



Demography and population growth rate of the tree *Prosopis flexuosa* with contrasting grazing regimes in the Central Monte Desert



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ABSTRACT

One of the most important current challenges for ecologists is to evaluate how human-induced changes in ecosystems would impact viability of populations. Demographic response to anthropogenic impact could help us to understand how to manage those impacts. Using demographic techniques and population projection models, here we assess if demography and population dynamics of the tree *Prosopis flexuosa* change in cattle grazed areas compared to ungrazed areas in the Central Monte desert, Mendoza, Argentina. To this end, we quantified vital rates and constructed a population projection matrix model to compare the deterministic population growth rate (λ) between grazed and ungrazed areas. We also estimated elasticities of vital rates to evaluate their potential importance for future changes in λ and performed a life table response experiment (LTRE) to identify the life cycle transitions that contribute the most to the observed differences in λ between the two treatments. Although we found differences in demographic processes, such as lower seed production and higher probability of reversion to smaller size classes in young individuals when cattle were present, our results indicate that cattle grazing had no significant effect on λ for this species. According to the elasticity analysis, survival of large trees is the main driver of the population growth rate (λ) of *P. flexuosa*, and the vital rates related to tree reproduction, such as seed production and germination, have a poor contribution to λ . Therefore, limitations of activities that can affect survival of large trees should be considered as part of the conservation strategy for this species. Our study provides a compilation of demographic information that can be useful to set policies connecting the conservation objectives for this woodlands with that of ranch managers of the area.

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1. Introduction

Changes in land use practices are the main driver of future biodiversity scenarios in terrestrial ecosystems (Sala et al., 2000). Therefore, one of the greatest challenges for ecologists is to evaluate how human induced changes in ecosystems impact population viability and conservation. Cattle ranching is one of the most common land uses in arid and semi-arid ecosystems in Argentina (Guevara et al., 2009). In woodlands worldwide, ungulates have been historically considered to have negative effects on plants by affecting their survival and growth, especially at the seedling,

sapling and juvenile stages (Harper, 1977; McInnes et al., 1992; López-Sánchez et al., 2014). However, ungulates can also exert positive effects on seed dispersal and the establishment of new individuals (Malo and Suárez, 1995; Rohner and Ward, 1999; Goheen et al., 2014). Thus, the interaction with ungulates has the potential to affect plant performance differently in consecutive phases of the life cycle, and the challenge is to weigh these contrasting effects to forecast the future trends of plant populations and communities.

In addition to ungulates, plants interact with multiple other animals during their life cycles. The interaction with different animals can often produce contrasting effects in plant vital rates. For example, Herrera (2000) showed that pollinators and herbivores had opposite effects on plant fecundity, almost canceling each other. In addition, in many long-lived, perennial plants the identity, magnitude and frequency of plant–animal interactions vary greatly in time and space, resulting in contrasting outcomes of the

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interactions (Gómez and Zamora, 2000; Herrera and Pellmyr, 2002; Knight, 2004). Given this complexity, a growing body of evidence highlights the need to monitor and integrate the effects of plant–animal interactions over different plant life cycle phases to assess their consequences (Calvo and Horvitz, 1990; Horvitz and Schemske, 1995; Ehrlén, 2002, 2003; García and Ehrlén, 2002; Gómez, 2005; Pulido and Díaz, 2005).

Population projection matrix models are a useful technique to integrate demographic information and to estimate population growth rate to assess effects of the biotic and abiotic variation that plants perceive (e.g., Ehrlén, 2002; Bruna and Oli, 2005). This approach has played a central role in population ecology and conservation biology (Morris and Doak, 2002), and it is also helpful to guide management decisions, as it allows combining, in a quantitative framework, the current understanding of species life histories and population status under different management alternatives (Crone et al., 2011; Menges, 2000a, 2000b; Maschinski et al., 2006). Population models are particularly valuable for guiding management of trees, as they allow us to integrate short-term vital rates into long-term estimates of population growth, even when high longevity would prevent us from observing changes in population size directly. These models also allow explicitly considering tree size, which is known to influence individual survival, growth and reproduction (Harper, 1977; Pacala et al., 1994; Clark and Clark, 1999). In addition, estimating the population growth rate as an integrated response variable can help to avoid the compartmentalized view of plant–animal interactions as acting only over particular life stages or single components of fitness (reproduction, survival or growth).

