecosystems of the world (Ludwig

Fig. 1 *Larrea divaricata*, showing a typical multistemmed architecture in the semiarid Chaco vegetation of central Argentina

et al. 1975; Lufafa et al. 2009; Murray and Jacobson 1982; Sampaio and Silva 2005; Vora 1988; Zeng et al. 2010), but only a few species-specific equations for shrubs from (or common to) the Chaco forest have been published to date (Gaillard de Benitez et al. 2002; Hierro et al. 2000; Iglesias et al. 2012; Iglesias and Barchuk 2010; Northup et al. 2005). In particular, there are several common shrub species in the Chaco ecosystems for which species-specific allometric models have not yet been developed, and there are not generalized multi-species models specifically for shrubs published to date. Iglesias and Barchuk (2010) and Iglesias et al. (2012) proposed some different allometric models for groups of functionally similar shrubs based on stem-related variables (diameter and height).

In this study, we aimed to develop species-specific biomass estimation models for eight common shrubs in the semiarid Chaco forest of central Argentina. We tested the relative performance of crown-related variables over stem-related ones to predict individual shrub aboveground biomass. We also developed a multispecies shrub model for the semiarid Chaco forest. Although this study includes only Chaco shrub species, we provide a basis for the standardization of useful variables to predict more accurately the aboveground shrub biomass component of open forests and woodlands.

2 Material and methods

2.1 Study area

The study was carried out in central-western Argentina (between 31°16′–31°37′ S and 65°25′–65°32′ W), covering

an area of about 450 km^2 within the semi-arid southern extreme of the Gran Chaco subtropical seasonal forest (Morello et al. 1977). The climate is monsoon-like with a mean annual precipitation of 550 mm concentrated to spring–summer (October–March) and a mean annual temperature of 20 °C (Capitanelli 1979). Soils are mainly sandy-loam aridisols of alluvial origin (Gorgas and Tassile 2003). The dominant vegetation is an open woodland whose canopy is dominated by the trees *Aspidosperma quebracho-blanco* and *Prosopis flexuosa*. The dense shrub layer is dominated by several multistemmed species of families such as Fabaceae and Zygophyllaceae, with *Mimozyganthus carinatus*, *Acacia gilliesii*, and *Larrea divaricata* being the most abundant species (Cabido et al. 1992). At present, the Chaco most "pristine" vegetation is represented by very small patches of well-preserved forest embedded in a mosaic of shrub-dominated ecosystem types in different stages of succession, degradation, or management.

2.2 Species selection

Following the floristic description of the area by Cabido et al. (1992), as well as our own field surveys, we selected eight subcanopy shrub species including *Acacia aroma*, *A. gilliesii*, *Aloysia gratissima*, *Capparis atamisquea*, *Celtis ehrenbergiana*, *L. divaricata*, *M. carinatus*, and *Moya spinosa*. Nomenclature followed Zuloaga and Morrone (1996, 1999) and their regular online updates at http://www2.darwin.edu.ar/Proyectos/FloraArgentina/FA.asp. In this study, we considered a shrub any individual woody plant with multiple basal stems growing from the same root system (Chojnacky and Milton 2008). In the case of *C. ehrenbergiana*, which includes trees as well as shrubs, we considered only the shrub form (formerly called *Celtis pallida*); therefore, we did not test the applicability of the equation to the tree form of this species (formerly called *Celtis tala*). A list of scientific and common names and their synonyms is included in Online Resource 1.

Although all species are common across the study area, some of them are more abundant in closed forest patches, while others appear predominantly associated to open shrublands and degraded sites. Among the selected species, *C. atamisquea*, *C. ehrenbergiana*, and *M. spinosa* are closed related to primary forests. Species like *A. gilliesii*, *M. carinatus*, and *L. divaricata* are widely distributed across all vegetation types in the area, but the first two species appeared as dominant in forests and closed shrublands, while *L. divaricata* clearly did so in open shrublands and degraded areas. *A. gratissima* and *C. ehrenbergiana* are especially abundant in selectively logged sites. *A. aroma* is the species with the lowest abundance in the area and seems to be more associated to roadsides and watering holes.

