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Individual plant and population biomass of dominant shrubs in Patagonian grazed fields

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ABSTRACT. Estimating aboveground biomass of vegetation is essential for population, community and ecosystem studies. In systems dominated or co-dominated by woody species, biomass estimation is difficult, and rapid and non-destructive methods are needed. In this study, we describe biomass distribution in different components (i.e., wood, leaves) and how this changes with shrub size for the three dominant species of shrubs in the Occidental District of the Patagonian steppe. We also describe the population size structure of the three species in grazed fields and estimate their contribution to total abundance and biomass through a non-destructive method. We developed allometric equations to estimate aboveground biomass components of individual shrubs from structural descriptors (i.e., diameter and height of the crown), sampling individual plants of different sizes. The variable that best predicted biomass of the three species was the sum of the height and the average diameter of the crown (calculated with the largest diameter and its perpendicular). Allometric models for each species explained more than 83% of the variability of individual aboveground biomass. At the individual level, species had different proportions of wood, leaves and specific wood weight. Increasing shrub size was accompanied by changes in the proportion of leaves to wood, and in some cases, the percentage of dead crown. At the population level, the three species differed in size distribution in moderately grazed fields. Development of allometric models from a population perspective is important to study demographic processes that drive community and ecosystem responses to environmental and land-use changes.

[Keywords: *Adesmia volckmannii*, allometric equations, *Mulinum spinosum*, semi-arid ecosystems, *Senecio filaginoides*, woody species]

RESUMEN. **Biomasa individual y poblacional de arbustos dominantes en estepas patagónicas pastoreadas**: La estimación de la biomasa aérea de la vegetación es clave para llevar a cabo estudios de Ecología de Poblaciones, de Comunidades y de Ecosistemas. En sistemas dominados o codominados por leñosas, esta estimación es dificultosa, y es importante contar con métodos rápidos y no destructivos. En este estudio describimos cómo se distribuye la biomasa aérea en distintos componentes (i.e., leño, hojas) y cómo cambia con el tamaño de arbusto para las tres especies dominantes de arbustos del Distrito Occidental de la estepa Patagónica. Además, describimos la estructura poblacional de tamaños de las tres especies en campos pastoreados y estimamos su contribución a la abundancia y la biomasa total a través de un método no destructivo. Desarrollamos ecuaciones alométricas para estimar la biomasa de los componentes aéreos de los individuos de arbustos a partir de descriptores estructurales (i.e., diámetros y altura de la copa). La variable que mejor predijo la biomasa aérea en las tres especies de arbustos fue la suma de

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la altura y el diámetro promedio (entre el diámetro mayor y el perpendicular) de la copa. Los modelos alométricos explicaron para cada especie más de 83% de la variabilidad de la biomasa aérea individual. En el nivel de individuo, las especies tuvieron distinta proporción de leño, hojas y distinto peso específico del leño. El aumento del tamaño individual de los arbustos fue acompañado por cambios en las proporciones de hojas/leño y en algunos casos por el porcentaje de copa muerta. En el nivel de población, las tres especies difirieron en la distribución de tamaños en pastizales pastoreados. La perspectiva poblacional utilizada para el desarrollo de los modelos alométricos es clave para estudiar los procesos demográficos que explican las respuestas de las comunidades y los ecosistemas áridos a los principales cambios ambientales y de uso.

[Palabras clave: *Adesmia volckmannii*, ecosistemas semi-áridos, ecuaciones alométricas, leñosas, *Mulinum spinosum, Senecio filaginoides*]

INTRODUCTION

The estimation of aboveground biomass and net primary productivity (NPP) is a central issue in Ecology (Flombaum & Sala 2007). Aboveground plant biomass provides important biological information and has been used for various purposes, such as estimations of net primary productivity, nutrient cycling, wood production, and recently, CO_2 dynamics and their greenhouse effect (Ter-Mikaelian & Korzukhin 1997; Nelson et al. 1999; Hierro et al. 2000; Keller et al. 2001; Sampaio & Silva 2005). It is also important to estimate forage availability and fuel characteristics, and to assess the effects of different fire and grazing management regimes (Hierro et al. 2000; Flombaum & Sala 2007). In general, all these descriptors of the structure and functioning of ecosystems have been studied ignoring aspects that we believe are essential, particularly for woody species. For example, species may present differences in the proportions of wood, leaves, and dead material in their crown, which in turn, can change with the size of the individual. On the other hand, at a higher level of organization, population size structure may be different for different species in a growth-form group or environmental condition. Knowledge of these differences in the distribution of population sizes allows inferences about ecosystems structure, and at the same time, provides knowledge about how the abiotic and biotic environment affects population vital rates.

In general, in systems dominated by grasses, biomass estimation is simple, whereas in systems dominated or co-dominated by woody plants, it is more difficult to achieve (Hughes et al. 1999). Because of the size of woody species, and because they have components with different densities (e.g., wood, leaves) that can change with the ontogeny of the plants, woody species biomass is difficult to quantify. Therefore, it is useful to have non-destructive methods to estimate biomass components that are quick, relatively accurate, and also require little training (Navar et al. 2004). One of the most common methods for determining biomass and productivity of woody species is the use of allometric regressions (Whittaker & Woodwell 1968; Usó et al. 1997). Normally, the biomass or volume is predicted by an equation that relates these variables with the diameter at breast height or height of the plant (Muukkonen 2007). In monospecific stands, this measure associated with an estimation of stand density allows assessment quickly, non-destructively and with low effort of components, ANPP, and basic data to estimate the C, N or other essential element pools. In natural systems composed of different species with different crown morphologies and different ages or size structures, this approach is valid, but also requires knowledge of whether the relationships vary among species and/or individual sizes.