Here we apply demographic techniques and population projection models to assess the population growth rate of *Prosopis flexuosa* in a protected area and the surrounding cattle ranches in the Central Monte Desert of Argentina. We particularly address the following questions: (1) is there an effect of land use on vital rates (reproduction, growth, and survival) and population growth rate?; (2) what are the relative contributions of vital rates to population growth rate?; and (3) how does the contribution to population growth rate of life cycle transitions (fecundity, growth, stasis, and reversion) change under protected and cattle grazed habitats? Because cattle trampling is expected to decrease survival or growth, especially of small plants, but passage of seeds through a cow's digestive tract is expected to increase seed germination, we expect these opposing effects of cattle grazing to at least partially cancel each other in their effects on population growth. We thus expect the population growth rate to be similar in cattle grazed and protected habitat with cattle exclusion since 1972 (MaB Reserve of Ñacuñán). Contrasting effects of grazing on two different vital rates would cancel each other completely if the contributions (sensu Caswell, 1996) of the two vital rates to the population growth rate are similar in magnitude but opposite in sign. Similar magnitudes but opposite signs could occur in two ways. First, the two vital rates could have similar sensitivities and grazing could increase one but decrease the other by similar amounts. Second, if one vital rate has a higher sensitivity than the other, a small change in the more sensitive rate could be compensated by a change in the less sensitive rate that is larger but opposite in direction.

2. Materials and methods

2.1. The study species and its life cycle

P. flexuosa (Leguminosae: Mimosoideae) is a long-lived arboreal (sometimes shrubby) species from arid and semiarid lands of South America, between 25° and 40°S latitude. It tolerates the coldest climate within the genus, can grow under 50–500 mm of average annual rainfall and tolerates saline soils (Alvarez and Villagra, 2009).

In the Monte desert of Argentina the open woodland of *P. flexuosa* provides resources for the subsistence of human communities due to the production of the hardest wood available within the plant community and various non-timber products (Ladio and Lozada, 2009; Abraham and Prieto, 1999). *P. flexuosa* trees also serve as nurse plant for other plants (Rossi and Villagra, 2003) and multiple interactions with native and exotic fauna (Cueto et al., 2006; Campos and Ojeda, 1997; Aschero and Vázquez, 2009). Thus, *P. flexuosa* can be considered an “umbrella” species in the ecosystem.

In the Central Monte desert, flowering of *P. flexuosa* occurs in spring, with a peak in early November, when the yellowish spikes are visited by many insect species (V. Aschero, pers. obs.). Insect pollination is needed for seed production (Aschero and Vázquez, 2009). Fruits are indehiscent pods that are ripe and available for animal and human consumption in summer (January). Fruits fall to the ground under the tree canopy and are quickly removed by local fauna. Fruit ripening is highly synchronized within individual trees, but varies substantially among trees in a population, with some trees still bearing fruit in March (V. Aschero, pers. obs.). Animal dispersal is an important process involved in the species' regeneration cycle, as seeds need scarification to germinate (Campos et al., 2008). Most germination occurs in late February and early March. The species does not have a permanent seed bank (Marone et al., 1998; Villagra et al., 2002a). Clonal growth is unusual, although resprouting and multiple trunk production after stem damage is common, and even if all aerial biomass is removed by herbivores, individuals usually survive, producing new aerial tissues a few months later (V. Aschero, pers. obs.). In the study area, trees grow ca. 1 mm per year in trunk diameter and live up to 200 years (Villagra et al., 2002b, 2005).