2.3 Species sampling

An average of 30 individuals per species were chosen in order to cover the widest possible range of plant sizes observed in the field for each species. The selected species were sampled across the study area keeping climatic and soil conditions as constant as possible. Several variables often used in allometric estimations of shrub biomass were measured in every individual plant prior to destructive sampling: total height (*H*, centimeters), defined as the distance between the ground surface and the highest crown point; diameter of the longest stem (DLS, centimeters) over the root collar (usually between 5 and 10 cm from the ground surface); number of ramifications emerging from the root collar (NR); maximum crown diameter (CD$_1$, centimeters), and its perpendicular diameter (CD$_2$, centimeters). Crown diameters were used to calculate crown area as follows:

$$CA = \pi \times (R_1 \times R_2)$$

where

CA   Crown area (square centimeters)
R_1 Radius from the longest crown diameter (CD$_1$) in centimeters
R_2 Radius from the crown diameter, perpendicular to CD$_1$ (CD$_2$) in centimeters

In addition, we tested the performance of two variables related to the crown shape, based on different geometric volumes, with respect to stem variables to predict shrub dry aboveground biomass (Ludwig et al. 1975). Models including crown shape-related variables are expected to be simpler and more accurate alternatives for biomass estimation in the case of shrubs than in the case of trees. We tested an inverted cone-shaped crown (CoC) following the form CD^{2}H and a hemisphere-shaped crown (HsC) following the form CD^3 as dry biomass predictor variables, using simple linear models. Formulas and calculations are shown in Online Resource 2.

Individual shrubs were cut down at ground level, and the total weight was obtained in the field using a hanging scale (Nops Goldenlark OEM BT-203, accuracy=0.1 kg). Fresh subsamples of wood and twigs with leaves were collected from five individuals per species, stored in sealed plastic bags, and transported to the laboratory where fresh and oven-dried weights (air-forced oven at 80 °C until constant weight) were obtained to estimate the water content (percent) per species. The resulting value of water content per species was therefore subtracted from the individual fresh mass weighted in the field to obtain the aboveground dry biomass (AGB) per individual per species (Whittaker and Woodwell 1968). This was the final variable used as dependent variable in the regression analysis.

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Wood specific gravity (WSG) is a trait usually included in biomass estimation, with proven predictive value in generalized tree models (Chave et al. 2005). We tested whether the inclusion of this specific trait improved the fitness of a multispecies aboveground biomass regression model. WSG is the oven-dry mass of a woody stem divided by its green volume in kilograms per cubic decimeter. WSG values per species were estimated over six samples collected from the thickest basal stem of six mature individuals in the field using a hatchet. In the lab, each fresh stem sample was totally immersed for 5 s in a volumetric flask of known weight filled with distilled water, and the increase in weight was recorded. The weight increment equals the green volume of the wood sample. After the volume measurement, the wood sample was oven-dried until it achieved constant weight. Wood specific density was then calculated as the oven-dry mass of the wood sample divided by the mass of water displaced by its green volume (Pérez Harguindeguy et al. 2013).

2.4 Statistical analysis

Species-specific regression analyses were performed between dry biomass and allometric variables, and their relative performances were compared. In addition, we constructed a set of multispecies aboveground biomass regression models considering all individuals from the eight shrubs species together (n =245). These models also estimated the individual shrub aboveground dry biomass without considering the species sampled. If necessary, variables were log-transformed in order to apply linear models. Three different allometric models were developed: (1) *single-variable model* refers to the model including the best fitted variable, (2) *multiple-variables model* refers to the best multiple model selected after include all variables, and (3) *crown model* refers to the model including only variables related to the crown shape. Single-variable and crown models were obtained using simple linear regression models. Multiple-variables models were obtained using multiple linear regression models.