Allometric equations have been developed for many plant species of different temperate and tropical biomes (Brown et al. 1989; Haase & Haase 1995; Schroeder et al. 1997; Ter-Mikaelian & Korzukhin 1997; Kumar et al. 1998; Nelson et al. 1999; Keller et al. 2001; Jenkins et al. 2001), but semi-arid biomes have received less attention, and biomass allometric relationships in these ecosystems have been less studied (Okello et al. 2001; Samba et al. 2001; Navar et al. 2004; Sampaio & Silva 2005). In Argentina, equations have been developed that relate structure descriptors and aboveground biomass in Espinal dominant shrubs in the Province of La Pampa (Hierro et al. 2000). In the Patagonian steppe, there are models to estimate plant biomass; however, these models estimate biomass using plant cover (Flombaum & Sala 2007), without estimating biomass at the individual level. Therefore, this method cannot asses the size structure of shrub populations. Research oriented at the population level has the potential to integrate information sources available at the plant and community level. These two research perspectives have not been effectively unified in an information base for vegetation management in grazed systems (Briske 1991). The population perspective is essential to study the demographic processes that explain community and ecosystem responses to environmental and land use changes.

About one third of the earth's land surface is composed of arid ecosystems (Noy-Meir 1973; Goodall & Perry 1979; Fernández & Busso 1999). The main feature of most of these ecosystems is low water availability (Noy-Meir 1973; Goodall & Perry 1979). Arid ecosystems are usually co-dominated by grasses and woody plants (Cabrera 1976; Walter 1977; Soriano et al. 1983; León et al. 1998). Shrubs are an important component of vegetation in semi-arid ecosystems around the world, and their ability to dominate these systems is a concern both ecologically and economically (Schlesinger et al. 1990; Sankaran et al. 2005). The steppes in the Patagonian Occidental district of Argentina are dominated by three shrub species of contrasting morphology and demography: *Adesmia volckmannii*, *Mulinum spinosum* and *Senecio filaginoides* (Soriano 1956; León & Aguiar 1985; Sala et al. 1989; Golluscio et al. 1998; Aguiar & Sala 1998; Cipriotti & Aguiar 2010). Our study was descriptive and had two goals, one allometric and one demographic. First, we studied the specific differences in the distribution of biomass in the different components of shrub crowns, and how it changes with individual size. With this information, we developed predictive biomass equations. Second, in grazed fields, we described the population size structure of the three shrub species and estimated their contributions to total biomass and abundance.

MATERIALS AND METHODS

Study Site Description

The study site is located at the INTA Experimental field, in Río Mayo, Province of Chubut, Argentina in South Central Patagonia (45º24′ S and 70º15′ W). The site is located in the Occidental District of the Patagonian phytogeographic province. Mean monthly temperature is between 2 °C in July and 14 °C in January. Mean annual precipitation is 154±44 mm, and most of the rainfall occurs between May and September (Jobbágy et al. 1995). Soils are of coarse texture (sandy), with a high content of pebbles of varying diameter (Paruelo et al. 1988). The dominant vegetation type is shrub steppe that is co-dominated by grasses and shrubs of low height, which contribute approximately 96% of total plant cover and biomass (Fernández et al. 1991; Golluscio & Sala 1993). Herbs are a group with great species richness but contribute less than 1% of plant cover (Fernández et al. 1991). The dominant shrub species are *Mulinum spinosum* (Cav.) Pers., *Adesmia volckmannii* Philippi (ex *A. campestris*) y *Senecio filaginoides* De Candolle, with a basal cover of 12% (Fernández et al. 1991). The three species show marked differences in their root systems (Fernández & Paruelo 1988; Golluscio et al. 2006) and hydraulic architecture (Bucci et al. 2009). These shrub species also differ in their palatability to sheep. Sheep preferentially browse the inflorescences of *Mulinum* (January-February), but avoid consuming other tissue due to sharp, spiny leaves and high concentrations of secondary metabolites (Bonvissuto et al. 1983; Cavagnaro et al. 2003). Sheep browse *Adesmia*'s twigs and leaves at the beginning of the growing season when tissues are not lignified. *Senecio* is not browsed due to its small, hairy, soft leaves with high concentrations of secondary metabolites (Cavagnaro et al. 2003). Secondary compounds dominating *Mulinum* and *Senecio* are mainly phenols and oils (Cavagnaro et al.

2003). The dominant grass species in the study site are *Pappostipa speciosa* (Trin. et Rupr.) (ex *Stipa speciosa*), *Pappostipa humilis* (Cav.) (ex *Stipa humilis*), *Poa ligularis* and *Bromus pictus* Hook. The studies were performed at the end of the growing season, in January 2001 and 2006, for studies 1 and 2, respectively. In 2000, the annual rainfall was 183 mm and 156 mm in 2005.