2.2. Experimental design

Data for this study were collected at the Man and Biosphere Reserve of Ñacuñán (34°20'S, 67°58'W; 13,200 ha) and the surrounding cattle ranches. We established a demographic study in June 2007 in 5 pairs of 0.25 ha plots inside and outside the protected area. The cattle ranches represented in our study are cow–calf production systems under extensive rangeland with continuous grazing; they have a cattle stock between 16 and 90 ha/AU (hectares per animal unit, one animal unit (AU) is defined as a 450 kg beef cow), most of which (3 of 5) at a mean of 27 ha/AU (Torres et al., 2008). The average carrying capacity for the study area was calculated between 15 and 26 ha/AU (Guevara et al., 2009). All *P. flexuosa* trees within the study plots were tagged, classified by developmental stage, and measured in the diameter at the base of all trunks (at ground level), total height, tree crown diameter (estimated as the average of the longest spread from edge to edge across the crown and the longest spread perpendicular to the first measurement), and trunk height from the ground to the crown. A total of 1245 individuals (914 in the cattle grazed plots and 331 inside the reserve) were followed from 2007 to 2009. Size and survival of marked individuals were monitored in June using annual post-breeding censuses (Morris and Doak, 2002) for two consecutive years (2008 and 2009).

The number of fruits and seeds produced per individual was estimated in the 2007–2008 and 2008–2009 reproductive periods. In each year, we counted the number of inflorescences produced on five branches per tree in both reproductive periods. Later we estimated the number of fruits and seeds produced per inflorescence. We also estimated the density of inflorescences in the tree crown on at least ten individuals per plot, using a wooden cube of 0.027 m³ placed at eight randomly selected points in the tree crown. With this information, we estimated the number of flowers/m³ under different land uses.

To estimate seed germination and early seedling survival (ESS), new seedlings were marked inside each plot with numbered plastic toothpicks in February and March 2008 and 2009. Survival was monitored in June the following year, when the annual census of the entire plot was conducted. Surviving seedlings were then permanently marked with an aluminum tag, as done for larger individuals in the plot.

2.3. The life cycle and the matrix model

We synthesized in a diagram the representation of the different transitions along the entire life cycle that we used to construct matrix models (Appendix A). The life cycle graph and life history pathways included in the diagram reflect the biology of the species and are also the mathematical blocks of the population projection matrix (Fig. 1a). To this end, individuals were classified by stage. Seedling stage refers to new individuals marked with cotyledons that form a clearly delimited class. Larger individuals were grouped by the diameter measured at the ground level of the trunk (DGL), using an equivalent combined diameter for multi-trunk individuals (Alvarez et al., 2006). Our classification resulted in five stage classes: (1) seedling, recently germinated plant with cotyledons; (2) sapling, individual with $DGL < 1$ cm; (3) juvenile, individual with $1 \text{ cm} \leq DGL < 7.5$ cm; (4) adult, individual with $7.51 \text{ cm} \leq DGL < 17.5$ cm; and (5) old, individual with $DGL \geq 17.51$ cm.

2.4. Estimation of the vital rates for matrix models

We calculated the following vital rates to construct the matrix models: seed production, germination probability, early seedling survival, growth, reversion, stasis and survival of each stage class. We used data from grazed and reserve habitats separately to estimate these vital rates. Vital rates were averaged over the two years to construct matrices for each land use.

2.4.1. Seed production

The average number of seeds produced per individual (f_i) was estimated for each class, habitat type and year. To estimate the

$$(a) \quad \mathbf{A} = \begin{pmatrix} 0 & 0 & F_{13} & F_{14} & F_{15} \\ 0 & a_{21} & a_{22} & a_{23} & 0 \\ 0 & 0 & a_{32} & a_{33} & a_{34} \\ 0 & 0 & a_{43} & a_{44} & a_{45} \\ 0 & 0 & 0 & a_{54} & a_{55} \end{pmatrix}$$

$$(b) \quad \mathbf{A}_{\text{cattle}} = \begin{pmatrix} 0 & 0 & 0.398 & 1.100 & 4.005 \\ 0.180 & 0.761 & 0.094 & 0 & 0 \\ 0 & 0.053 & 0.842 & 0.021 & 0 \\ 0 & 0 & 0.009 & 0.951 & 0.016 \\ 0 & 0 & 0 & 0.009 & 0.997 \end{pmatrix}$$

$$(c) \quad \mathbf{A}_{\text{reserve}} = \begin{pmatrix} 0 & 0 & 0.043 & 0.743 & 2.000 \\ 0.285 & 0.649 & 0.036 & 0 & 0 \\ 0 & 0.142 & 0.913 & 0.040 & 0 \\ 0 & 0 & 0.012 & 0.934 & 0.012 \\ 0 & 0 & 0 & 0.009 & 0.997 \end{pmatrix}$$

