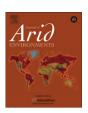
FISEVIER

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv



Wood productivity of *Prosopis flexuosa* D.C. woodlands in the central Monte: Influence of population structure and tree-growth habit

J.A. Alvarez a,*, P.E. Villagra a,c,1, R. Villalba a,1, M.A. Cony b, M. Alberto c

- ^a Departamento de Dendrocronología e Historia Ambiental, Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA), CONICET, CC 330, 5500, Mendoza, Argentina
- b Unidad de Ecofisiología Vegetal, Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA), CONICET, CC 507, 5500, Mendoza, Argentina
- ^c Facultad de Ciencias Agrarias, Universidad Nacional de Cuyo, M5528AHB. Chacras de Coria, Mendoza, Argentina

ARTICLE INFO

Article history: Received 20 August 2009 Received in revised form 10 May 2010 Accepted 6 September 2010

Keywords: Growth rate One-versus multi-stemmed individuals Prosopis biomass

ABSTRACT

A balance between forest production and protection is hard to achieve in arid zones due to their low potential for wood production. *Prosopis flexuosa* woodlands are the major woody formations in the Monte desert and are currently in a degraded state due to intense use. The main degradation factors in the study area are overgrazing and firewood extraction. We developed allometric models to estimate the aerial biomass of *P. flexuosa*, compared annual growth rates of one- and multi-stemmed individuals through dendrochronological methods, and estimated the productivity of four structurally different woodlands in the central Monte. Total dry weight was best estimated by power equations. Annual increments in basal area and dry weight were initially larger for multi- than one-stemmed individuals. However, whereas multi-stemmed individuals rapidly decreased their growth rates after 60 years of age, one-stemmed trees maintained steady growth rates during the first 100 years. Depending on woodland density and tree size, total woodland biomass varied between 4000 and 15 000 kg ha⁻¹. Wood productivity was similar in all four woodlands studied (121.6–173.7 kg ha⁻¹ year⁻¹). Our results reveal the importance of tree growth habit to productivity, and suggest that regulated extraction of firewood and poles from old multi-stemmed individuals could optimize wood productivity and contribute to the sustainable use and conservation of these woodlands.

© 2010 Elsevier Ltd. All rights reserved.

1. Introduction

The main challenge to the forestry sector is finding a balance between production and forest protection (F.A.O., 1999); this goal is hard to achieve in arid zones due to the strong pressure on wood resources and their low potential for wood production. Although most native woodlands in arid areas have limited economic possibilities from a classical forestry perspective, they benefit local inhabitants by providing non-traditional forest products (poles, firewood, fodder, fruit) and environmental services (soil, water and diversity conservation) (Burkart, 1976; F.A.O., 1999).

Open woodlands of *Prosopis flexuosa* are the major woody formations in the Monte desert. From a bioclimatic point of view, the Monte includes the arid or semiarid lands lying in the eastern and southern parts of the Arid Diagonal in South America. Total annual rainfall ranges between 30 and 350 mm. *Prosopis*

woodlands only occur in areas with accessible groundwater (between 8 and 15 m depth). Intense use of these woodlands, irrespective of their growth rates, has caused degradation of these resources (Villagra et al., 2004, 2005b). In addition, the natural recovery of these systems after disturbance is extremely slow because of the reduced establishment of dominant species and their low rates of growth (Villagra et al., 2004). Therefore, a proper estimation of woodland productivity, considering the particular structures of these woodlands, is essential to promote their sustainable use.

Most *Prosopis* species show distinct annual growth rings which allow determination of radial growth rates and biological culmination ages (Castro, 1994; Villalba et al., 2000). Most tree-ring based studies with *P. flexuosa* have been conducted with onestemmed individuals or considering the main trunk of multistemmed trees (Duff et al., 1994; Perpiñal et al., 1995; Ríos et al., 2001; Villagra et al., 2005a, 2005b). Nevertheless, other studies suggest that radial growth significantly differs between one- and multi-stemmed trees in a population (Cao and Peters, 1998). In the central Monte, multi-stemmed trees of *P. flexuosa* represent 60% of the woodland population (Alvarez et al., 2006). In consequence,

^{*} Corresponding author. Tel.: +54 261 5244207; fax: +54 261 5244200. E-mail address: jalvarez@mendoza-conicet.gov.ar (J.A. Alvarez).

¹ Tel.: +54 261 5244207; fax: +54 261 5244200.

accounting for the differences in growth between one- and multistemmed trees may provide a better estimation of woodland productivity. The objectives of this study were: a) to develop allometric models to estimate the aerial biomass of *P. flexuosa* from tree structure data, b) to compare annual growth rates of one-versus multi-stemmed individuals using dendrochronological methods, and c) to estimate the productivity of *P. flexuosa* woodlands from northeastern Mendoza.

