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Reproductive costs of herbivory in small-sized populations

Abstract

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The effect of two herbivory regimes by cattle on plant growth and reproductive traits was studied in a small population of the endangered *Erodium paularense* (*Geraniaceae*), a narrow endemic of Central Spain. Results varied in time and according to the type of herbivory showing that the problem of managing herbivory for conservation purposes is not simple and cannot always be optimally solved by fencing.

Introduction

Herbivory has generally been assumed to reduce plant reproduction and fitness (Harper 1977), although both negative (Louda 1984; Parker & Salzman 1985; Karban & Strauss 1993) and positive (McNaughton 1985) effects of herbivores on population dynamics have been documented. Vegetative herbivory may reduce the resources available for reproduction, while destruction of reproductive structures may increase the resource level of the surviving ones (Fellows & al. 1979; Garrish & Lee 1989; Ehrlén 1992; Krupnick & Weis 1999). Foliar and floral herbivory can affect plant fitness indirectly by altering pollinator visitation patterns to damaged plants (Strauss & al. 1996; Strauss 1997; Lehtilä & Strauss 1999). Grazing can positively regulate a species' abundance, by eliminating competitors and by creating suitable conditions for germination, seedling emergence and growth. On the other hand, plant size and survival may be negatively affected by defoliation (Silvertown & al. 1992).

Effects of herbivory on rare plant biology have been scarcely documented. So, we analyzed the effect of herbivory by cattle on a small population of endangered *Erodium paularense* Fern. Gonz. & Izco (*Geraniaceae*) in Central Spain. In order to determine the species' conservation needs, understanding how herbivores may affect plant reproductive success and survival, and how they impact the potential for the species persistence or population growth is crucial.

Methods

Two experiments were established in order to evaluate the reproductive costs imposed by direct ingestion of reproductive organs and vegetative plant portions. In the first one, plant reproduction under the effect of herbivory and habitat alteration in an area of public transit where cattle passes through while grazing ("Type 1 herbivory") was compared to plant reproduction in absence of herbivores (a fenced area of 18 x 15 m where cows could not access, "Control"); in the second one, plant reproduction on a private property where cattle was permanently stationed and practiced more intensive grazing ("Type 2 herbivory") was compared to plant reproduction in the same control area without herbivores. Experimental units could not be replicated due to the small size of the population.

Twelve plots of 0,7 x 1 m were established within each area. Plots were placed at distances of 1 m in two or three lines along the area, with lines separated 2 m from each other. All *E. paularense* plants found in plots were marked and monitored for two consecutive years. Plant survival, plant size, measured as maximum rosette diameter (González-Benito & al. 1995), and seedling emergence were recorded in autumn. Reproductive traits, number of flower stalks, number of flowers and number of fruits per plant were monitored. The second year, the reproductive cost of herbivory was also tested by means of other reproductive variables such as number of flowers per stalk and flower size, considering that plant fitness may be influenced by petal size as it affects rates of pollinator visitation (Lehtilä & Strauss 1999). Plant cover of all other perennial species within each plot was also quantified.

Comparison of means of flower and fruit number was carried out by Repeated Measures-ANOVA for each experiment with SPSS statistical package. In 1999, flower size (maximum diameter and petal length) and number of flowers per flower stalk were compared by standard t tests or the Mann-Whitney test when necessary. Survival of individuals from one year to another was also compared by the Mann-Whitney test.

We used structural equation modeling (SEM) to analyze a set of hypothesized relationships among the variables (Hayduk 1987; Loehlin 1987). The model (Fig. 1) proposes that fruit production is mainly influenced by plant size and flower production, as has been previously shown (Albert & al. 2001), and that these variables (plant size, flowers and fruits) are also influenced by the intensity or type of herbivory and by the level of plant competition, measured as total plant cover of other perennial species within each plot. We constructed separate models for each herbivory experiment and year. In order to prevent biased responses due to different starting plant sizes, the first year plants were selected to equalize mean plant size between treatments.

SEM analysis was performed with the CALIS procedure of the SAS statistical software package (SAS Institute 1990). Standardized path coefficients were estimated by the maximum likelihood method. Multisample analyses were carried out to determine whether the relationships between variables differ between herbivory types (see Albert & al. 2001 for detailed methods).