Fig. 1. (a) Projection matrix **A**. Each matrix element represents the probability of an average individual in class j to be in class i at time $t + 1$. Separate matrices were constructed for cattle grazed and protected populations of *P. flexuosa*. (b and c) Annual transition matrices estimated for trees belonging to cattle grazed and protected habitats.

number of seeds produced per individual, we used the formula for the volume of an ellipsoid to describe the total volume of the crown in each individual. We made the assumption that the reproductive part of each individual was approximately 1/3 of the crown, as flowers are present only in the outer shell of the tree crown. Therefore, we then multiplied 1/3 of the total volume of the crown by mean flower production per m^3 estimated in each individual. To calculate seed production per tree, we multiplied the average number of seeds per inflorescence by total number of inflorescences in the crown of each tree.

2.4.2. Germination probability and early seedling survival

We estimated the germination probability (GP) by dividing the number of seedlings by the sum of all the seeds produced per individual under each habitat type and year. Early seedling survival (ESS) was calculated as the number of surviving seedlings counted in the annual census (June 2008 and 2009) divided by the total number of seedlings marked each year in February, March and June. Thus, ESS represents probability of seedling survival in their first 3–4 months of life.

2.4.3. Growth, reversion and stasis

To estimate growth for each class (g_i) we calculated the proportion of surviving individuals that changed to a higher class i relative to all of surviving individuals that were initially counted in each class in the previous census. The reversion probability (r_i), representing individuals that shrank to smaller classes, was calculated as the number of survivors shrinking to smaller classes i divided by the number of individuals that did not grow. Stasis (t_i), the probability of staying in the same stage class the next year, was defined as $(1 - g_i) * (1 - r_i)$. By definition of seedlings, the probability of sapling shrinking to seedling was equal to one.

2.4.4. Survival

Seedling survival was directly estimated by counting the proportion of plants that were still alive after one year in the annual censuses because seedlings had no diameter measurements and thus could not be included in the logistic regression. For sapling, juvenile, adult and old trees we estimated stage specific survival probability (s_i) with logistic regressions of proportion of trees that survived to the next stage vs. DGL and year for each stage. We first performed logistic regressions models for each habitat with survival as response and, DGL and “year” as predictor variables. Then, we take the midpoint of DGL in each stage class, substitute into the logistic equation as independent variable and use the resulting value as the estimated survival rate for the stage class (Morris and Doak, 2002). Regressions were statistically significant ($p < 0.05$) in both types of habitat, and indicated that there was a greater probability of survival with increasing tree size. Only one regression model was used for the Reserve habitat because “year” was not statistically significant in the general model. Instead, in cattle grazing habitat, both DGL and “year” were significant, therefore, a regression model separately for each year was used to predict tree survival rate. Thus, tree survival in cattle grazed habitat was the average survival in both years.

2.5. Data analysis

2.5.1. Demography

Differences in reproduction at cattle grazed and reserve habitats were tested considering seed production per individual as response variable, and trunk diameter at the base and land use (cattle/reserve) as explanatory variables. We applied zero inflated negative binomial models to analyze differences in seed production because they had the best fit when compared to generalized linear models assuming Poisson, negative binomial, and zero

inflated Poisson distributions of errors. We based model comparisons on Akaike’s Information Criterion (AIC), using the threshold $\Delta AIC > 2$ to distinguish among two competing models (Burnham and Anderson, 1998).

To analyze growth we adjusted linear and quadratic models between size at time $t + 1$ as response variable and size at t and habitat type as explanatory variables. Size was described by trunk diameter measured at ground level (DGL, cm). Both models were compared with likelihood ratio tests.

To test for differences in survival between grazed and ungrazed habitat, we applied logistic regression analysis with survival as the response variable and DGL and habitat type (cattle/reserve) as explanatory variables.