The best statistical model developed for either individual species or all species considered together was selected according to the Akaike Information Criterion (AIC), a likelihood criterion that penalizes the number of parameters (Burnham and Anderson 2002; Johnson and Omland 2004), where the best statistical model has the lowest value of AIC. We also reported the predictive mean squared error of the regression as an alternative statistic reflecting the accuracy of the estimator. Although models including all variables are expected to have a better fit than simpler models, a greater number of predictor variables increases the model complexity and the sources of uncertainty, and thus decreases the precision of the resulting predictions. The principle of parsimony stipulates that the "best" regression model is the model that explains the largest amount of response variability with the fewest predictor terms (Logan 2010). We followed this criterion to select the best regression models used for inference. All statistical analyses were carried out with the statistic software InfoStat v. 2011 (Di Rienzo et al. 2011).

Together with the statistical parameters of log-transformed models, a correction factor (CF) was presented for the bias entailed for the log transformation of the data in the final biomass estimation (Baskerville 1972). Estimations of biomass on the basis of log-transformed variables are expected to underestimate the real value. We thus calculated a CF to be applied to AGB in those cases where log-transformed variables intervened in the equation. The CF must to be applied to biomass estimation as follows:

$$AGB = CF \times e^{\ln(AGB)}$$

where,

$$CF = e^{\left(\frac{SEE^2}{2}\right)}$$

CF   Correction factor
SEE   Standard error of the estimation.

3 Results

Among the species considered, *A. gilliesii* showed the highest weights while *A. gratissima* and *C. ehrenbergiana* were the smallest in terms of total aboveground dry biomass and height per individual. *M. carinatus* and *L. divaricata* were the tallest and most branched species, with individuals taller than 400 cm and with more than 20 ramifications. However, they showed intermediate individual aboveground dry biomass. In contrast, *A. aroma* presented lower height and fewer ramifications than these species, but the highest crown area. Finally, *C. atamisquea* and *M. spinosa* had intermediate height, number of ramifications and weight (see Table 1 for the ranges of values of biometric variables and aboveground dry biomass observed per species and for the complete dataset).

3.1 Species-specific aboveground dry biomass regression models

The best-fitted models developed per species, corresponding parameters, correction factors, and statistical descriptors are presented in Table 2. Among the single-variable models, CA was the best predictor variable of aboveground dry biomass for all except one species, accounting at least for 50 % of the variability in all cases. The best fit corresponded to *A. gratissima* (R^2=0.90, p<0.0001). The exception was *C. atamisquea*, where DLS instead of CA was the variable that

Table 1 Summary of the range of values of biometric variables and total aboveground dry biomass per species

Shrub species	Family	N	DLS (cm)	H (cm)	NR	CA (cm^2)	CV (cm^3)	WSG (kg dm^{-3})	AGB$_o$ (kg)
Acacia aroma	Fabaceae	29	0.7–3.4	80–365	1–14	11,015–161,163	655,350–13,860,078[a]	0.74 (0.06)	1–21.4
Acacia gilliesii	Fabaceae	29	0.5–2.7	108–345	1–12	6,300–92,000	397,820–8,944,114[a]	0.82 (0.05)	0.6–25.2
Aloysia gratissima	Verbenaceae	30	0.8–3.0	68–229	1–15	147–7,854	13,708–2,398,082[a]	0.79 (0.05)	0.1–2
Capparis atamisquea	Capparaceae	28	0.7–5.4	52–300	1–11	4,775–77,911	82,770–7,012,034[a]	0.81 (0.05)	0.1–8.3
Celtis ehrenbergiana	Celtidaceae	29	0.5–3.8	46–200	1–13	2,160–28,425	33,117–1,895,009[a]	0.71 (0.03)	0.1–2.4
Larrea divaricata	Zygophyllaceae	40	0.4–1.9	170–416	2–22	7,540–111,448	448,986–14,441,273[a]	0.78 (0.03)	0.5–21.1
Mimozyganthus carinatus	Fabaceae	30	0.6–2.3	129–444	1–20	8,953–56,548	633,227–6,295,751[a]	0.84 (0.03)	1.1–18.3
Moya spinosa	Celastraceae	30	1.5–6.0	50–250	1–15	3,141–51,129	71,896–4,601,386[b]	0.73 (0.04)	0.1–6.9
Total dataset	–	245	0.4–6.0	46–444	1–22	147–161,163	13,708–14,441,273[a]	–	0.1–25.2

Values in brackets represent the standard deviation (SD)

