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Proximity to other plants determines the effect of livestock exclusion on eight species in the semiarid scrublands of Mexico

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ABSTRACT

Exclusions are one of the most used methodologies to study the effects of herbivores on ecosystems. Although long periods are needed to detect changes in species composition, the responses of perennial plants may be visible in the short term. The ability of plants to tolerate herbivory may be influenced by the availability of resources and nearby vegetation. The aim of this study is to assess the effect of proximity to other plants on the response of adult plants to livestock exclusion. After 3 years of exclusion, we quantify the differences in size (height and canopy size) and reproductive organ production in eight predominant shrubs species. We consider three neighborhood conditions: Alone, Partially or Completely covered. Our results showed that palatable species present larger sizes inside the exclusion areas. Neighborhood influence depended on the studied species. The density of reproductive organs decreased with exclusion for four species, and proximity to neighboring plants had different effects depending on the species. The species that showed greater size inside the exclusion areas when they were Partially and/or Completely covered by other plants and did not show the same pattern for reproductive organ production, which indicated a possible process of light competition. Four of the eight species presented greater size and/or density of reproductive organs on Alone plants, especially inside the exclusion areas, which suggested that herbivore exclusion can intensify competition among plants. The present study showed that the effect of the exclusion of livestock grazing was affected by plant–plant interactions, which may affect the changes in the composition of the plant community found after permanent removal of livestock.

1. Introduction

The intensification of human activities has dramatically altered the geographic distribution, specific composition and population density of large herbivores on the planet (Milchunas and Lauenroth, 1993; Oesterheld et al., 1992). Although there are many studies on plant-herbivore interactions, the consequences of the modification of those interactions on the plant community are not fully known. Plant-herbivore interactions are complex, with consequences that depend not only on two main elements (i.e., the herbivore and plant consumed) but also on surrounding biotic (other plant interactions, symbionts...) and abiotic (light, water...) conditions (Baraza et al., 2007). The availability of resources such as light and nutrients can determinate not only plant defenses against herbivory but also plant recovery after herbivore damage (Baraza et al., 2010b). For example, the concentration of defense compounds such as compounds as tannins and terpenes may be related to light availability (Baraza et al., 2004, 2010a). Wise and Abrahamson (2007) demonstrated that the availability of resources affects plant tolerance to herbivory depending on the relationship among the limiting growth resource and the resources affected by herbivory. In the same way, the ability of plants to recover after herbivore damage may be directly influenced by the presence of neighbors (Rand, 2004). This is because other plants growing nearby can compete for resources, decreasing the availability of resources for the recovery of a target plant after herbivory (Baraza et al., 2010b; Wise and Abrahamson, 2007). On the other hand, the micro-environment provided by the neighborhood could decrease abiotic stress, increasing the capacity of the plant for recuperation after herbivory (Rand, 2004; Soliveres et al., 2011). Neighbors can have a protective role for the target plant against herbivores, compensating for the competitive effect by reducing the probability of herbivore attack, resulting in a net positive effect between plants (Baraza et al., 2006; Smit et al., 2007) that disappears after herbi-

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vore exclusion. In fact, several studies have demonstrated complex interactions between plants, neighboring plants and herbivores; due to these interactions, the elimination or reduction of herbivores can change plant–plant interactions from facilitation to competition (Graff and Aguilar, 2011; Veblen, 2008).

From these processes, it is evident that the presence of herbivores not only changes the vegetation by direct consumption of plants but can also have indirect effects by modifying the dynamics of interactions between plants (Cipriotti and Aguiar, 2012; Van der Wal et al., 2000). This effect of herbivores on plant–plant interactions is extremely important for the composition and structure of communities because the balance between competition and facilitation determines the assemblage of plant species (Bruno et al., 2003). However, livestock exclusion studies rarely consider plant interactions as an important component of vegetation recuperation after herbivory. Variations in growth and reproduction after the experimental exclusion of herbivores can provide us an idea of the changes in important components of plant fitness and their ability to compensate for herbivore damage (Collar et al., 2010; Van der Wal et al., 2000). Moreover, the influence of neighbors on plant response to the cessation of grazing in the short term can provide a more appropriate picture of the long-term changes in the plant community.

The aim of this study is to assess the effect of the proximity to other plants on the response of shrubs to grazing cessation. We analyzed the variation in the size and production of reproductive organs of 8 species of low-stature shrubs that reach heights of no more than 1.5 m as adults and that grow inside and outside of livestock exclusions under different neighborhood conditions. We expect that if domestic herbivore exclusion promotes competition, species will recover better only when growing without neighbors, whereas species that are facilitated by other plants will better recuperate when growing under the canopies of other plant.