2.5.2. Constructing projection matrices from the estimated vital rates

Because the main objective in this study is to compare the performance of *P. flexuosa* populations between habitat types, we pooled together data from all sites sampled in each habitat to estimate vital rates. Average annual vital rates were used to characterize demography and construct deterministic matrix models under cattle grazing and habitat protection. Different vital rates were combined to construct the elements of the projection matrix using conventional methods for using stage based models and post-breeding censuses (Morris and Doak, 2002). For example, the fertility element of the projection matrix (F_{13} , F_{14} and F_{15}) includes seed production (f_i), germination probability (GP) and ESS (Table 2). A transition matrix was calculated for each land use with the average vital rates from two years, 2007–2008 and 2008–2009.

The total population effect of land use was assessed by comparison of the deterministic population growth rate (λ) between reserve and cattle grazed sites. We used the asymptotic population growth rate for the density-independent population model $n(t + 1) = \mathbf{A}n(t)$ (Caswell, 2001). The matrix \mathbf{A} for each land use describes how individuals in each stage class in vector $\mathbf{n}(t)$ contribute to the stage classes in $\mathbf{n}(t + 1)$. The dominant eigenvalue of the matrix \mathbf{A} is the asymptotic population growth rate (λ). If the size of the population in one year is larger than in previous years then $\lambda > 1$, and the population is considered to be growing, but if $\lambda < 1$ the population is considered to be declining.

To obtain the 95% confidence intervals of λ , we used bootstrap resampling for each land use and year (Caswell, 2001). Each bootstrap data set included information on the fate of individuals and fecundity; the number of plants in each size class selected in each iteration equaled the original number in the data. The bootstrap resampling was repeated 2000 times; for each sample, we estimated vital rates as described before, constructed transition matrices, and computed λ values. From the 2000 bootstrapped λ values, we computed 2.5th and 97.5th percentiles, to get a 95% confidence interval for λ .

The relative contribution of vital rates to λ was estimated by calculation of their elasticities using small perturbations, and then dividing the new λ by the original λ (Caswell, 2001). For simplicity, we calculated the elasticity for the vital rates and not for matrix elements, as matrix elements in our model include more than one vital rate. Because elasticities for a particular vital rate are calculated while all other elements are held constant, they add up to one in a matrix and can thus be combined to calculate the effects of multiple vital rates.

We applied life table response experiment (LTRE) analysis to decompose and estimate the contribution of different vital rates on the observed differences in λ between habitat types. In our LTRE the total effect of treatments (cattle/reserve) on λ is decomposed into specific effects of each vital rate and not for matrix entries in order to distinguish for example between contributions from effects on survival, growth and reproduction individually

(Caswell, 1996). We used a one-way fixed design according to the following equation:

$$\lambda^{treatment} - \lambda^m = \sum (v_i^{treatment} - v_i^m) \times (\partial\lambda/\partial v_i) \tag{1}$$

where *treatment* denotes either the reserve or cattle grazed habitat, *m* denotes the mean of the vital rate, v_i denotes vital rates, and $(\partial\lambda/\partial v_i)$ the sensitivity of λ to v_i , evaluated on an average matrix that is “midway” between the matrices from the two treatments (Caswell, 2001; Ehrlén et al., 2005). Thus, the LTRE analysis gives the positive or negative contribution of each vital rate to differences in λ under each land use. Sensitivities were estimated using the vitalsens function in the Popbio R package (Stubben and Milligan, 2007).

3. Results

3.1. Demography

Seed production per individual and survival probability increased significantly with increasing trunk diameter (DGL) and differed significantly between land use regimes (Table 1). The logistic regression results are driven by survival differences mostly in smaller plants, because we did not record deaths in large trees during the study period. Land use was not a statistically significant predictor of tree growth in regression models. For tree growth,

Table 1

Results of zero-inflated negative binomial model to evaluate the relationship between trunk diameter measured at ground level (DGL), land use (cattle/reserve) and seed production, and results of logistic regression model of survival as function of trunk diameter (DGL) and land use.

Adjusted model	Coefficient	Estimate	Std. error	z value	Pr (> z)
Count model	Intercept	7.68	0.31	24.61	***
	DGL	0.08	0.01	5.82	***
	Land use	0.84	0.21	3.86	***
	Log(Theta)	-0.48	0.11	-4.2	***
Zero-inflated model	Intercept	2.11	0.27	7.85	***
	DGL	-0.18	0.02	-8.53	***
Logistic regression	Intercept	0.58	0.33	1.73	***
	DGL	7.38	1.06	6.94	***
	Land use	-0.09	0.55	0.17	***

*** $p < 0.001$.

Table 2

Estimated vital rates used for construction of deterministic matrix models in cattle grazed and reserve habitat.