N number of individuals, *DLS* diameter of the longest stem, *H* height, *NR* number of ramifications, *CA* crown area, *CV* crown shape variable, *WSG* wood specific gravity, *AGB$_o$* observed aboveground dry biomass

[a] Corresponding to the conical crown variable used in the final crown volume model (see Table 2)

[b] Corresponding to the hemispherical crown variable used in the final crown volume model (see Table 2)

best explained aboveground dry biomass ($R^2=0.85$, $p<0.0001$), although CA also performed well ($R^2=0.82$, $p<0.0001$). After CA, DLS was the second best predictor variable for species-specific biomass in almost all cases. H showed intermediate predictive capability, with the highest value for *C. atamisquea* ($R^2=0.79$, $p<0.0001$). NR showed the lowest predictive capacity in all cases, with the highest regression coefficient for *A. gilliesii* ($R^2=0.34$, $p=0.0009$).

In terms of multiple-variables models, those developed for *C. atamisquea* and *A. gratissima* had the best predictive capacity ($R^2=0.96$ and $R^2=0.94$ at $p<0.0001$, respectively).

As for crown models, the conical crown model (CoC) was the best predictor of AGB, except in the case *M. spinosa* for which the hemispherical crown model (HsC) showed a better fit (Table 2).

3.2 Multispecies aboveground dry biomass regression models

Simple- and multiple-variables models for all species considered together ($n=245$), their fitted parameters, and statistical descriptors are shown in Table 3. Similar to the species-specific models, CA was the variable that best predicted AGB for the complete dataset, followed by height (Fig. 2a, b). The regression between DLS and AGB clearly showed the existence of two groups of species with different dimensional relationships (Fig. 2c). *A. aroma*, *A. gilliesii*, *L. divaricata*, and *M. carinatus* showed more biomass at a given DLS than did *A. gratissima*, *C. atamisquea*, *C. ehrenbergiana*, and *M. spinosa*. This could be indicating two different branching patterns; therefore, DLS cannot be considered as a good predictor variable in the generalized multispecies shrub model, at least for systems including these species. NR showed poor predictive capacity and its inclusion in the multiple-variables model did not improved the fit of the model (Fig. 2d).

H and CA were the only variables included in the multiple-variables model. As expected, the inclusion of WSG improved the fit of the models. The best crown volume model was the conical one (model V, Table 3), explaining 85 % of aboveground dry biomass variation in the dataset.

Figure 3 shows the performance of the best fitted multispecies model (model IV, Table 3) including H, CA, and WSG. In any case, it is important to note that regression models should not be used beyond their range of validity. Models proposed here are valid between the ranges of allometric variables shown in Table 1, stressing that in the models DLS and H should be measured in centimeters, CA in square centimeter, CoC and HsC in cubic centimeters, and WSG in kilograms per cubic decimeter.