Results and discussion

As previously shown (Albert & al. 2001), flower and fruit production of *E. paularense* is mainly determined by plant size (Fig. 1). Results show two different types of effect of herbivores on plant reproduction. Type 1 herbivory did have some positive effects on fruit production in 1998, although effects on flower production were negative in the following year (Fig. 1; Repeated Measures-ANOVA: F Greenhouse-Geisser for Year x Herbivory type effect = 16,544, P < 0,001; data log transformed). This may result from a compensatory response of plants to defoliation and direct flower stalks consumption. Plants may be able to divert most resources to fruit maturation after herbivory, so mitigating the negative effects from damage or removal of reproductive structures (Lowenberg 1994). Thus, when resources are in some way decreased by herbivory, plants may maximize their total fitness by allocating energy to female reproduction (Krupnick & Weis 1999; Lehtilä & Strauss 1999). In this way, lower flower availability in 1999 (due to greater flower consumption) did not result in decreased fruit production. According to some models of plant compensation (Maschinski & Whitham 1989; Vail 1992), this response is possible because herbivory in this area occurs sporadically in the reproductive season and it's restricted to a short period of time relative to the plant's development. Greater flower availability in the ungrazed area in 1999 was due to a greater number of flowers per flower stalk, more than to higher flower stalk production (Table 1).

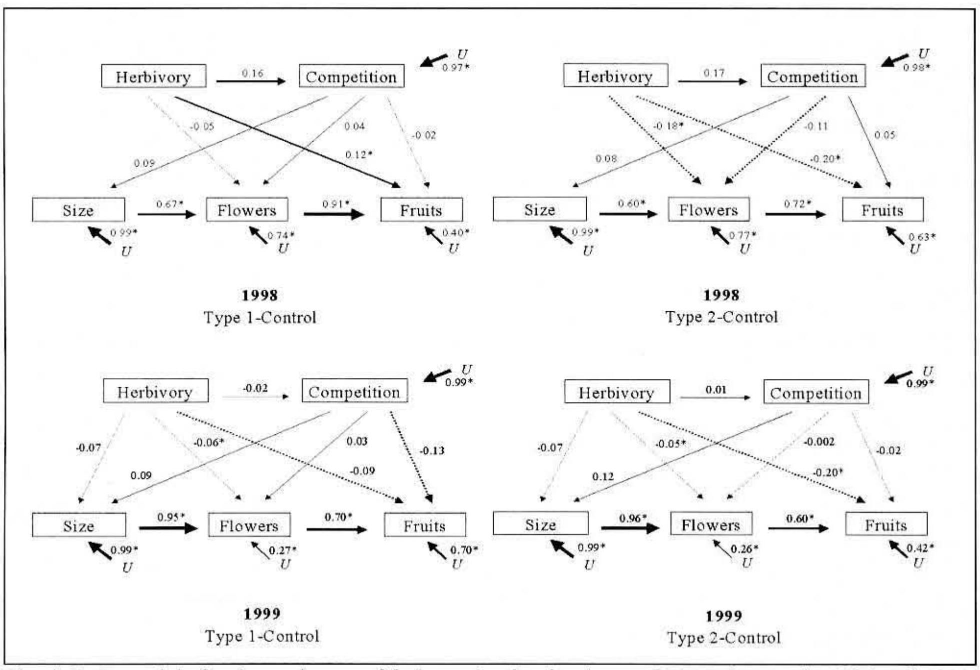

Fig. 1. Path models for determinants of fruit production in plants of *E. paularense* in 1998 and 1999, in two herbivory experiments. Positive effects are indicated by solid lines and negative effects by dashed lines. Arrow widths are proportional to path coefficients. Asterisks denote path coefficients that are significantly different from 0 as assessed by the multivariate Wald test. Numbers near the paths indicate standarized path coefficients. Goodness-of-fit statistics for each model are: 1998 Type 1-Control: NFI = 0,98, GFI = 0,98; 2 =3,11, df = 2, P =0,21; 1998 Type 2-Control: NFI = 0,99, GFI = 0,99; 2 = 1,28, df = 2, P =0,52. 1999 Type 1-Control: NFI = 0,99, GFI = 0,99; 2 =3,01, df = 1, P = 0,08; 1999 Type 1-Control: NFI = 0,99, GFI = 0,99; 2 =0,40, df = 1, P = 0,53. U = effect of unexplained causes. NFI = Bentler-Bonett normed fit index. GFI = goodness-of-fit index.

Table 1. Number of flowers per flowering stalk in 1999. Data log transformed.