Study 1. Variation of the crown allometric relationships with individual size

For each shrub species (*A. volckmannii, M. spinosum, S. filaginoides*), we selected individuals (n=30) in moderately grazed areas. Individuals had different sizes and represented the range sizes within the population (30-130 cm of average diameter and 32-120 cm of height in *Adesmia*, 35-130 cm of average diameter and 30-80 cm of height in *Mulinum*, 30-140 cm average diameter and 20-80 cm of height in *Senecio*). For each individual, we estimated the percentage of dead crown (dead leaves and stems) and measured two diameters of the crown (larger diameter and its perpendicular), along with the height. Crown architecture was thus represented by these measures. Afterwards, shrubs were cut at the soil level (stem-root transition) and fresh biomass was weighed with a portable scale (Salter, Model 235 6S, England, ±5 g of error). To obtain dry weight, we made a sub-sampling. A representative branch of each shrub crown was weighed for fresh biomass estimation and brought to the laboratory to separate different fractions (wood, leaves, reproductive structures) and weigh dry biomass (oven at 65 °C for 72 h). During the processing period, samples were kept in a freezer at -8 °C. These data were used to extrapolate the dry weight of the entire plant. Dry weights were correlated with diameters and heights. Sub-samples were used to estimate the proportion of leaves and wood of each species of shrub in the total range of sizes. Individual shrub size was then correlated with proportions of wood and leaves, and percentage of dead crown.

To characterize the three species of shrubs, we also estimated the specific wood weight, or wood density. We harvested the base of the main stem of small, medium and large size individuals (approximately 40, 80 and 110 cm average diameter, respectively) of the three species (n=3 for each size and each species). Each stem was dried and then weighed. Volume was estimated by immersing the stem in a graduated cylinder with distilled water and recording the difference in level. Results were presented as the mean and standard error of the specific weights for each species.

Study 2. Population size structure of shrubs in grazed fields

We estimated population size structure of shrub species in a community moderately and continuously grazed by sheep (ca. 0.2 equivalent sheep/ha). We delimitated a total of nine plots of 50 m^2 (50 m x 1 m transects) distributed in four different paddocks >100 ha in area. We avoided sampling areas near water points or fences, because grazing pressure is higher in these areas. Within each plot, all established individuals (with more than 10 cm height and at least one branch) of the three species under study were surveyed. For each shrub, we measured two diameters of the crown (the largest and its perpendicular), and height. These values were converted to biomass with equations obtained from the Study 1. We used individual plant biomass to calculate cumulative relative frequency of plant size for the three shrub species. We also estimated species density and total biomass of the three species in the paddocks (n=4).

Data Analysis

We used regression analysis to estimate the relationship between size and biomass for the three species. We tested different types of models (i.e., linear, potential and exponential). Final models were selected according to the best adjustment. The parameters (exponent and constant) of the selected models for each species were compared (sum of squares *F* test) (GraphPad Prism software 5.0 2007). Regression analysis was also used to correlate the size of individual plants with the proportion of wood, leaves and dead crown. The results of the different fractions (wood, leaves) were analyzed with ANOVA, comparing the variables among the shrub species. The weight of reproductive structures was not analyzed, and data is only presented as an orientation, because the three species differ in their phenology (Golluscio et al. 2005), and sampling was conducted at a single time (peak production in January). Specific wood weight was analyzed with ANOVA to reveal species and size effects. To compare the populations' size structure in the three species, we compared the distributions of the cumulative relative frequency of different sized individuals with Kolmogorov-Smirnov nonparametric test. Finally, the three species were characterized by biomass and density, and were compared with ANOVA.

Table 1. Potential equations for predicting aboveground dry biomass in shrubs using structure descriptors as independent variables. b=aboveground dry biomass (g); h=height (cm); d1=largest diameter (cm); d2=diameter perpendicular to d1 (cm); dx=average of the largest diameter (d1) and its perpendicular (d2) (cm); dh=sum of average diameter and height (cm). All models were statistically significant ($P<0.01$). The sample size was 30 shrubs per species (n=30). A numeral sign (#) identifies equations with the highest adjustment.

Tabla 1. Ecuaciones potenciales para predecir biomasa seca aérea en arbustos utilizando descriptores de estructura como variables predictoras. b=biomasa aérea (g); h=altura (cm); d1=diámetro mayor (cm); d2=diámetro perpendicular al mayor (cm); dx=diámetro promedio entre el mayor y su perpendicular (cm); dh=diámetro promedio+altura (cm). Todos los modelos fueron estadísticamente significativos ($P<0.01$). El tamaño de muestra fue de 30 arbustos por especie (n=30). Con signo numeral (#) se señalan las ecuaciones de mayor ajuste.

Species	Potential equation	r^2
Adesmia volckmannii	$b=0.0126 * h^{2.7014}$	0.6611
	$b=0.0648 * d1^{2.2643}$	0.6825
	$b=0.0072 * d2^{2.7993}$	0.7905
	$b=0.0095 * dx^{2.7254}$	0.7882
	$b=0.0002 * dh^{3.1402\,\#}$	$0.8375^{\#}$
Mulinum spinosum	$b=0.00009 * h^{4.0415}$	0.6939
	$b=0.0002 * d1^{3.3986}$	0.7773
	$b=0.0011 * d2^{3.0418}$	0.7847
	$b=0.0002 * dx^{3.4255}$	0.8349
	$b=0.000003 * dh^{3.9321\,\#}$	$0.8424^{\#}$
Senecio filaginoides	$b=0.0083 * h^{3.0204}$	0.7149
	$b=0.005 * d1^{2.7681}$	0.8401
	$b=0.0424 * d2^{2.2657}$	0.6555
	$b=0.003 * dx^{2.8883}$	0.8411
	$b=0.0002 * dh^{3.1876\,\#}$	$0.8564^{\#}$

All ANOVA analyses were performed using Infostat 2.0 software (2002). We controlled data normality and homogeneity of variances. Tukey tests were used for comparisons of means post-hoc ANOVA.