Table 2 Species-specific aboveground dry biomass regression models

Specie	Model	Fitted parameters	R^2	PMSE	CF
Acacia aroma	Single-variable model	$\ln(AGB_p) = -8.38 + 0.97 \times \ln(CA)$	0.72	0.21	1.018
	Multiple-variables model	$AGB_p = -1.43 + 4.07 \times DLS - 0.05 \times H + 1.7E - 04 \times (H^2) + 0.41 \times NR + 6.4E - 05 \times CA$	0.87	8.64	N/A
	Crown model	$\ln(AGB_p) = -1052 + 0.83 \times \ln(CoC)$	0.79	0.15	1.01
Acacia gilliesii	Single-variable model	$AGB_p = -1.44 + 2.4E - 04 \times CA$	0.61	16.8	N/A
	Multiple-variables model	$\ln(AGB_p) = -4.44 + 0.72 \times \ln(DLS) + 0.01 \times H + 0.45 \times \ln(NR) + 0.37 \times \ln(CA)$	0.87	0.13	1.005
	Crown model	$\ln(AGB_p) = -11.57 + 0.91 \times \ln(CoC)$	0.67	0.32	1.037
Aloysia gratissima	Single-variable model	$AGB_p = 0.02 + 1.4E - 04 \times CA + 1.58E - 08 \times (CA)^2$	0.90	0.02	N/A
	Multiple-variables model	$\ln(AGB_p) = -6.05 + 1.69 \times \ln(DLS) + 0.46 \times \ln(NR) + 0.48 \times \ln(CA)$	0.94	0.11	1.003
	Crown model	$AGB_p = 0.05 + 7.87E - 07 \times CoC$	0.91	0.02	N/A
Capparis atamisquea	Single-variable model	$\ln(AGB_p) = -1.47 + 2.07 \times \ln(DLS)$	0.85	0.21	1.018
	Multiple-variables model	$\ln(AGB_p) = -8.27 + 1.11 \times \ln(DLS) + 0.61 \times \ln(H) + 0.47 \times \ln(CA)$	0.96	0.08	1.003
	Crown model	$\ln(AGB_p) = -11.95 + 0.9 \times \ln(CoC)$	0.87	0.20	1.015
Celtis ehrenbergiana	Single-variable model	$\ln(AGB_p) = -12.5 + 1.28 \times \ln(CA)$	0.68	0.42	1.060
	Multiple-variables model	$\ln(AGB_p) = -11.32 + 0.67 \times DLS + 0.91 \times \ln(H) + 0.28 \times \ln(NR) + 0.47 \times \ln(CA)$	0.89	0.17	1.006
	Crown model	$\ln(AGB_p) = -13.72 + 1.00 \times \ln(CoC)$	0.78	0.28	1.029
Larrea divaricata	Single-variable model	$\ln(AGB_p) = -8.70 + 0.96 \times \ln(CA)$	0.71	0.29	1.034
	Multiple-variables model	$\ln(AGB_p) = -7.6 + 1.26 \times \ln(DLS) + 0.96 \times \ln(H) + 0.05 \times NR + 0.31 \times \ln(CA)$	0.92	0.10	1.002
	Crown model	$\ln(AGB_p) = -11.18 + 0.84 \times \ln(CoC)$	0.78	0.22	1.018
Mimozyganthus carinatus	Single-variable model	$AGB_p = -4.66 + 7.4E - 04 \times CA - 8.5E - 09 \times (CA)^2$	0.50	10.70	N/A
	Multiple-variables model	$\ln(AGB_p) = -8.30 + 0.96 \times \ln(DLS) + 0.72 \times \ln(H) + 0.29 \times \sqrt{NR} + 0.52 \times \ln(CA)$	0.77	0.13	1.004
	Crown model	$\ln(AGB_p) = -10.1 + 0.82 \times \ln(CoC)$	0.62	0.19	1.013
Moya spinosa	Single-variable model	$\ln(AGB_p) = -13.95 + 1.45 \times \ln(CA)$	0.71	0.36	1.046
	Multiple-variable model	$\ln(AGB_p) = -10.25 + 1.28 \times \ln(DLS) + 0.12 \times NR + 0.89 \times \ln(CA)$	0.82	0.23	1.016
	Crown model	$\ln(AGB_p) = -12.99 + 0.96 \times \ln(HsC)$	0.69	0.37	1.052

Parameters and statistical descriptors are shown for the best fitted model. All regressions were statistically significant ($p<0.0001$)

AGB_p predicted aboveground dry biomass (kg), DLS diameter of the longest stem (cm), H total height (cm), NR number of ramifications, CA crown area (cm²), CoC conical crown variable (cm³), HsC hemispherical crown variable, $PMSE$ predictive mean squared error, CF correction factor, N/A no applicable