Herbivory type	Mean ± st. desv.	*t* test
Control	4,31 ± 1,14	
Type 1	3,69 ± 0,83	*t*=2,907 **
Control	4,31 ± 1,14	
Type 2	4,04 ± 0,65	*t*=1,497 ns

** *P*<0,01; ns non significant

The effect of Type 1 herbivory contrasted with Type 2 herbivory, the last one having negative effects on both flower and fruit production, both years (Fig. 1; Repeated Measures-ANOVA: F Greenhouse-Geisser for flowers, Year effect = 19,359, P < 0,001; fruits: Year effect F = 30,577, P < 0,001, Herbivory type effect F = 13,995, P < 0,001; data log transformed). The more intensive grazing in this area, and more constant over the reproductive season, did not allow for the recovery of plants, at least in the period of time studied. As observed in *Salix arizonica* (Maschinski 2001), the amount of time necessary for recovery may be much longer. Lower values of flower and fruit production in this area resulted from direct ingestion of reproductive structures; the threshold of damage was overcome and compensatory responses were not possible.

Models described for both types of herbivory were not identical in 1998, since when path coefficients were forced to be constrained to the other herbivory type data, 4 of 16 possible constraints were rejected, with a significantly higher x^2. However, in 1999 there was not a significant increase in x^2, indicating that both models are similar. Thus, two years after the beginning of the experiment both types of herbivory seem to have similar effects on plant reproduction. A possible explanation for this result may lay in the fact that the fenced plot (control) was built at the expense of the area which was under Type 1 herbivory. The setting of the experiment may have intensified the effects in the remaining Type 1 herbivory area by forcing cattle to pass through a narrower area, and increasing herbivory and specially habitat alteration.

Both flower diameter and petal size were negatively influenced by grazing (Table 2). This response has been also found in other species exposed to herbivory (Lehtilä & Strauss 1999). Greater corollas may be more attractive to pollinators and thus may affect both female (seed set) and male (pollen removal) fitness (Lehtilä & Strauss 1999). If undamaged plants receive more pollinator visits (Krupnick & al. 1999), greater flower sizes of ungrazed plants may be another reason for their greater fruit production.

Plant survival was not affected by herbivory. Small plants suffered more mortality than greater ones, but survival rates were of the same order (Control 55%, Type 1 Herb. 44%, Type 2 Herb. 59%). Only plants of Type 2 Herbivory treatment with sizes between 5-15 cm were a little affected (survival of control plants: 100%, Type 2 Herb. plants: 89%; Mann-Whitney U = 893,00, P < 0,05).

Results presented here are an early response of herbivory protection and more years are necessary to know how fencing would affect future growth and reproduction. The decline in alpine gentians density, for example, only began three years after imposed protection

Table 2. Variables of flower size (maximum diameter and petal length) and tests for differences between herbivory types (n=50 for each herbivory type).

Variable	Herbivory type	Mean ± st. desv.	*t* test	Mann-Whitney test
Flower diameter	Control	3,13 ± 0,33		
	Type 1	2,88 ± 0,26	*t*=4,623 ***	
Petal	Control	1,44 ± 0,18		*U*=814,00 ***
	Type 1	1,33 ± 0,16		
Flower diameter	Control	3,13 ± 0,33		
	Type 2	2,76 ± 0,34	*t*=5,640 ***	
Petal	Control	1,44 ± 0,18		*U*=692,00 ***
	Type 2	1,29 ± 0,17		

*** $P<0,001$

from grazing (Miller & al. 1999). Taller and denser perennial vegetation in the ungrazed area may reduce the amount of bare soil and result in the loss of potential gaps for seed germination and seedling establishment (Miller & al. 1999). Vegetation structure may also pose difficulties for seed dispersion in ungrazed sites.

If damage from herbivores is so moderate that compensation may occur, the effect of herbivory on population dynamics can be minimal. The compensatory response depends on the interaction between the timing and intensity of herbivory rather than intensity itself (Lowenberg 1994).

Thus, it can be concluded that the problem of managing herbivory for conservation purposes is not simple and cannot always be optimally solved by fencing. A proper management of herbivores may provide much better results. In the case of *E. paularense*, it would be advantageous to reduce grazing pressure from March to June, when *E. paularense* plants are flowering and fruiting, and to allow grazing just before this period and once seed dispersion has finished. Nevertheless, further monitoring in time will be necessary to reach definite conclusions.

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