2. Materials and methods

2.1. Study area

The study area is located in the central plains of northeastern Mendoza, Argentina (32–33°S, 67–68°W; 500–550 m elevation). This area, including the Telteca Reserve and surrounding lands, is representative of the central part of the Monte Biogeographic Province (Morello, 1958; Rundel et al., 2007). The area lies in a sedimentary basin between two geological structures with positive relief, the Uspallata range on the west and San Luis Sierras to the east. Aeolian reworking of Holocene sediments originated a system of transverse sand dunes up to 20 m high separated by 100–200 m wide troughs (González Loyarte, 1992). The climate is arid with a total annual precipitation of around 156 mm (1972–2007 average), and large daily and annual temperature ranges. Mean temperature is 18.5 °C, with the absolute maximum and minimum being respectively 48 °C and –10 °C (Estrella et al., 1979).

P. flexuosa D.C. (Fabaceae, Mimosoideae), called "algarrobo dulce", is one of the 44 Prosopis species recognized by Burkart (1976), most of them distributed across arid and semiarid South America. In Mendoza, a high proportion (69%) of *P. flexuosa* trees is multi-stemmed, reaching 5-12 m in height (Alvarez et al., 2006). A well-developed root system enables trees to tap groundwater located at 7 m depth (Guevara et al., 2010). Logging activities are less intensive at the study area than in other Monte woodlands, because sand dunes prevent access to the area. Four P. flexuosa woodland units have been indentified in Northeastern Mendoza: (1) Semi-closed canopy woodland (with Atriplex lampa and Lycium tenuispinosum in inter-dune valleys), (2) Open woodland with Trichomaria usillo and Suaeda divaricata, (3) Semi-open woodland with Trichomaria and (4) Semi-open woodland with Atriplex (Alvarez et al., 2006). Population structure differs among these woodlands (Alvarez et al., 2006). The highest density of trees was sampled in the Semi-open woodland with Trichomaria (233.3 individuals ha⁻¹), while in the Semi-closed canopy woodland was 181.4. The lowest total density was recorded in Open woodland (155 individuals ha⁻¹). For the Semi-closed canopy woodland, the density of adult trees (117.4 individuals ha^{-1}), height (5.7 m), crown diameter (5.3 m) and coverage of *Prosopis* (32.3% by ha) was higher than the other three woodlands (adults = trees with a basal diameter greater than 7.5 cm).

2.2. Allometric variables and regression models

To estimate dry weight, we generated regression equations from the allometric variables of 39 *P. flexuosa* trees representing the different diameter classes larger than 3 cm identified in the study area (Alvarez et al., 2006). For each tree we recorded the following allometric variables: number of stems per tree, stem base diameter (SBD), tree height, and largest and smallest crown diameters (used to estimate mean crown diameter). Due to the low height of the stems, we preferred to use SBD instead of diameter at breast height (Pajtík et al., 2008). For multi-stemmed trees, basal area (*BA*) was determined as the sum of the cross-sections of their stems. The

diameter corresponding to this total area was then termed as the 'equivalent basal diameter' of the tree (EBD).

Trees were then cut at the base. Each tree was divided into fractions and weighed in a hanging scale or a precision scale. Foliar, small branch (<3 cm diameter in adult trees), and root biomass was not evaluated. In other *Prosopis* species, no allometric model relate the small parts of the tree (leaves and branches with diameter <2 cm) to dasometric variables (Padrón and Navarro, 2004).

To estimate dry biomass, the water content of each fraction was determined. For this, transverse sections of the main trunk, green branches, and dead wood were weighed in the field with 0.01 g precision, oven-dried at 70 $^{\circ}$ C, and weighed again after the dry weight of the samples became constant (61 days). For determination of specific gravity, we used the water displacement method (Paul et al., 2008).

In agreement with previous studies (Pajtík et al., 2008), we proposed a power model for the determination of *Dry Weight* based on tree height, equivalent basal diameter and crown diameter. Because the stem is not a perfect cylinder, weight should be proportional to the power transformations of height, equivalent basal diameter and crown diameter.

Dry Weight = α . *Height*^{β}. *EBD* $^{\gamma}$. *Crown Diameter* $^{\sigma}$

where α , β , γ , σ , are the model coefficients.

In addition, to assess the possible effects of different growth habits (number of stems) we incorporated this parameter to the model. As a result, we adjusted a covariance model by log transformation:

$$\log(Dry \ weight_i) = \log(\alpha) + \beta\log(Height_i) + \gamma\log(EBD_i) + \sigma\log(crown \ diameter) + \varphi_i + \epsilon_i$$

where ϕ_i represents the effects of stem number.

The analysis of variance showed that the effects of stem number were not significant (p = 0.7758); thus, for the estimation of dry weight, all individuals were considered as belonging to a single population. As a consequence, regressions were developed using as predictors the individual variables in the previous equation and their combinations (Crow and Schlaegel, 1988).