RESULTS

Study 1. Variation of crown allometric relationships with individual size

The sum of the height and the average diameter (largest diameter and its perpendicular) was the variable that best predicted aboveground biomass in the three shrub species (Table 1). In all cases, the best fitted model was a potential equation with one predictor variable. Allometric models for each dominant shrub species explained more than 83% of the variability in the estimation of individual aboveground biomass in this Patagonian steppe (Figure 1). In *Adesmia*, there were two large individuals with a disproportionate weight for their size (Figure 1a). The relationship between size and aboveground dry weight did not vary among species ($P=0.49$). A single model that included the three species explained 81% of the variability ($b=0.0001 * dh^{3.2604}$; $r^2=0.81$; n=90; $P<0.01$; where b=aboveground dry biomass, dh=average diameter+height).

Wood was the most important component of aboveground biomass of individual plants (>70% of the biomass per individual), followed by the leaves, showing very small amounts of reproductive structures (on average, 0.2% in *Adesmia*, 1.7% in *Mulinum* and 3.5% in *Senecio*). The three species exhibited differences in the relative proportions of wood (*Adesmia>Senecio>Mulinum*) and leaves (*Mulinum>Senecio>Adesmia*) (Figure 2).

Shrub size was related to the proportion of leaves and wood, and in some cases, with the percentage of dead crown. In the three species, the leaf weight/wood weight ratio decreased with shrub size (Figure 3a, b and c). In *Adesmia* and *Mulinum,* the percentage of dead crown increased with size (Figure 3d, e and f).

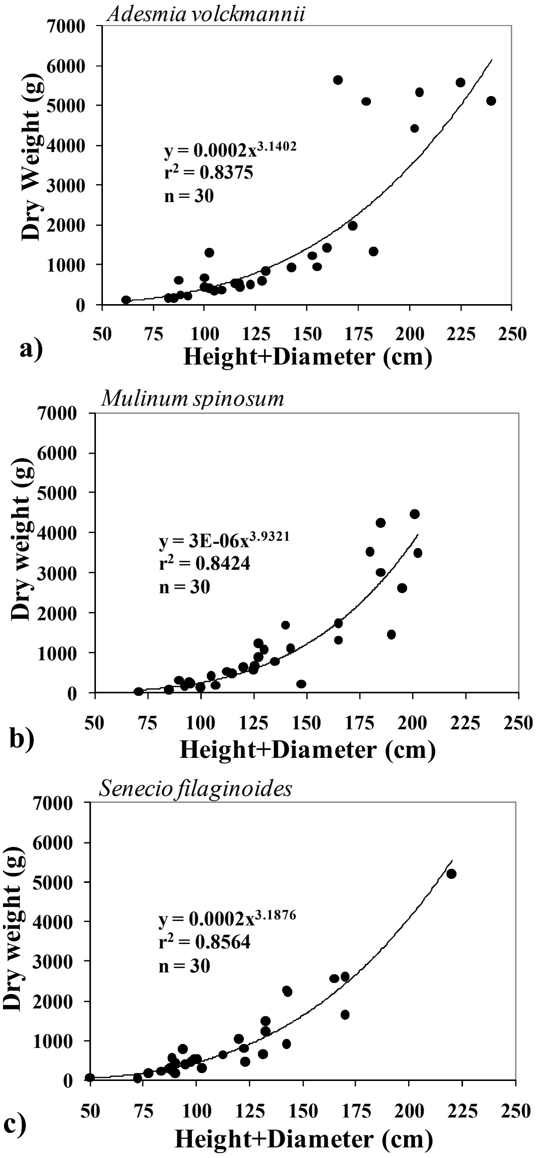

Figure 1. Relationship between individual size and aboveground dry weight of dominant shrub species: a) *Adesmia volckmannii*; b) *Mulinum spinosum*; c) *Senecio filaginoides*. Size is estimated as the sum of height and average diameter (average of the largest diameter and its perpendicular) of the crown (Height+Diameter). All equations were statistically significant (P<0.01).

Figura 1. Relaciones entre el tamaño y peso seco aéreo de individuos de las especies dominantes de arbustos; a) *Adesmia volckmannii*; b) *Mulinum spinosum*; c) *Senecio filaginoides*. Height+Diameter=suma de la altura y el diámetro promedio entre el mayor y el perpendicular de la copa. Las tres ecuaciones fueron estadísticamente significativas (P<0.01).

Specific stem weight differed among the three species (P<0.001), and significant differences were not found across the range of shrub sizes studied (P=0.25). *Adesmia* had the highest specific wood weight (0.89 g.cm^{-3}±0.04), followed by *Mulinum* (0.77 g.cm^{-3}±0.06) and *Senecio* (0.68 g.cm^{-3}±0.06).

Study 2. Population size structure of shrubs in grazed fields

The population density and specific total aboveground biomass did not vary significantly among the shrub species in grazed fields (P=0.33 and P=0.35, respectively), probably due to high variability shown by the data (the coefficient of variation was 64% for density and 42% for biomass). However, *Adesmia* presented the lowest values of average density; *Senecio* showed the lowest average

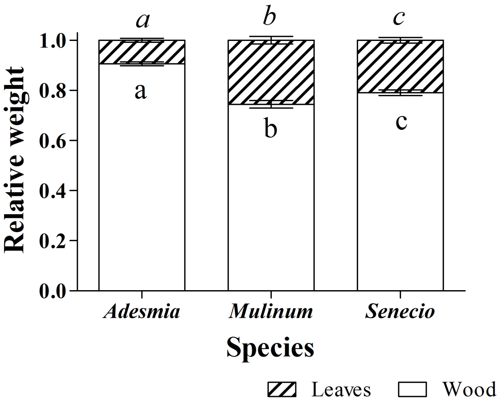

Figure 2. Proportion of biomass corresponding to wood and leaves in relation to total dry weight for the entire size range in the three dominant shrub species (*Adesmia volckmannii, Mulinum spinosum* and *Senecio filaginoides*). Bars correspond to mean values and vertical lines indicate standard errors. Different letters in italics (leaves) and different letters in print (wood) indicate significant differences (P<0.05) among species (Sp).