Table 3 Multispecies aboveground dry biomass regression models

Model	Parameters	R^2	PMSE	AIC	CF
I. Single- variable model	$\ln(\mathrm{AGB_p}) = -9.58 + 1.06 \times \ln(\mathrm{CA})$	0.76	0.57	561.44	1.176
II. Single-variable model including WSG	$\ln(\mathrm{AGB_p}) = -16.15 + 1.02 \times \ln(\mathrm{CA}) + 8.83 \times \mathrm{WSG}$	0.81	0.43	494.50	1.097
III. Multiple-variable model	$\ln(\mathrm{AGB_p}) = -13.79 + 1.44 \times \ln(H) + 0.71 \times \ln(\mathrm{CA})$	0.86	0.34	433.24	1.060
IV. Multiple-variable model including WSG	$\ln(\mathrm{AGB_p}) = -17.55 + 1.22 \times \ln(H) + 0.75 \times \ln(\mathrm{CA}) + 5.92 \times \mathrm{WSG}$	0.88	0.28	389.41	1.040
V. Crown model	$\ln(\mathrm{AGB_p}) = -14.14 + 1.06 \times \ln(\mathrm{CoC})$	0.85	0.35	439.60	1.063
VI. Crown model including WSG	$\ln(\mathrm{AGB_p}) = -17.33 + 1.02 \times \ln(\mathrm{CoC}) + 4.82 \times \mathrm{WSG}$	0.86	0.31	416.89	1.049

Parameters and statistical descriptors are shown for the best fitted model. All regression analyses were statistically significant ($p<0.0001$)

AGB_p predicted aboveground dry biomass (kg), H total height (cm), CA crown area (cm^2), WSG wood specific gravity (kg dm^{-3}), CoC Cone shaped crown variable (cm^3), HsC hemisphere-shaped crown variable, R^2 regression coefficient, $PMSE$ predictive mean squared error, AIC Akaike information criterion, CF correction factor, N/A no applicable

4 Discussion

Biomass allometric models specifically developed for shrubs are scarce in the literature. This article makes a contribution in that sense by testing the validity of several equations and variables, including crown-related variables, for the prediction of individual shrub aboveground dry biomass in the semiarid Chaco forest of central Argentina.

Although the results presented in this study showed that the multiple-variables models performed better than single-variable and crown models, the later ones seem to have more

applicability since were more parsimonious while still retaining good predictive capability. In practice, dealing with several variables could be very laborious and attention has to be paid to the range of validity of each variable separately, so models including fewer variables are convenient and therefore preferred.

Since crown models had an intermediate fit between multiple- and single-variable models and include just two allometric variables combined (H and CA) in a single variable, we recommend using those models to predict aboveground dry biomass of shrub species. The final selection criterion