The determination coefficient (r^2) and the Bayesian Information Criterion (BIC) were used to select the best regression equations. Smaller BIC values are related to more stable, unbiased models (Bolker, 2007). Basic statistical assumptions were verified with the Shapiro—Wilk test (normality) and the Breusch-Pagan/Cook—Weisberg test (homoscedasticity).

2.3. Growth in one-stemmed and multi-stemmed individuals

Previous studies indicated the existence of annual rings of this species which are defined by the presence of a narrow band of terminal parenchyma and by the difference in diameter between earlywood and latewood vessels (Giantomasi et al., 2009; Villalba, 1985). Cross-sections were removed from the base of all stems used in the biomass study. Samples were polished with progressively finer grained sandpaper to achieve clear visualization of the annual growth rings across two perpendicular radii. Ring widths were measured using a Unislide TA 4020H1-S6 Velmex, with 0.001 mm precision. The quality of dating was checked using the COFECHA program (Holmes, 1983).

To compare growth and productivity of one- and multi-stemmed individuals, we calculated the annual, cumulative and mean increments in equivalent basal diameter, basal area, and dry weight from the radial increments obtained for each stem using the AGE program (Holmes, 1994). For each stem, we calculated current annual diameter increment (*CAId*). Current annual increment in basal area (*CAIb*) for each stem was estimated from:

$$CAIb_t = \pi \Big(r_t^2 - r_{t-1}^2 \Big)$$

where $CAIb_t$ is the increment in basal area in year t, r_t is the radius of the tree in year t and r_{t-1} is the radius in year t-1 (minor radius). For multi-stemmed individuals, the current annual increment in basal area (CAIb) was estimated as the summation of current annual increments of individual stems in year t.

The cumulative basal increment (*CBI*) in year t results from the summation of current annual increments in basal area in year t. Based on *CBI*, the cumulative diameter increment (*CDI*) and the current annual diameter increment (*CAI*d) for each tree in year t was determined as follows:

$$CDI_t = \sqrt{CBI_t/\pi}$$

$$CAId_t = \sqrt{CBI_t/\pi} - \sqrt{CBI_{t-1}/\pi}$$

The rate of wood productivity (*DWI*) for one- and multi-stemmed individuals was estimated using the regression equations relating *EBD* to total dry weight. We applied this equation to the cumulative diameter increments to estimate the cumulative dry weight increments (*CDWI*). The current annual increment in dry weight (*CAI*dw), which represents the wood productivity for each tree at year t, was estimated from *CDWI* as follows:

$$\textit{CAI} dw_t \, = \, \textit{CDWI}_t - \textit{CDWI}_{t-1}$$

Mean annual increment in basal area (MAIB) and dry weight (MAIdw) for both types of trees (one- and multi-stemmed) was calculated as the average of annual increments in basal area and dry weight up to year t, respectively.

Interannual variability of the growth series was smoothed using a 32-year cubic spline function (Cook, 1985; Fritts, 1972). The theoretical biological rotation age (or culmination age) occurs when *MAI* is equal to *CAI* (Assman, 1970).

2.4. Estimation of woodland biomass and productivity

Woody biomass for the different woodlands was calculated from the combination of the diameter structure of P. flexuosa populations and the best allometric equations according to the r^2 and BIC statistics. For diameter structure, we used the data collected from 90 plots (20×50 m) established for a previous study in all four woodlands. In each plot, we measured density of P. flexuosa trees and, for each individual, number of stems, SBD, height, and crown diameter (Alvarez et al., 2006).

As differences in growth rates were observed between one- and multi-stemmed individuals (see results), to estimate the woodland productivity, we reanalyzed the data on woodland structure to obtain separate diameter structures for one- and multi-stemmed individuals (Alvarez et al., 2006). Total productivity for each diameter class in the different woodlands was estimated as the product of the mean *CAI*dw and number of individuals for that class. Finally, we summed the yields from all diameter classes to calculate total productivity of each woodland.

Differences in biomass and productivity among the four woodland types were compared using a one-way analysis of variance. Tukey's tests were used for *a posteriori* mean comparisons (Zar, 1984).

2.5. Relationship between equivalent basal diameter and crown

We used the relationship between EBD and crown area as a first indicator of both leaf area and the photosynthetic capacity of one-stemmed and multi-stemmed individuals. We performed logistic regression models for both types of trees using the data of all individuals sampled for the structure analysis. We compared both models using the extra-sum-of-square F test (Ratkowsky, 1990). This method entails development of one equation for each type of individual and one equation for the whole data set, and assessment of the differences between the model parameters for the whole data set and the model parameters for each type of tree.

3. Results

3.1. Regression equations

All selected models had determination coefficients higher than $r^2 > 0.87$; hence they are good predictors of *P. flexuosa* woody biomass. The model combining equivalent basal diameter, tree height and crown diameter yielded the highest determination coefficient and the lowest BIC value and should be regarded as the most accurate estimator of aerial biomass (Table 1). However, the regression based on *EBD*, the most commonly recorded variable in the field, also showed acceptable prediction.