Figura 2. Proporciones de biomasa de las fracciones leño y hojas en relación al peso seco total, para todo el rango de tamaños estudiado. Especies de arbustos: *Adesmia volckmannii, Mulinum spinosum y Senecio filaginoides*. Las barras corresponden a los valores medios y las líneas verticales a los errores estándar. Letras distintas en cursiva (hojas) y letras distintas en imprenta (leño) indican diferencias significativas (P<0.05) entre las especies (Sp).

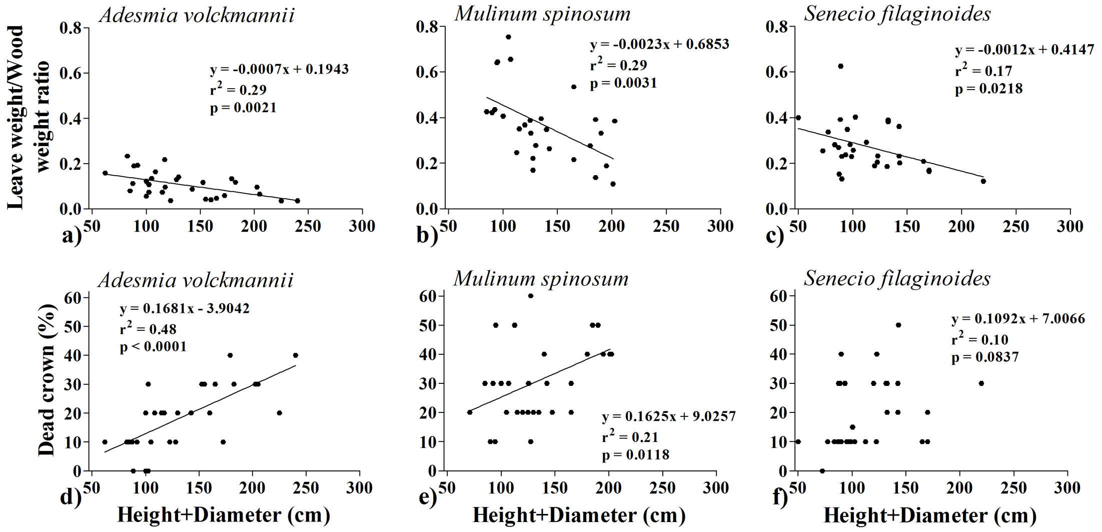

Figure 3. Relationship between shrub size (Height+Diameter=sum of average crown diameter and height), and ratio of leaf weight/wood weight and percentage of dead crown in the three species of shrubs (*Adesmia volckmannii, Mulinum spinosum* and *Senecio filaginoides*).

Figura 3. Relaciones entre el tamaño de arbusto (Height+Diameter=suma del diámetro promedio de la copa y la altura) y la relación peso hojas/peso tallo y el porcentaje de copa muerta en las tres especies de arbustos (*Adesmia volckmannii, Mulinum spinosum* y *Senecio filaginoides*).

specific biomass values, and *Mulinum* had the highest mean values for both variables (Figure 4a). The size structure differed among species (Figure 4b). *Adesmia* had a lower frequency of small individuals (less than 3 kg) than *Mulinum* (P<0.0001), and a lower frequency of small and intermediate individuals than *Senecio* (P=0.001). Furthermore, *Mulinum* had a lower frequency of small and intermediate shrubs (0.5 to 4 kg) than *Senecio* (P<0.0001). The largest individuals found were of *Adesmia* (one individual weighed >7.5 kg), with an average individual weight of 982 g (median=201 g). Mean individual weight for *Mulinum* was 690 g (median=43 g), and the largest individual found weighed 6 kg. *Senecio* was the species with the lowest average individual size (386 g) (median=142 g), and the largest individual was <4 kg (Figure 4b).

DISCUSSION

Our study has made advances in two important aspects relevant to understanding of Patagonian shrub populations: biomass partitioning at the individual level, and population size structures in grazed fields. At the individual level, the developed equations allow a precise, quick and easy estimation of aboveground biomass of dominant shrub species in the studied community. Moreover, the estimation is non-destructive and requires little training. The crown architecture characterized by the sum of the average diameter and height is a good predictor of individual shrub biomass in the species studied. Equations were adjusted for each species because shrubs differ significantly in their morphology. *Adesmia* is tall (120 cm) with an open canopy architecture in the form of an inverted cone; *Mulinum* is low in height (70 cm) with a cushion form, hemispherical; and *Senecio* is a low shrub (60 cm), globose and evergreen. However, the parameters of the three adjusted equations did not differ among species. This result suggests that a single equation can be used to estimate biomass in the three species of shrubs, with a slightly inferior fit than the equations developed for each species. Assuming that stoichiometry of the species is not different,