Fig. 2 Relationship between the aboveground dry biomass (kg) and **a** crown area (CA, cm^2), **b** height (H, cm), **c** diameter of the longest stem (DLS, cm), and **d** number of ramifications for the complete dataset. *Different symbols* and *colours* represent different species. Only CA and H were useful variables to predict multispecies aboveground shrub biomass
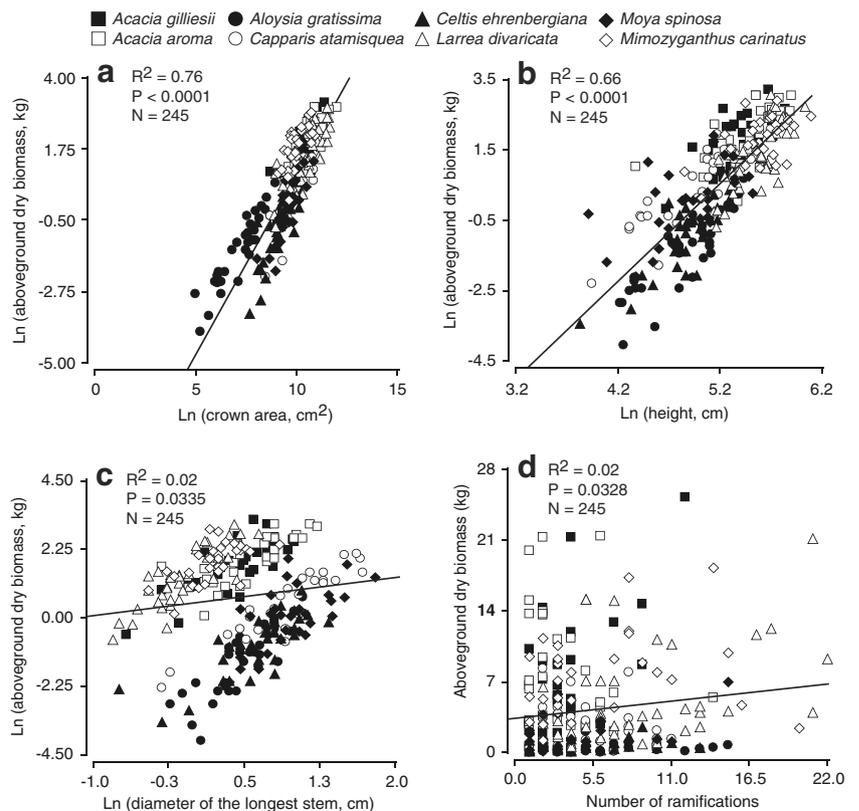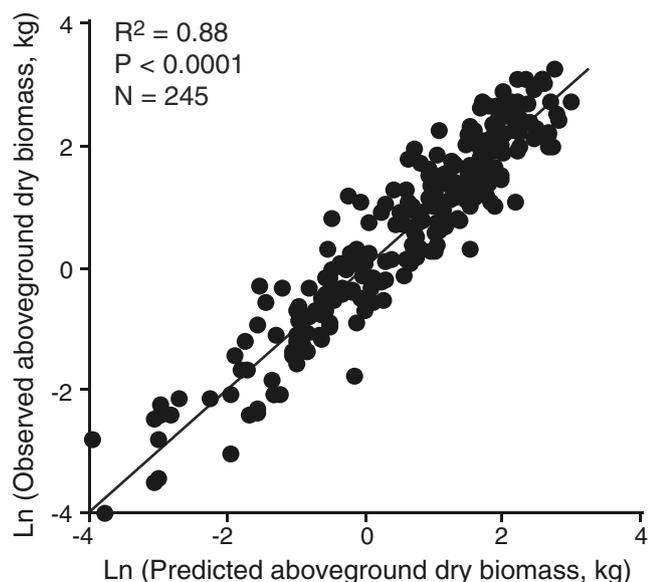
Fig. 3 Capacity of model IV for predicting shrub aboveground biomass, considering all species together. Each *dot* corresponds to an individual weighted shrub $\ln(\mathrm{AGB_p}) = -17.55 + 1.22 \times \ln(H) + 0.75 \times \ln(\mathrm{CA} + 5.92 \times \mathrm{WSG}$

between the presented models will depend on the data available for the biomass estimation as well as on the aim of the research project at hand.

After developing 24 species-specific equations for eight shrub species, we strongly recommend the use of crown- and height- related variables over other common allometric variables as predictors of individual aboveground biomass of shrubs in semiarid Chaco forests and woodlands. Among the allometric variables sampled, we found that crown-related variables were the best predictors of shrub biomass in both species-specific and multispecies models, which is in agreement with the size–biomass relationship found for shrubs in other semiarid ecosystems (Ludwig et al. 1975; Murray and Jacobson 1982; Northup et al. 2005). Several other studies that applied crown-volume equations to the estimation of individual shrub biomass in different ecosystems or vegetation types, such as Mediterranean shrublands (Castro and Freitas 2009; Paton et al. 2002), the Chihuahan desert (Ludwig et al. 1975), the Monte desert in western Argentina (Hierro et al. 2000), and the shrub component of pine forests from subtropical China and southern USA (Sah et al. 2004; Zeng et al. 2010) have also obtained good fits. The fact that shrub aboveground biomass could be accurate predicted using a single variable of crown area across different ecosystems regardless of species identity makes an important contribution in the improvement of global biomass estimates, since it provides a very powerful tool to estimate shrub aboveground biomass from remote sensing data (Phua and Saito 2003). Our results also confirmed that the use of natural log–log models is the most appropriate form for providing a common statistical basis for describing

size–biomass relationships in almost all cases presented, as was found for others shrub species around the world (Hierro et al. 2000; Hofstad 2005; Oñatibia et al. 2010; Sah et al. 2004; Smith and Brand 1983; Tietema 1993).

