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Mechanic defences and reproduction in desert trees under different habitat management

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Abstract

Herbivory can have deleterious effects on plant reproduction by limitation of photosynthates that are either lost by consumption, used to re-growth or invested in defences. In addition, herbivores can also exert direct impact on plant reproduction by consuming flowers. Spine length can act as an inducible defence in plants, because it tends to increase with increasing herbivore pressure. I hypothesized that almost 40 years of different habitat management (cattle exclusion within a protected area vs. cattle grazing in adjacent areas) could affect inflorescence abundance, spine length and fruit production in *Prosopis flexuosa* trees. The study area was located in the Central Monte desert of Argentina. I estimated differences in spine length, number of inflorescences and fruit production in trees inside the Man and Biosphere Reserve of Ñacuñán and in the adjacent cattle ranches surrounding the protected area. Inflorescence abundance in the tree canopy was similar in cattle grazed and protected sites, but the presence of large herbivores was associated with limited fruit production. Spines were 37% shorter and fruit production three times higher in trees inside the reserve than in trees in cattle ranches. A negative exponential model was used to describe the relationship between reproduction and spine length in trees. The results indicate that after almost four decades of cattle exclusion, trees inside the protected area show higher reproduction and shorter spines than cattle-browsed trees in surrounding areas. The negative association between defence and reproduction may be due to competition for photosynthates. The present results could be useful and relevant in conservation because they provide evidence on how anthropogenic habitat use can affect plant phenotypes and fitness, which in turn can affect the long-term ecological and evolutionary dynamics of plant populations.

Zusammenfassung

Herbivorie kann eine schädliche Wirkung auf die Fortpflanzung von Pflanzen haben, indem Photosyntheseprodukte durch Fraß verloren gehen, für den Wiederaustrieb verbraucht oder in Verteidigung investiert werden. Außerdem können Herbivore auch direkt auf die Reproduktion einwirken, indem sie Blüten fressen. Die Dornenlänge kann als eine induzierte Abwehr bei Pflanzen fungieren, da sie dazu tendiert, mit zunehmendem Herbivorendruck zuzunehmen. Ich stellte die Hypothese auf, dass fast 40 Jahre unterschiedlicher Bewirtschaftung (Ausschluss von Rinderbeweidung in einem Schutzgebiet versus Beweidung durch Rinder in benachbarten Gebieten) die Häufigkeit der Blütenstände, die Dornenlänge und die Fruchtproduktion von *Prosopis flexuosa*-Bäumen beeinflussen sollten. Das Untersuchungsgebiet lag in der Zentralen Monte-Wüste (Argentinien). Ich bestimmte die Unterschiede bei Dornenlänge, Anzahl der Blütenstände und Fruchtproduktion im MaB-Reservat von Nacunan und auf angrenzenden Rinderfarmen. Die Dichte der Blütenstände war ähnlich für beweidete und geschützte Flächen, aber die Anwesenheit von Rindern war mit einer begrenzten Fruchtproduktion verbunden. Verglichen mit Bäumen auf Rinderfarmen waren die Dornen an Bäumen im Reservat 37% kürzer und die Fruchtproduktion dreimal höher. Ein negatives Exponentialmodell

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wurde benutzt, um die Beziehung zwischen Produktion und Dornenlänge der Bäume zu beschreiben. Die negative Beziehung zwischen Abwehr und Reproduktion könnte aus einer Konkurrenz um Photosyntheseprodukte resultieren. Die gegenwärtigen Resultate könnten nützlich und bedeutsam für den Naturschutz sein, weil sie zeigen, wie anthropogene Nutzung Phänotyp und Fitness von Pflanzen beeinflussen kann, was seinerseits auf die langfristige ökologische und evolutive Dynamik von Pflanzenpopulationen einwirken kann.