3.2. Growth in one-stemmed and multi-stemmed Prosopis flexuosa individuals

From 15 to 80 years of age, current annual increments in basal area (CAIb) and in dry weight (CAIdw) were larger for multistemmed than for one-stemmed individuals (Fig. 1). However, the CAIb and CAIdw in multi-stemmed trees decreased after 60 years, whereas a positive trend still persists in one-stemmed trees at least up to 100 years old. Both one-stemmed and multi-stemmed individuals reached their maximum diameter growth between 20 and 30 years (2.47 and 3.21 mm respectively). After that, the decrease was more pronounced in multi-stemmed trees. Multi-stemmed individuals reached their maximum CAIb (5 cm²) between 40 and 80 years of age, whereas one-stemmed individuals continued to increase their CAIbs, at least, for at least 100 years. The CAIb from one-stemmed trees surpassed the CAIb from multi-stemmed trees after 80 years (Fig. 1b). The largest yield in CAIdw in one-stemmed individuals occurred after 80 years (annual mean being 1.5 kg), and corresponded to individuals with an EBD close to 27 cm (Fig. 2a). In multi-stemmed individuals, the largest yield occurred between 60 and 85 years (average being 2 kg), and corresponded to individuals with EBD between 20 and 27 cm (Fig. 2a). The growth culmination age for multi-stemmed Prosopis was around 80 years, based on the moment when CAIdw and MAIdw intercept (Fig. 1). In one-stemmed trees, instead, culmination age is over 104 years, the age of the oldest sampled tree.

3.3. Woodland biomass and productivity

The Semi-closed canopy woodland has the largest *Prosopis* woody biomass (15 390.70 kg ha⁻¹), whereas the lowest (3263.17 kg ha⁻¹) is

Table 1 Regression equations tested for the estimation of total dry weight (*TDW*) of *Prosopis flexuosa*. *EBD*: equivalent basal diameter. H: tree height. CD: mean crown diameter. r^2 : determination coefficient. BIC: Bayesian information criterion. The basal diameter of the sampled trees was higher or equal to 3 cm (n = 39).

Model	r ²	BIC
$TDW = 0.07977 \ EBD^{1.131617} \ e^{0.4953181 \ log(H)^2} \ CD^{1.480073}$	0.974	36.1
$TDW = 0.03569 \ EBD^{2.374869}$	0.946	60.4
$TDW = 1.2304 e^{1.362872 \log(H)^2}$	0.914	78.7
$TDW = 0.02391 \ CD^{6.749443}$	0.876	91.8
$TDW = 0.06211 \ EBD^{1.431773} \ e^{1.491206 \ \log(H)^2}$	0.966	46.3

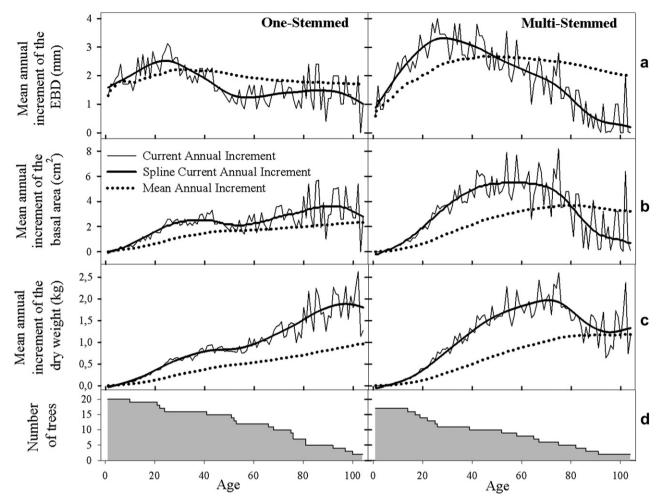


Fig. 1. Current (solid line) and Mean (dotted line) annual increment: (a) Equivalent Basal Diameter (mm), (b) Basal Area (cm²) and (c) Dry Weight (kg) for one- and multi-stemmed *Prosopis* trees. (d) Number of individuals sampled for each type of tree.

found in the Open woodland (Fig. 3a). Intermediate values of biomass were recorded in the Semi-open woodlands with *Trichomaria* and *Atriplex* (10 419.54 and 7778.26 kg ha $^{-1}$, respectively). Most of the woody volume was contributed by trees larger than 35 cm equivalent diameter. In consequence, total biomass of the woodlands was related to the amount of trees with diameters above 35 cm.

Wood productivity did not differ statistically among the different woodlands, varying from 119.7 kg ha $^{-1}$ year $^{-1}$ and 172.6 kg ha $^{-1}$ year $^{-1}$ (number of sites = 30, d.f. = 3, F = 1.07, p = 0.37) (Fig. 3b). However, differences were recorded among woodlands in the diameter classes with largest biomass productivity, depending on the density and proportion of one- and multistemmed individuals within each different diameter class (Fig. 4a). In the Semi-closed canopy woodland, the largest biomass was related to one-stemmed individuals larger than 25 cm EBD, whereas in the Open and Semi-open woodlands with Atriplex the largest yield was from multi-stemmed individuals with EBD between 7.5 and 17.5 cm. The Semi-open woodland with Trichomaria, biomass is largely associated with multi-stemmed individuals with EBD larger than 17.5 cm (Fig. 4a).

3.4. EBD - crown area relations

Regression models for the relationship between *EBD* and crown area of each type of individual were significantly different from the whole data set model, indicating significant differences between

one-stemmed and multi-stemmed individuals (Table 2, Fig. 2b). Multi-stemmed individuals smaller than 28 cm in *EBD* showed larger crown area than one-stemmed individuals, while individuals larger than 28 cm *EBD* showed similar crown areas. B2 parameter indicated the rate of crown area increase, which was higher in multi-stemmed than in one-stemmed individuals. B1 parameter indicated the point where the crown area becomes stable, being larger in one-stemmed than in multi-stemmed individuals (Table 2, Fig. 2b).

4. Discussion

Woody biomass in woodlands can be precisely estimated using power function models. Power equations of the type $M=a\ D^b$ (M= biomass and D= diameter of the main stem) are widely used in North America with high determination coefficients (between 0.66 and 0.99) (Ter-Mikaelian and Korzukhin, 1997). These power functions represent a good compromise between prediction accuracy and data requirements (Ter-Mikaelian and Korzukhin, 1997). For *Prosopis* woodlands in the central Monte desert, the best allometric equation includes *EBD*, tree height, and crown diameter. Nonetheless, *EBD* alone provides high determination coefficients, representing a valid alternative when additional allometric variables have not been recorded or dendrochronological methods have been used to estimate productivity from annual diameter increments.

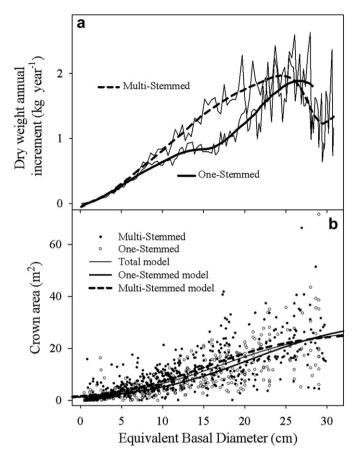


Fig. 2. a) Relation between the equivalent basal diameter (cm) and the dry weight annual increment (kg year $^{-1}$) for one- and multi-stemmed individuals (fine lines). To emphasize the long-term variations, the increments for one- (solid) and multi-stemmed (dotted) individuals were smoothed with a cubic spline designed to reduce 50% of the variance in a sine wave with a periodicity of 15 years. b) Logistic regression models for the relation between the equivalent basal diameter (cm) and the crown area (m^2) for one- and multi-stemmed individuals.

Growth differences between one- and multi-stemmed individuals agree with the proposed hypothesis, suggesting that growth habits are a determinant of growth rate. Hence, the proportion of multi-stemmed individuals in woodlands from arid areas should be considered in estimating wood productivity and its temporal evolution. Similar rates of growth were recorded for both forms during the first years of development. At this stage, growth rings in P. flexuosa are concentric (Villalba, 1985; Villalba and Boninsegna, 1989; Villalba et al., 2000) and no evidence of interference between young stems is recorded. Growth differences between one- and multi-stemmed trees start at around 15 years old and would be a response to different photosynthetic capacities between growth habits. It has been observed that branching patterns, which are defined in juvenile stages, directly affect the photosynthetic capacity of trees (Fisher, 1986). Between 15 and 80 years, the larger foliar area in multi-stemmed individuals would determine a higher photosynthetic rate than in one-stemmed trees (Duff et al., 1994). Finally, above a certain crown size, competition for light would start between the different crowns of a multi-stemmed tree, inducing a marked decrease in the rate of biomass increment. On the contrary, one-stemmed Prosopis would maintain an increasing rate of photosynthetic capacity, at least during the 100 years analyzed. First evidences supporting these postulates are the larger crown areas observed in multi-stemmed than one-stemmed individuals with EBD smaller than 28 cm, and the lack of difference observed in