Diameter of the longest stem, which was a good predictor for species-specific models, as found by Hierro et al. (2000), is not recommended for multispecies models because species in this region seem to belong to different groups characterized by different branching patterns. Height appeared as a more relevant variable in the case of multispecies models than for species-specific models. Unlike trees, the estimation of shrub height is very simple and can be made using a simple tape. Finally, the number of ramifications showed very little predictive value and it is very laborious to measure at field, particularly in thorny multistemmed shrubs, such as some of the species measured in this study. Our results differ from those by Vilà (1993) for Mediterranean resprouting shrub species, where the variable "number of branches" significantly improved the fit of the allometric biomass models.

Iglesias and Barchuk (2010) and Iglesias et al. (2012) presented equations for different groups of Chaco shrubs: *A. gilliesii* and *M. carinatus* separately and together; *L. divaricata*, as well as different equations for two groups of shrubs species including *A. grattissima*, *C. ehrenbergiana*, and *Lycium ciliatum* on the one side and *C. atamisquea* and *Condalia microphylla* on the other. Although useful, these equations are only applicable for individuals having a lower number of ramifications since the authors only include basal stem diameter and height considering each of the basal stems of a shrub as a separate individual. The stem diameter, easily obtainable in the case of trees, can be particularly time consuming to obtain in shrub species commonly having more than 10 (and sometimes up to 20) ramifications per plant. In comparison, measuring crown diameters and height of shrubs is considerably quicker, easier, and more accurate (Northup et al. 2005). Gaillard de Benitez et al. (2002) obtained very precisely estimations of the biomass of *L. divaricata* using an equation with the predictive variables basal perimeter, crown perimeter, ramification number, and crown volume (but not crown area). However, the best predictor variable found in that study, crown perimeter, is notoriously time consuming and difficult to measure in the field, as pointed out by the same authors. Our work, on the other hand, set out to find accurate yet simple estimations of several shrub species individually and together without the need to measure different predictor variables for different shrubs species, or to include difficult or time-consuming variables.

Hierro et al. (2000) developed biomass equations for *L. divaricata* in the Monte shrublands, using an inverted cone volume as the best predictor variable, similar to those reported in our study. The parameters finally included in

both equations of Hierro et al. and ours are quite similar, suggesting that the individuals in the Monte ecosystems are equivalent in terms of size and architecture to the individuals sampled in the Chaco region for this particular species. The same pattern applied to the comparison with the total aboveground dry biomass model for *C. ehrenbergiana* (formerly called *C. pallida*) developed in the subtropical thornscrub parklands of southern Texas and using crown area as a predictor variable (Northup et al. 2005).

Different multispecies models for the estimation of aboveground dry biomass showed similar predictive capacity with no relevant difference in the number of variables included (e.g., multiple-variable models included the same variables needed to estimate the conical crown models). Based on the AIC, the best predictive model founded in the present work was the one that included *H*, CA, and WSG (model IV in Table 3). Even when WSG—a trait commonly measured and reported in the forestry literature—improved the fit of the models, differences in their predictive capability were not large enough to justify measuring WSG, since it involves the additional time-consuming activities of extracting the samples, processing, and measuring them in the laboratory. Accordingly, we recommend model III because of its good balance between number of input variables needed and predictive capacity. However, and for practical purposes, model I including just crown area as a predictive variable offer an accurate, practical, fast, and inexpensive way to estimate shrub aboveground biomass in open forest ecosystems. Crown area is a variable easily obtained using fine spatial-resolution data (i.e., aerial photographs,) allowing an indirect estimation of individual shrub aboveground biomass.

All models included in Table 3 should perform well in predicting shrub aboveground biomass in semiarid Chaco forests. The decision about the best predictive model to use for the biomass estimation is thus to be made on the basis of the available variables.

Although species-specific equations often provide more accurate estimates of biomass than multispecies aboveground biomass regression models, as was found in this study, generalized (multispecies) regression models could provide useful estimations in similar woody open ecosystems where species-specific equations are not yet available and the proposed variables could be correctly measured. Furthermore, it is preferable to use region or site-specific relationships whenever possible, since species size–biomass relationship could differ as plants alter allocation patterns in response to soils, climate and disturbance (Northup et al. 2005).

The models provided here should contribute to the inclusion of shrubs in open woodland and forest biomass estimations to biological carbon stocks as well as providing tools for a methodological standardization for the quantification of individual dry biomass in shrub species.

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