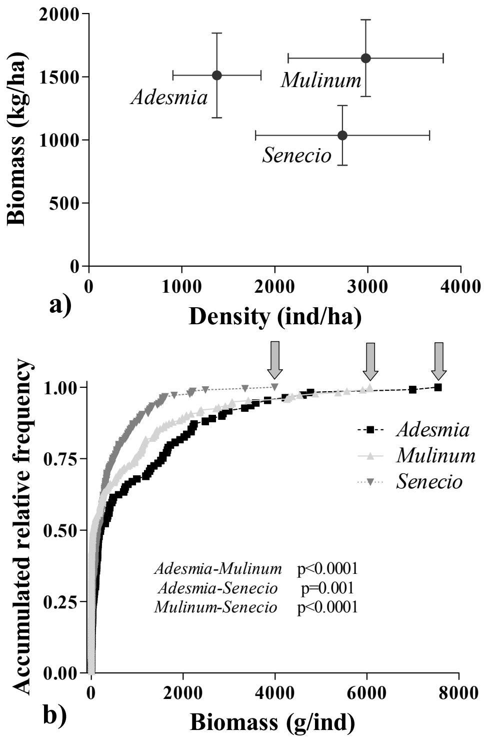

Figure 4. a) Population density (individuals/ha) and specific total aboveground biomass (kg/ha) of *Adesmia volckmannii, Mulinum spinosum* and *Senecio filaginoides* in grazed fields. Values indicate the mean±1 standard error. b) Accumulated relative frequency of shrub size (g of biomass/individual) for the three species in grazed fields. *P* values ≤0.001 indicate significant differences between each pair of curves. Vertical arrows indicate the maximum size for each species.

Figura 4. a) Densidad poblacional (individuos/ha) y Biomasa aérea total específica (kg/ha) de *Adesmia volckmannii, Mulinum spinosum* y *Senecio filaginoides* en campos pastoreados. Los valores indican la media±1 error estándar. b) Frecuencia relativa acumulada de tamaños (g de biomasa/individuo) de las tres especies de arbustos en campos pastoreados. Los valores *P* ≤ 0.001 indican diferencias significativas entre cada par de curvas. Las flechas verticales indican los tamaños máximos de arbusto para cada especie.

this general model is useful in conducting expeditious studies of biomass/nutrient reservoir pools and productivity at the ecosystem level, since species composition is usually less relevant in these inquires. It may be particularly useful in cases with relatively homogeneous environments, where species do not change in abundance (e.g., only one condition of grazing intensity). In contrast, in population or community studies where is important to distinguish between species, or in studies of stress or disturbance gradients, it is recommended to use specific models to estimate individual biomass precisely and avoid propagation errors.

The adjustments of specific equations were somewhat lower than the adjustments of other potential equations developed for shrub species in the semi-arid Argentinean Espinal (Hierro et al. 2000). However, our adjustments were higher than those for relationships found for the same shrub species, using plant cover as the independent variable (Flombaum & Sala 2007). The use of plant cover to estimate biomass in this study generated controversy (Montès 2009; Flombaum & Sala 2009), since it was proposed that plant architecture generates differences in biomass that is not captured with plant cover (Montès 2009). Our approach, biomass estimation at the individual level, avoids this discussion and provides information for monitoring biomass dynamics at different levels: individual plant, population, community and ecosystem.

Shrub species differed in their individual biomass distribution, although relationships between crown architecture and total biomass did not differ. On average, individuals of the three shrub species had different proportions of wood and leaves (Figure 2) and different specific wood weight. *Adesmia* was the species with the highest proportion of wood and the lowest proportion of leaves, which corresponds to a specific net aboveground productivity lower than *Mulinum* and *Senecio* (Fernández et al. 1991). In addition, *Adesmia* was the species with the highest specific wood weight, a characteristic that is positively related to drought tolerance (Hacke et al. 2001). The proportion of leaves/wood and the percentage of dead crown of the three species changed with individual sizes. The decrease in the ratio of leaf weight/wood weight as plant size increased in the three species could correspond to a decrease in productivity with increasing shrub age. This would occur if the carbon respired by live shoots exceeds the amount of carbon fixed by photosynthesis in leaves (Hierro et al. 2000). In addition to these changes in the proportions of components, the percentage of dead crown increased with shrub size in *Adesmia* and *Mulinum*, which would also indicate that productivity per unit biomass decreases with age in these species. Besides being relevant to productivity, differences at the species or single plant level are important when considering decomposition rates. Recently, it has been shown that the rate of decomposition is mainly determined by biomass lignin content (Austin & Ballaré 2010), so differences in the proportion of wood or its specific weight would have a significant impact on the rate of decomposition. In general, our results do not depend on the characteristics of the year (i.e., dry, normal or wet), mainly because crown biomass is composed of wood and therefore integrates plant growth over several years. In addition, shrub growth would be largely independent of annual rainfall due to the deep roots of these plants that allow the use of deep water horizons. They should thus be independent of the dynamics of surface water that are controlled by the characteristics of the year (Golluscio et al. 1998).

At the population level in the grazed fields studied, the species did not differ in population density and biomass. The low density of *Adesmia* compared to *Senecio* and *Mulinum* (almost half) could be compensated for in terms of biomass due to the higher individual weights of *Adesmia*. On the other hand, from the difference in population size distributions, it is possible to propose new hypotheses about the vital rates of these three shrub species in Patagonian grazed fields. The higher frequency of small individuals of *Senecio* might be explained by a lower mortality of these shrub sizes, since its growth rate is higher than *Adesmia* and similar to *Mulinum* (Fernández et al. 1991). Lower mortality may be explained by lower sheep impact due to low sheep preference (Bonvissuto et al. 1983). Furthermore, the difference with *Mulinum* may result from grazing preference for *Mulinum*, which would lower the frequency of small individuals through floral herbivory and lower recruitment (Cipriotti & Aguiar, personal communication). On the other hand, the large individuals of *Adesmia*, together with this species' slow individual growth (Fernandez et al. 1991) may be indicative of a long life span (Adrián Núñez, unpublished data).