Keywords: Cattle; Habitat protection; Inflorescence abundance; Fruit production; Mesquite; *Prosopis flexuosa*; Spine length; Monte desert

Introduction

Herbivory can have deleterious effects on plant survival, growth and reproduction (Crawley 1989). Plants use several strategies to defend themselves against this risk (Fritz & Simms 1992). Plant anti-herbivore defences are traditionally classified into two main categories: chemical and mechanical. The first category includes a variety of substances that are toxic, repellent, or that render plant tissues indigestible to animals. The second category involves a series of physical barriers to avoid being eaten. These include structures such as thorns, spines, trichomes and hard or sticky surfaces. Defensive mechanical traits, such as spines and thorns, can limit the behaviour of large herbivores, reducing loss of twigs or shoots by enforcing smaller bite size or lower feeding rate (Cooper & Owen-Smith 1986; Gowda 1996; Young & Okello 1998; Lucas, Turner, Dominy, & Yamashita 2000).

Many defensive strategies by plants against herbivores are dynamic in time and space (Coley, Bryant, & Chapin 1985; Rhoades 1985; Agrawal & Rutter 1998). Thus, even though constitutive mechanic defences are the default defensive strategy in plants, some species can also regulate the production of defences in response to variable herbivore pressure (Karban & Baldwin 1997). For example, in the African Savannah, large herbivores induced mechanic defences in *Acacia* trees with longer spines produced in individuals under high levels of herbivory than in individuals excluded from herbivores (Young 1987; Young, Stanton, & Christian 2003; Goheen, Young, Keesing, & Palmer 2007). Conversely, a relaxation of spine length in *Acacia* was observed in plants protected from herbivores (Young & Okello 1998). Inducible defences are considered advantageous over non-inducible defences because the photosynthetic products that are not used to maintain defensive structures can be allocated to increase individual performance in the absence of herbivory (Agrawal 1998; Karban & Agrawal 2002). That is, inducible defences allow plants located in a herbivore-free environment to avoid investing in unnecessary defences, and can have more resources available for reproduction (Gómez & Zamora 2002). In a recent meta-analysis, a trade-off between fitness and anti-herbivore defences has been proposed as a general pattern in plants (Koricheva 2002).

Herbivores can indirectly affect plant reproduction through decreasing available energy by removing photosynthetic tissues (Hendrix 1988; Gadd, Young, & Palmer 2001), or by promoting compensatory regrowth (Strauss & Agrawal 1999; Pratt et al. 2005). Herbivores can also exert direct impact on plant reproduction by consuming flowers. Flower and fruit abundance is a key factor assumed to limit reproductive success in plants (Primack 1997). Thus, flower consumption by ungulates can severely decrease plant reproductive output (Gómez 2005). However, the effects of large herbivores on flower production are not easy to predict, as some plant species can compensate completely and some species can even overcompensate (Belsky 1986; Strauss & Agrawal 1999). The effects of large herbivores on reproductive structures in plants have been studied in non-arboreal plants but little is known about this potential direct effect of herbivory in trees. To my knowledge, no previous studies have dealt with the effects of ungulate herbivores on the magnitude of floral abundance and consequently on fruit production in trees. This is probably because of the methodological difficulties of estimating flowering magnitude given the large size of trees and the small size of their flowers.

Prosopis spp. are common trees in arid lands of Asia, Africa and America. In *Prosopis* spp. woodlands grazing with large domestic ungulates is one of the main land uses and thus it is reasonable to expect effects of cattle herbivory on trees. I hypothesized that cattle herbivory can (1) induce mechanic defences in *Prosopis flexuosa*, and (2) affect its reproductive success. I explore here the idea that the effect on reproduction could be through modification of flower abundance in the tree canopy, and I discuss the idea that fruit production could be in part explained by reduced allocation of energy towards reproduction. To test these hypotheses I studied *P. flexuosa* trees on cattle ranches and inside a protected area, from which large herbivores have been excluded for the last 40 years. I expected to find larger spines, lower number of inflorescences and lower fruit production in trees exposed to cattle grazing than in trees inside the protected area.

Materials and methods

Study area and species

The study area lies within the central Monte desert of Argentina (Cabrera 1976). The climate is semi-arid and most rainfall occurs in spring and summer (October–March); average rainfall in the study region is 280 mm. The open-woodland is one of the typical plant communities in the Monte, where *P. flexuosa* is accompanied by the small tree