Vital rate	Cattle	Reserve
f_3 : average seeds produced by a juvenile individual	1570	1059
f_4 : average seeds produced by an adult individual	4331	18,110
f_5 : average seeds produced by an old individual	15,768	48,806
GP: germination probability of seeds	0.000529	0.000057
ESS: early seedling survival	0.48	0.71
s_1 : survival probability of seedling	0.18	0.28
s_2 : survival probability of sapling after 1 year	0.815	0.893
s_3 : survival probability of juvenile after 1 year	0.894	0.98
s_4 : survival probability of adult after 1 year	0.969	0.995
s_5 : survival probability of old after 1 year	0.993	0.997
t_2 : stasis of sapling individual	0.85	0.72
g_2 : growth of sapling to juvenile	0.06	0.15
r_3 : reversion of juvenile to sapling	0.09	0.03
t_3 : stasis of juvenile	0.86	0.93
g_3 : growth of juvenile to adult	0.009	0.012
r_4 : reversion of adult to juvenile	0.02	0.04
t_4 : stasis of adult	0.95	0.94
g_4 : growth of adult to old	0.01	0.01
r_5 : reversion of old to adult	0.016	0.012

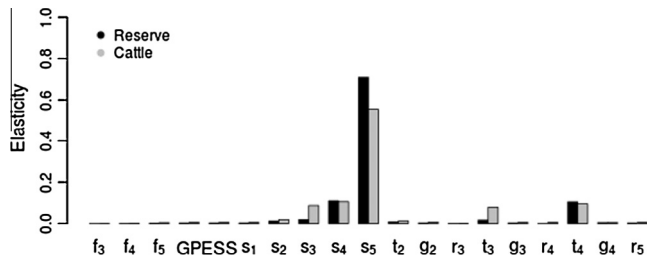


Fig. 2. Elasticities of vital rates. Vital rates in the figure are denoted as in Table 2.

DGL_{t+1} was best described by a linear function of DGL_t , and a quadratic term did not improve model fit ($DGL_{t+1} = 5.58 + 0.01 * DGL_t$, $T = 16.57$, $p < 0.001$).

3.2. Matrix model

Average vital rates estimated for the construction of matrix models are shown in Table 2. Note that the estimated germination probability was lower inside than outside the reserve, while ESS showed the opposite effect. When the vital rates were combined in transition matrices, fecundity (values in the first row in Fig. 1b and c) was higher in cattle ranches than inside the reserve. In turn, reversion was higher in cattle ranches than inside the reserve, particularly for small individuals, while growth was higher inside the reserve.

A slightly higher λ was recorded in *P. flexuosa* populations inside the reserve, but the 95% confidence intervals of λ overlapped almost completely between the two land use regimes (cattle grazed habitat: $\lambda = 1.003$, 95% CI = [0.98, 1.03]; reserve: $\lambda = 1.007$, 95% CI = [0.98, 1.05]).

Elasticities of vital rates were qualitatively similar outside and inside the reserve. Elasticities were greatest for survival rates of old and adult trees (Fig. 2). A small change in survival for all size classes has a relatively large effect on λ , both in cattle grazed habitat and in the Reserve, but if vital rates related to fecundity are modified the effect on population growth rate is expected to be less important. A 1% increase in adult survival would mean more than 0.1% increase in λ in both habitat types, while a 1% increase in any vital rate related to fecundity will not increase λ more than 0.01% (Fig. 2).

LTRE analysis showed that in cattle ranches germination probability contributed positively to λ , while seed production and ESS contributed negatively to λ in the grazed treatments (Fig. 3a). Therefore, higher abundance of seedlings in cattle ranches is driven by higher seed germination, not by higher seed production. Survival in all stage classes made only a small contribution to differences in λ between the reserve and cattle grazed areas (Fig. 3b). Grazing had negative effects on the transition to larger stage classes (Fig. 3c) and positive effects on reversion, particularly from juvenile to sapling (Fig. 3d).