In the Patagonian steppe, shrubs are an important structural component of the community, since they play key role in the vegetation mosaic organization (Aguiar & Sala 1998, 1999; Cipriotti 2006). Therefore, monitoring the structure and dynamics of the biomass of these populations is important for the management of vegetation in relation to grazing (Cipriotti 2006). In this regard, methodologies such as those developed in this work are essential for accurate monitoring of the effects of extensive grazing at different hierarchical scales (plant, population, life form, ecosystem) and on variables such as shrub biomass dynamics, productivity and forage availability (Hierro et al. 2000).

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LITERATURE CITED

AGUIAR, MR & OE SALA. 1998. Interaction among grasses, shrubs, and herbivores in Patagonian grass-shrub steppes. *Ecología Austral*, **8**:201-210.

AGUIAR, MR & OE SALA. 1999. Patch structure, dynamics and implications for the functioning of arid ecosystems. *Trends in Ecology and Evolution*, **14**:273-277.

AUSTIN, AT & CL BALLARÉ. 2010. Dual role of lignin in plant litter decomposition in terrestrial ecosystems. *PNAS*, **107**:4618-4622.

BONVISSUTO, G; O MORICZ DE TECSO; O ASTIBIA & J ANCHORENA. 1983. Resultados preliminares sobre los hábitos dietarios de ovinos en un pastizal semidesértico de Patagonia. *Informe Investigación Agropecuaria (INTA)*, **36**:243-253.

BRISKE, DD. 1991. Developmental morphology and physiology of grasses. Pages 85-108 in: Heitschmidt, RK & JW Stuth (eds.). Grazing management. An ecological perspective. Timber Press, Portland.

Brown, S; AJR Gillespie & AE Lugo. 1989. Biomass estimation methods for tropical forests with applications to forest inventory data. *Forest Science*, **35**:881-902.

Bucci, SJ; FG Scholz; G Goldstein; FC Meinzer & ME Arce. 2009. Soil water availability and rooting depth as determinants of hydraulic architecture of Patagonian woody species. *Oecologia*, **160**: 631-641.

Cabrera, A. 1976. Regiones Fitogeográficas Argentinas. *Enciclopedia Argentina de Agricultura y Jardinería*, Tomo 2, Fascículo 1. ACME, Buenos Aires.

Cavagnaro, FP; RA Golluscio; DF Wassner & DA Ravetta. 2003. Caracterización química de arbustos patagónicos con diferente preferencia por los herbívoros. *Ecología Austral*, **13**:215-222.

Cipriotti, PA. 2006. *La dinámica de los parches de vegetación en la estepa Patagónica*. Tesis doctoral. Escuela para Graduados "Ing. Agr. Alberto Soriano". Facultad de Agronomía. Universidad de Buenos Aires, Argentina.

Cipriotti, PA & MR Aguiar. 2010. Interactions network enable coexistence in a shrub-grass steppe. *Journal of Vegetation Science*, en prensa.

Fernández, OA & CA Busso. 1999. Arid and semi-arid rangelands: two-thirds of Argentina. *Rala Reports*, **200**:41-60.

Fernández, RJ & JM Paruelo. 1988. Root systems of two patagonian shrubs: A quantitative description using a geometrical method. *Journal of Range Management*, **41**:220-223.

Fernández, RJ; OE Sala & RA Golluscio. 1991. Woody and herbaceous aboveground production of a Patagonian steppe. *Journal of Range Management*, **44**:434-437.

Flombaum, P & OE Sala. 2007. A non-destructive and rapid method to estimate biomass and aboveground net primary production in arid environments. *Journal of Arid Environments*, **69**: 352-358.

Flombaum, P & OE Sala. 2009. Cover is a good predictor of aboveground biomass in arid systems. *Journal of Arid Environments*, **73**:597-598.

Golluscio, RA & OE Sala. 1993. Plant functional types and ecological strategies in Patagonian forbs. *Journal of Vegetation Science*, **4**:839-846.

Golluscio, RA; OE Sala & WK Lauenroth. 1998. Differential use of large rainfall events by shrubs and grasses: a manipulative experiment in the Patagonian steppe. *Oecologia*, **115**:17-25.

Golluscio, RA; VA Deregibus & JM Paruelo. 1998. Sustainability and range management in the Patagonian steppes. *Ecología Austral*, **8**:265-284.

Golluscio, RA; M Oesterheld & MR Aguiar. 2005. Phenology of twenty five Patagonian species related to their life form. *Ecography*, **28**: 273-282.

Golluscio, RA; A Faigón & M Tanke. 2006. Spatial distribution of roots and nodules and ?15 N evidence of nitrogen fixation in *Adesmia volckmannii*; a Patagonian leguminous shrub. *Journal of Arid Environments*, **67**:328-335.

Goodall, DW & RA Perry. 1979. Arid-lands ecosystems: Structure, Functioning and Management. Volumen 1. *Cambridge University Press*, Cambridge, p. 881.

GraphPad Prism 5.0. 2007. GraphPad Software, Inc. San Diego, California. USA.

Haase, R & P Haase. 1995. Above-ground biomass estimates for invasive trees and shrubs in the Pantanal of Mato Grosso, Brazil. *Forest Ecology and Management*, **73**:29-35.

Hacke, U; JS Sperry; WP Pockman; SD Davis & KA McCulloh. 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pres-sure. *Oecologia*, **126:** 457-461.

Hierro, JL; LC Branch; D Villareal & KL Clark. 2000. Predictive equations for biomass and fuel characteristics of Argentine shrubs. *Journal of Range Management*, **53**:617-621.