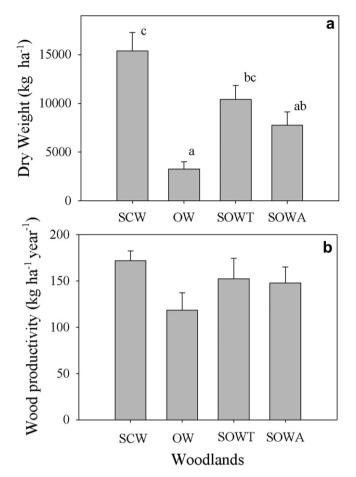


Fig. 3. a) Woody biomass of *Prosopis* woodlands from northeastern Mendoza (kg ha⁻¹). (n=30, d.f. = 3, F=8.15, p<0.0005). b) Wood productivity from northeastern Mendoza woodlands (kg ha⁻¹ year⁻¹) (n=30, d.f. = 3, F=1.07, p=0.37). Bars are mean values and vertical lines the standard errors. Different letters indicate significant differences at p<0.05. Number of sample sites per woodland: 9 for Semi-closed canopy woodland (SCW), 4 for Open woodland (OW), 9 for Semi-open woodland with *Trichomaria* (SOWT) and 8 sites for Semi-open woodland with *Atriplex* (SOWA).

individuals more than 28 cm in *EBD*. Nevertheless, additional studies are needed to supplement these observations and support our initial results. Increased replication with older individuals is necessary to validate the growth trends after 80 years.

Forestry practices in the *P. flexuosa* woodlands should take into account the different growth rates recorded between one- and multi-stemmed trees. Based on basal area and dry weight increments, we estimated culmination ages for multi-stemmed *Prosopis* trees in around 80 years. In addition, productivity was higher in one- than multi-stemmed trees for individuals with *EBD* larger than 27 cm. In consequence, removal of secondary stems or major branches when the main stem of trees is larger than 27 cm may increase the growth rate of the remaining stems by reducing light competition and improving, as a secondary effect, the wood quality of the selected stem (Cornejo-Oviedo et al., 1992).

In spite of the structural differences observed between wood-lands (Alvarez et al., 2006) and the larger biomass accumulated in the Semi-closed canopy woodland, there are no significant differences in productivity between woodlands. This is due to the decreased productivity in old trees, especially in multi-stemmed individuals after 50 years. The woodland with largest amount of old trees (Semi-closed canopy woodland) has a lower density of individuals in the most productive diameter classes (Fig. 4). Alvarez

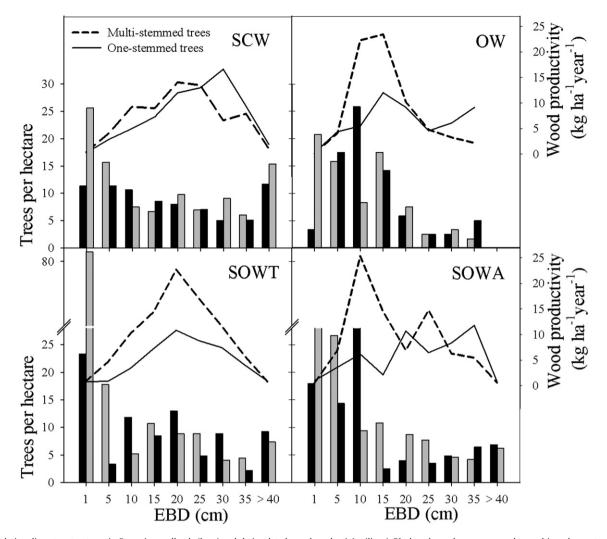


Fig. 4. Population diameter structures in *Prosopis* woodlands (bars) and their related wood productivity (lines). Black and grey bars correspond to multi- and one-stemmed trees. SCW: Semi-closed canopy woodland, OW: Open woodland, SOWT: Semi-open woodland with *Trichomaria* and SOWA: Semi-open woodland with *Atriplex*. Trees larger than 40 cm in EBD were grouped in the >40 diameter class.

et al. (2006) recorded a higher proportion of unhealthy individuals with decumbent growth habit, which in turn reduces the quality of forestry products. These observations reinforce the idea that regulated extraction of firewood and poles is a suitable forestry practice because it would favor the productivity of these woodlands and prolong the period of maximum growth rate in larger individuals. Therefore, it is necessary to quantify the amount of existing dry wood, its production rate, and the effects of wood extraction in these woodlands to determine the best management strategies.

Table 2Parameter for fitted logistic model regression between EBD and crown area, and results of the extra sum of squares F test performed to compare one- and multistemmed models.

Model	Crown area = $\frac{B1}{1 + \exp(-B2(EBD - B3))}$			
Parameter	Whole data set	One-stemmed	Multi-stemmed	
	model	model	model	
B1	27.86 (1.66)	31.48 (3.92)	26.28 (1.60)	
B2	0.1600 (0.0111)	0.1515 (0.0166)	0.1732 (0.0152)	
B3	17.35 (0.95)	20.63 (1.92)	15.39 (0.96)	
d.f. E.S.S. F calc. = 10.6	1021 32514.92 8; <i>P</i> < 0.00001	415 11812.73	606 19713.18	

Wood availability and productivity in the central Monte woodlands is lower than in other *Prosopis* woodlands in the arid areas of Argentina. Woody biomass is 60 000 kg ha⁻¹ in Cafayate (Salta) (Calzon Adorno, 1995) and oscillates between 63 100 and 31 000 kg ha⁻¹ in Pipanaco (Catamarca) (Villagra et al., unpublished data). In the most productive sites in Pipanaco and Cafayate, wood productivity is 950.8 and 1007.5 kg ha⁻¹ year⁻¹, respectively (Calzon Adorno, 1995; Villagra et al., unpublished data). These values represent around six-fold the productivity recorded for Telteca (120–170 kg ha⁻¹ year⁻¹). Although these large differences in productivity may be related to environmental factors such as mean temperature, water availability, extent of growth period, frost-free period, and land-use history, they may also relate to genetic variability within *P. flexuosa* populations in the Monte desert (Cony, 1996; Duff et al., 1994).

The results from this study contribute to our knowledge of the rates of woody growth and related productivity of *P. flexuosa* woodlands. In addition, they reveal the importance of tree growth habits to wood production and, in consequence, to woodland productivity. The reduced rate of growth, growth habits and low diameter of stems at the age of growth culmination hinder the economic use of these woodlands under traditional forestry management practices. However, the relatively high rate of growth

of young multi-stemmed individuals and the low difference in productivity among woodlands with different biomass accumulation suggest that the use of other forest products (firewood and poles), could optimize wood productivity and contribute to the sustainable use and conservation of these woodlands. However, additional studies addressing *Prosopis* establishment rates, the importance of vegetative propagation versus sexual reproduction, and the evaluation of forestry practices and their effects on ecosystems, are needed before sound management practices can definitely be established.

Acknowledgements

This research was supported by the Agencia Nacional de Promoción Científica y Tecnológica of Argentina (PICT-03220) and the Universidad Nacional de Cuyo (Programa de Investigación 06-P05). We thank A. Miner, G. Zalazar, H. Debandi and E. Cesca for their field assistance, A. Giantomasi in measuring the growth rings. We thank M. E. Soler and N. Horak for their English version. We appreciate helpful suggestions and comments from J. Boninsegna and J. Aranibar.

References

- Alvarez, J.A., Villagra, P.E., Cony, M.A., Cesca, E., Boninsegna, J.A., 2006. Estructura y estado de conservación de los bosques de *Prosopis flexuosa* D.C. en el Noreste de Mendoza, Argentina. Revista Chilena de Historia Natural 79, 75–87.
- Assman, E., 1970. The Principles of Forest Yield Study: Studies in the Organic Production, Structure, Increment, and Yield of Forest Stands. Press, P, Oxford. p. 506.
- Bolker, B., 2007. Likelihood and all that. In: Ecological Models and Data in R. Princeton, pp. 228–291 (Chapter 6).
- Burkart, A., 1976. A monograph of the genus *Prosopis* (Leguminosae subfam. Mimosoideae). Journal of the Arnold Arboretum 57 (219–249), 450–455.
- Calzon Adorno, M.E., 1995. Estudio de la productividad económica de un bosque de algarrobo en el Departamento de Cafayate. Tesis Profesional. Universidad Nacional De Salta.Salta, Pcia de Salta, 69 pp.
- Cao, K.-F., Peters, R., 1998. Structure and stem growth of multi-stemmed trees of Fagus engleriana in China. Plant Ecology 139, 211–220.
- Castro, M.A., 1994. Maderas Argentinas de Prosopis. Atlas Anatómico., Secretaría General de la Presidencia de la Nación, República Argentina, 101 pp.
- Cony, M.A., 1996. Genetic variability in *Prosopis flexuosa* D.C., a native tree of the Monte phytogeographic province, Argentina. Forest Ecology and Management 87, 41–49.
- Cook, E.R., 1985. A Time Series Analysis Approach to Tree-ring Standardisation. Published by Tree- Ring Laboratory Lamont-Doherty Geological Observatory Palisades. New York. EUA. 171.
- Cornejo-Oviedo, E., Gronski, S., Felker, P., 1992. Mature mesquite (*Prosopis glandulosa* var *glandulosa*) Stand description and preliminary effects of understory removal and fertilization on growth. Journal of Arid Environments 22, 339–351.
- Crow, T.R., Schlaegel, B.E., 1988. A guide to using regression equations for estimating tree biomass. Northern Journal of Applied Forestry 5, 15—22.
- Duff, A.B., Meyer, J.M., Pollock, C., Felker, P., 1994. Biomass production and diameter growth of nine half-sib families of mesquite (*Prosopis glandulosa* var. *glan-dulosa*) and a fast growing *Prosopis alba* half-sib family grown in Texas. Forest Ecology and Management 67, 257/266.