2. Material and methods

2.1. Study area

The study was conducted within the Biosphere Reserve of the Tehuacán-Cuicatlán in the area surrounding the town of San Juan Raya, (18°11′N 97°23′W, 1750 m a.s.l.), which is located in the river basin of Zapotitlán, in the state of Puebla, Mexico. This area has an annual mean rainfall of 380 mm, most of which occurs during the summer months, and an annual mean temperature of 21 °C, with rare frosts.

The vegetation present in the area is xerophytic shrubland dominated by columnar cacti, legume shrubs and *Agave* species, among others shrubs (Valiente-Banuet et al., 2000).

2.2. Experimental design and data collection

In January 2006, four excluded plots of ca. 400 m^2 separated from each other by more than 500 m were established in a natural non-managed area in which domestic goats browse daily, especially during the drought season (Osorno-Sánchez, 2005), and other livestock, such as free-grazing cows and donkeys, are occasionally present. The effect of livestock exclusion was analyzed in June, July and September of 2008. In September, only three excluded areas were considered. The study focuses on shrubs for two main reasons: one, because it is the dominant vegetation and the only one that provides food resources to herbivores throughout the year, and two, because the main herbivore is the domestic goat, which behaves like a browser and mainly consumes shrubs (Baraza et al., 2010a). To select plants completely randomly, we focused on plants

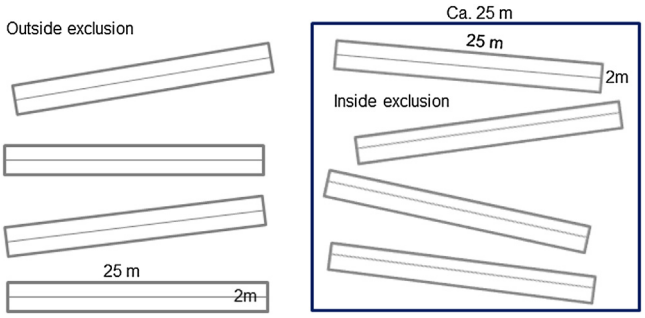

Fig. 1. Schematic representation of the location of transects. This design was repeated for the four exclusion fences.

inside four transects of 25 × 2 m randomly distributed both inside and outside each of the four fenced plots (Fig. 1).

Only the species that presented a high enough number of individuals in all transects were included in the study, which represented a total of 8 species: *Aeschynomene compacta* Rose, *Bouvardia erecta* (DC.) Standl., *Croton ciliato-glanduliferus Ortega.*, *Echinopterys eglandulosa* (A.Juss.) Small, *Hibiscus elegans* Standl., *Justicia candicans* (Nees) L.D. Benson, *Lippia graveolens* Kunth. and *Turnera diffusa* Willd. ex Schult.

Due to the small stature of most of the plants, which reach no more than 1.5 m in height, they are prone to be covered by other species after the cessation of grazing, which affects their performance. These species are consumed by domestic goats (Baraza et al., 2010b; Osorno-Sánchez, 2005). Considering the frequency of consumption by domestic goats in relation to the relative abundance of the vegetation, all species could be classified as palatable (consumed above or in a similar proportion to its abundance), with the exception of *C. ciliato-glanduliferus*, which was consumed at a lower proportion than its abundance (Osorno-Sánchez, 2005).

The proportion of individuals presenting reproductive organs was quantified in each transect during each monitoring visit. In July and September, the height and the highest and smallest diameters of the canopy and the total number of reproductive organs of each plant were quantified.

All analyzed species bloomed between May and December with one or more peaks. Flowering and fruiting peaks were distributed randomly during the rainy season depending on the intensity and distribution of rainfall (Pavón and Briones, 2001). Thus, we quantified all reproductive organs (buds, flowers, unripe and ripe fruits) for each plant in both monitoring periods. In the case of *Croton ciliato-glanduliferus*, due to the low number of flowers and the strong relationship between the number of flowers and total number of branches (data not shown), we quantified the proportion of branches that had reproductive organs. In the cases of *L. graveolens* and *E. eglandulosa*, reproductive organs are grouped in inflorescences, so the number of inflorescences/infructescenses was quantified.

For each plant, the neighborhood conditions were annotated as Alone (A), when no other plant grows above; Partially Covered (PC), when the plant was partially covered by the canopy of other species; and Completely Covered (CC), when the canopy of the plant is completely covered by one or more other plants.

2.3. Data analysis

The effect of the livestock exclusion and neighborhood conditions on the size of reproductive plants was analyzed considering the logarithmic transformation of height and canopy size as the response variables. We estimated the canopy size of each plant as the area that its canopy would occupy with an elliptical shape with maximum and minimum diameter values measured in the field.