Hughes, RF; J Kauffman & V Jaramillo. 1999. Biomass, carbon, and nutrient dynamics of secondary forests in a humid tropical region of México. *Ecology*, **80**:1892-1908.

Infostat 2.0. 2002. Grupo Infostat. FCA. Universidad Nacional de Córdoba, Argentina.

Jenkins, JC; RA Birdsey & Y Pan. 2001. Biomass and NPP estimation for the mid-Atlantic region (USA) using plot-level forest inventory data. *Ecological Applications*, **11**:1174-1193.

Jobbagy, E; JM Paruelo & RJC León. 1995. Estimación del régimen de precipitación a partir de la distancia a la cordillera en el noroeste de la Patagonia. *Ecología Austral*, **5**:47-54.

Keller, M; M Palace & G Hurtt. 2001. Biomass estimation in the Tapajos National Forest, Brazil: examination of sampling and allometric uncertainties. *Forest Ecology and Management*, **154**: 371-382.

Kumar, M; SJ George; V Jamaludheen & TK Suresh. 1998. Comparison of biomass production, tree allometry and nutrient use efficiency of multipurpose trees grown in woodlot and silvopastoral experiments in Kerala, India. *Forest Ecology and Management*, **112**:145-163.

León, RJC & MR Aguiar. 1985. El deterioro por uso pasturil en estepas herbáceas patagónicas. *Phytocoenologia*, **13**:181-196.

León, RJC; D Bran; M Collantes; JM Paruelo & A

SORIANO. 1998. Grandes unidades de vegetación de la Patagonia extra-andina. *Ecología Austral*, **8**: 125-144.

MONTÈS, N. 2009. A non-destructive method to estimate biomass in arid environments: A comment on Flombaum and Sala (2007). *Journal of Arid Environments*, **73**:599-601.

MUUKKONEN, P. 2007. Generalized allometric volume and biomass equations for some tree species in Europe. *European Journal of Forest Research*, **126**: 157-166.

NÁVAR, J; E MÉNDEZ; A NÁJERA; J GRACIANO; V DALE; ET AL. 2004. Biomass equations for shrubs species of Tamaulipan thornscrub of North-eastern Mexico. *Journal of Arid Environments*, **59**:657-674.

NELSON, BW; R MESQUITA; JLG PEREIRA; SGA SOUZA; GT BATISTA; ET AL. 1999. Allometric regressions for improved estimate of secondary forest biomass in the central Amazon. *Forest Ecology and Management*, **117**:149-167.

NOYMEIR, I. 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics*, **4**:25-41.

OKELLO, BD; TG O'CONNOR & TP YOUNG. 2001. Growth, biomass estimates, and charcoal production of *Acacia drepanolobium* in Laikipia, Kenya. *Forest Ecology and Management*, **142**:143-153.

PARUELO, JM; MR AGUIAR & RA GOLLUSCIO. 1988. Soil water availability in the Patagonian arid steppe: gravel content effect. *Arid Soil Research and Rehabilitation*, **2**:67-74.

SALA, OE; RA GOLLUSCIO; WK LAUENROTH & A SORIANO. 1989. Resource partitioning between shrubs and grasses in the Patagonian steppe. *Oecologia*, **81**:501-505.

SAMBA, SAN; C CAMIRÉ & HA MARGOLIS. 2001. Allometry and rainfall interception of *Cordyla pinnata* in a semi-arid agroforestry parkland, Senegal. *Forest Ecology and Management*, **154**: 277-288.

SAMPAIO, EVSB & GC SILVA. 2005. Biomass equations for Brazilian semiarid caatinga plants. *Acta Bot. Bras*, **19**:935-943.

SANKARAN, M; NP HANAN; RJ SCHOLES; J RATNAM; DJ AUGUSTINE; ET AL. 2005. Determinants of woody cover in African Savannas. *Nature*, **438**:846-849.

SCHLESINGER, WH; JF REYNOLDS; GL CUNNINGHAM; LF HUENNEKE; WM JARRELL; ET AL. 1990. Biological feedbacks in global desertification. *Science*, **247**: 1043-1048.

SCHROEDER, P; S BROWN; J MO; R BIRDSEY & C CIESZEWSKI. 1997. Biomass estimation for temperate broadleaf forest of the United States using inventory data. *Forest Science*, **43**:424-434.

SORIANO, A. 1956. Aspectos ecológicos y pastoriles de la vegetación Patagónica relacionados con su estado y capacidad de recuperación. *Revista de Investigaciones Agrícolas*, **10**:349-372.

SORIANO, A; CP MOVIA; & RJC LEÓN. 1983. Vegetation In: Deserts and semi-deserts of Patagonia. Pp. 440-454 in: West, NE (ed.). *Temperate deserts and semi-deserts of the world*. Vol. 5 of Ecosystems of the World (ed. in chief: Goodall, DW). Elsevier Publ. Co. Amsterdam-Oxford-New York.

TER-MIKAELIAN, MT & MD KORZUKHIN. 1997. Biomass equations for sixty-five North American tree species. *Forest Ecology and Management*, **97**:1-24.

USÓ, JL; L MATEU; T KARJALAINEN & P SALVADOR. 1997. Allometric regression equations to determine aerial biomasses of Mediterranean shrubs. *Plant Ecology*, **132**:59-69.

WALTER, H. 1977. *Vegetation of the Earth and ecological systems of the geobiosphere*. Springer-Verlag, Berlin. Pp. 318.

WHITTAKER, RH & GM WOODWELL. 1968. Dimension and production relations of trees and shrubs in the Brookhaven Forest, New York. *Journal of Ecology*, **56**:1-25.