- Estrella, H.A., Heras, V.A., Guzzeta, V.A., 1979. Registro de elementos climáticos en áreas críticas de la provincia de Mendoza. Cuaderno Técnico (IADIZA-Mendoza) 1. 49–71.
- F.A.O., 1999. Situación de los bosques del mundo. F.A.O., 129 pp.
- Fisher, J.B., 1986. Branching patterns and angles in trees. In: Givnish, T.J. (Ed.), On the Economy of Plant Form and Function. Cambridge University Press, Cambridge, p. 717.
- Fritts, H.C., 1972. Tree rings and climate. Scientific American 226, 92-100.
- Giantomasi, M.A., Roig Juñent, F.A., Villagra, P.E., Srur, A., 2009. Annual variation and influence of climate on the ring width and wood hydrosystem of *Prosopis flexuosa* DC. Trees 23, 117–126.
- González Loyarte, M.M., 1992. Reserva Faunística y Florística Telteca. In: Las Áreas
- Protegidas de la Provincia de Mendoza. IADIZA, pp. 32–35. Guevara, A., Giordano, C.V., Aranibar, J., Quiroga, M., Villagra, P.E., 2010. Phenotypic plasticity of the coarse root system of *Prosopis flexuosa*, a phreatophyte tree, in the Monte Desert (Argentina). Plant and Soil 330 (1–2), 447–464.
- Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bulletin 43, 69–78.
- Holmes, R.L., 1994. Dendrochronology Program Library Users Manual. In: Research, L.o.T.-R. University of Arizona, Tucson, Arizona, USA, 40 pp.
- Morello, J., 1958. La Provincia Fitogeográfica del Monte. Opera Lilloana 2, 5–115. Padrón, E., Navarro, R.M., 2004. Estimation of above-ground biomass in naturally occurring populations of *Prosopis pallida* (H. & B. ex. Willd.) H.B.K. in the north
- of Peru. Journal of Arid Environments 56, 283–292.
 Pajtík, J., Konopka, B., Lukac, M., 2008. Biomass functions and expansion factors in young Norway spruce (*Picea abies* [L.] Karst) trees. Forest Ecology and
- Management 256, 1096—1103.

 Paul, K.I., Jacobsen, K., Koul, V., Leppert, P., Smith, J., 2008. Predicting growth and sequestration of carbon by plantations growing in regions of low-rainfall in
- southern Australia. Forest Ecology and Management 254, 205–216. Perpiñal, E., Balzarini, M., Catalán, L., Pietrarelli, L., Karlin, E., 1995. Edad de culminación del crecimiento en *Prosopis flexuosa* D.C. en el Chaco árido argentino.
- Investigación Agraria: Sistemas y Recursos Forestales 4, 45–55. Ratkowsky, D., 1990. The Handbook of Nonlinear Regression Models. Marcel Dekker Inc., New York, 241 pp.
- Ríos, N.A., Giménez, A.M., Moglia, J.G., 2001. Crecimiento de itín (*Prosopis kuntzei* Harms) en la región chaqueña argentina. Madera Y Bosques 7, 47—56.
- Rundel, P., Villagra, P.E., Dillon, M.O., Roig-Juñent, S.A., Debandi, G., 2007. Arid and semi-arid ecosystems. In: Veblen, T.T., Young, K., Orme, A. (Eds.), The Physical Geography of South America. Oxford University Press, pp. 158–183.
- Ter-Mikaelian, M.T., Korzukhin, M.D., 1997. Biomass equations for sixty-five North American tree species. Forest Ecology and Management 97, 1–24.
- Villagra, P.E., Boninsegna, J.A., Alvarez, J.A., Cony, M., Cesca, E., Villalba, R., 2005a. Dendroecology of *Prosopis flexuosa* woodlands in the Monte desert: implications for their management. Dendrochronologia 22, 209–213.
- Villagra, P.E., Cony, M.A., Mantován, N.G., Rossi, B.E., González Loyarte, M.M., Villalba, R., Marone, L., 2004. Ecología y Manejo de los algarrobales de la Provincia Fitogeográfica del Monte. In: Arturi, M.F., Frangi, J.L., Goya, J.F. (Eds.), Ecología y Manejo de Bosques Nativos de Argentina. Editorial Universidad Nacional de La Plata.
- Villagra, P.E., Villalba, R., Boninsegna, J.A., 2005b. Structure and growth rate of Prosopis flexuosa woodlands in two contrasting environments of the central Monte desert. Journal of Arid Environments 60, 187–199.
- Villalba, R., 1985. Xylem structure and cambial activity in *Prosopis flexuosa* D.C. IAWA Bulletin n.s 6, 119–130.
- Villalba, R., Boninsegna, J.A., 1989. Dendrochronological studies on *Prosopis flexuosa* D.C. IAWA Bulletin 10, 155–160.
- Villalba, R., Villagra, P.E., Boninsegna, J.A., Morales, M.S., Moyano, V., 2000. Dendroecología y dendroclimatología con especies del género *Prosopis*. Multequina 9 (2), 1–18.
- Zar, J.H., 1984. Biostatistical Analysis, second ed. Prentice-Hall International Editions, 718 pp.