4. Discussion

Population growth rate of *P. flexuosa* was similar in woodlands inside the ungrazed MaB Reserve of Nacuñán and in the surrounding cattle ranches. Even though demographic processes differed between the land use regimes, such as lower seed production and higher probability to revert to smaller size classes for young individuals in cattle ranches, our results indicate no significant overall effects of cattle grazing on the asymptotic deterministic growth rate (λ) for this species.

Land use affected survival and reproduction probability. Both survival and seed production increased with increasing tree trunk

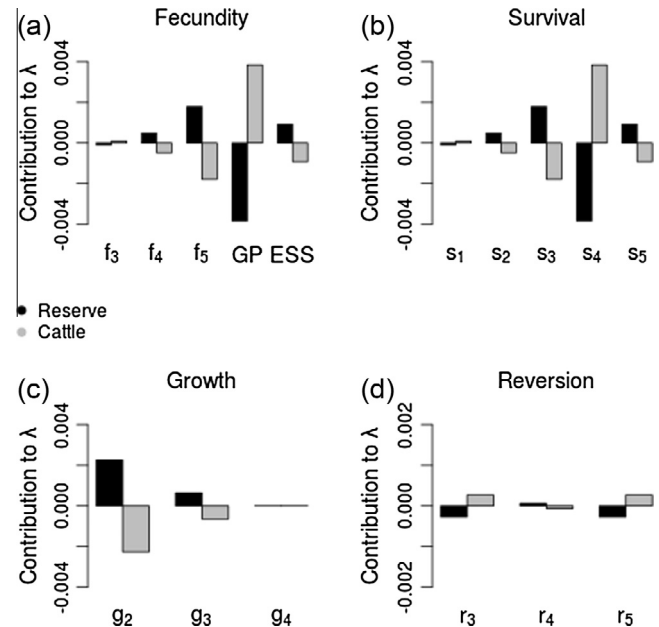


Fig. 3. Differences in contribution to population growth rate (λ) of vital rates from habitats inside the MaB Reserve of Nacuñán (black bars) and under cattle grazing (gray bars). Vital rates in the figure are denoted as in Table 2. (a) Vital rates related to fecundity. (b) Vital rates related to survival. (c) Vital rates related to growth. (d) Vital rates related to transition to smaller stage classes.

diameter, supporting the idea that size is a good predictor of the fate of individuals in this species, as found previously for other tree species (e.g., Pacala et al., 1994; Zuidema et al., 2010). Differences in seed production between different land uses could be explained by limited pollination (Aschero and Vázquez, 2009) and the increased allocation to mechanic defences in young trees in cattle grazed habitats (Aschero, 2014). Growth rate for trees was unrelated to land use. Yet, the transition probability from sapling to juvenile stages was lower outside than inside the reserve. Reversion from juvenile to sapling was greater in cattle grazed habitat, probably due to cattle browsing. Reversion from juvenile to sapling was also observed in the absence of large herbivores inside the reserve, which could be due to herbivory by *Ctenomys mendocinus*, the most frequent consumer of leaves and shoots of small trees in the reserve during our study (V. Aschero, pers. obs.). *C. mendocinus* is known to be more abundant inside the reserve (Tabeni and Ojeda, 2003) than in the surrounding cattle ranches, which suggests that its negative effects on sapling growth could be qualitatively similar to those of cattle.

Our results suggest that the contrasting effects of grazing on different demographic rates can compensate one across the life cycle of our study species. For example, in cattle ranches seed germination was higher but seedling survival was lower than in the Reserve, and these effects cancelled each other. Greater fecundity in cattle grazed habitat probably results from enhanced germination of seeds after passage through a cow's digestive tract (Campos and Ojeda, 1997). This result highlights the importance of considering the whole life cycle when evaluating the consequences of human-induced environmental changes for a particular species. Our results also warn against drawing conclusions about human impacts on species performance in studies focused exclusively on particular stages of the life cycle.

Elasticity values indicated that population growth is most sensitive to demographic parameters related to survival, and that vital rates related to fecundity, such as seed production and seed germination, are less important. This is a pattern expected for a long-lived woody species (Franco and Silvertown, 2004). Problems with the estimation of adult survival are frequent in long-lived

species, given the limited sampling effort and the low mortality rates in adult categories in most studies (Zuidema and Boot, 2002). In our study, we recorded no deaths in adult and old classes, which probably resulted from sampling issues, not from a true lack of mortality. To circumvent this problem, we used logistic regressions of survival vs. size, which allowed us to estimate the increase of survival with tree diameter. Such estimation was lower in cattle grazed habitat for saplings and juveniles, probably because of higher mortality from cattle trampling and browsing. We believe that the detected importance of survival rates in large trees is due to life history of the species, in particular its high longevity. For this reason, a limitation of human activities that affect survival of large trees seems an adequate recommendation as a conservation strategy for the species.

Our study has at least three important caveats to consider. First, the time span of the study was short, with only two years of demographic data, which is a problem for the estimation of variation in vital rates; this led us to use a deterministic matrix using average vital rates. Second, our matrix models were deterministic, not stochastic, because they are accurate given the data we had and the most simple approximation to compare demography of *P. flexuosa* trees under contrasting habitat management. Using deterministic models is not ideal, because they are considered to be poor predictors of population performance through time compared to stochastic models. However, we believe this limitation of deterministic models is not a problem in our study, as our objective was to compare demography under cattle grazed and protected habitats, not to predict the development of populations over time. In a recent review, Crone et al. (2011) suggested that relative to stochastic population growth rates, deterministic population growth rates could be more precise under some conditions (e.g., high variance and <5 years of data), which suggests deterministic models may be the most appropriate analysis for the actual available data set for *P. flexuosa*. Third, we did not consider the type, intensity and frequency of cattle grazing in our study system, which would be arguably important to understand and quantify the effects of grazing on plants (Riginos and Hoffman, 2003; Tadey, 2006). For example, cow–calf production by continuous free grazing, the type of activity studied here, might differ in its environmental impact and consequences for woody vegetation from other types of livestock, such as goats and sheep with different behavior and diet. The spatial distribution of cattle is known to be heterogeneous in the Monte desert, as they tend to associate with water sources (Gonnet et al., 2003), facilitating woody encroachment (Asner et al., 2003). This effect of the heterogeneous spatial distribution of cattle cannot be detected in our study, as our data were not collected near water sources, where trampling and browsing by cattle should be more intense.

4.1. Management and conservation implications

We found contrasting effects in both land uses on some vital rates, including seed production, seed germination and seedling survival. The LTRE analysis indicates that the lack of difference in λ between reserve and non-reserve sites resulted from the fact that some vital rates that change under contrasting land uses, for example seed germination and seedling survival, had contributions to λ that were similar in magnitude but opposite in sign. According to our elasticity analysis, survival of large trees is the main driver of the population growth rate of *P. flexuosa*. Although we found a negative effect of cattle on seedling survival, this effect becomes negligible in larger stage classes. We also found that population growth rate did not differ significantly between cattle ranches and the reserve. A plausible reason for this lack of difference in λ between land uses is that the vital rate with the highest sensitivity did not differ significantly between reserve and non-reserve sites.

Therefore, it seems reasonable to conclude that the population performance and conservation status of *P. flexuosa* are similar under both land use regimes.

In Mendoza Province, where our study was conducted, *P. flexuosa* woodlands are protected and logging is forbidden by law (Gobierno de Mendoza, 1997). In our opinion, this policy represents an unreasonably extreme protection, because moderate levels of pruning and wood collection are unlikely to affect the survival of adult trees (Alvarez et al., 2011a), which in light of our results is the vital rate with the most influence on population growth. In a recent study, Alvarez et al. (2011b) suggested 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. Furthermore, whether to worry or not about cattle effects on seedlings and saplings would depend on the management or study goals. For example, if the objective is to produce wooden poles or wood boards, probably the effects on seedling survival by cattle browsing and trampling, sapling growth and abundance of multi-stemmed trees could be considered problematic. Finally, because of the small contribution of fecundity to population growth rate, regulated human harvesting of fruits of *P. flexuosa* for flour production (Alvarez and Villagra, 2009), should not affect its long term conservation. Our study suggests that combining demographic data collected in the field and population dynamic models could be a useful guide for management decisions.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2016.03.028>.

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