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# Role of disturbance in maintaining a savanna-like pattern in Mediterranean *Retama sphaerocarpa* shrubland

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**Abstract.** Can the interaction of episodic and chronic disturbances explain the maintenance of savanna-like patterns? We explored the morphological and spatial patterns of the leguminous shrub *Retama sphaerocarpa* in a Mediterranean environment in relation to disturbance. Various morphological variables of *R. sphaerocarpa* shrubland were found to be determined by a combination of two types of disturbance: (1) mechanical cutting: an episodic, heavy, short-term disturbance of anthropogenic origin for management purposes, and (2) herbivore activity primarily by rabbits: generally a chronic, more lenient, long-term disturbance. The intensities of these two types of disturbance were not correlated. Mechanical cutting effects on *R. sphaerocarpa* shrubland morphology predominated quantitatively over herbivore effects. Herbivores generally produced open shrubland with fewer, more scattered, thicker branched, larger *R. sphaerocarpa* shrubs. In contrast, intense sprouting after cutting produced a higher density of smaller *R. sphaerocarpa* shrubs with denser aerial biomass. However, heavy herbivory in abnormally dry periods produced some effects similar to those of mechanical cutting. The size of *R. sphaerocarpa* shrubs was positively related to seed production. Thus, the means of propagation depended upon the type of disturbance: episodic disturbances resulted in intense sprouting, whereas chronic herbivore activity resulted in the formation of thick branches that produced a large number of seeds. The combination of these two disturbances determine, in part, space occupancy patterns of dominant woody species in this Mediterranean landscape and similar savanna-type ecosystems. Investigations of environmental constraints on vegetation distribution and abundance should take into account the historical role of herbivores in shaping present systems.

**Keywords:** Animal-plant interaction; Chronic disturbance; Episodic disturbance; Herbivory; Mechanical cutting; Rabbit; Seed production; Shrubland management; Sprouting.

## Introduction

Disturbance interferes with a settled state; it can be defined as any event in time that removes biomass or organisms. Disturbances can be classified into episodic, sudden changes such as intense fire and cutting or more chronic, continuous changes such as herbivory. Although the joint influence of different types of disturbance on various characteristics of plant community structure has been considered in several studies (e.g. Vieira et al. 1994; Frelich & Reich 1995; Greenberg et al. 1995; Hobbs & