



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



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## ARTICLE INFO

### Article history:

Received 30 July 2015

Received in revised form 8 March 2016

Accepted 11 March 2016

Available online 28 March 2016

### Keywords:

Algarrobo

Cattle grazing

Life table response experiment

MaB Reserve of Nacuñán

Matrix model

Monte desert

## 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 ( $\lambda$ ) between grazed and ungrazed areas. We also estimated elasticities of vital rates to evaluate their potential importance for future changes in  $\lambda$  and performed a life table response experiment (LTRE) to identify the life cycle transitions that contribute the most to the observed differences in  $\lambda$  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  $\lambda$  for this species. According to the elasticity analysis, survival of large trees is the main driver of the population growth rate ( $\lambda$ ) of *P. flexuosa*, and the vital rates related to tree reproduction, such as seed production and germination, have a poor contribution to  $\lambda$ . 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 m<sup>3</sup> placed at eight randomly selected points in the tree crown. With this information, we estimated the number of flowers/m<sup>3</sup> under different land uses.

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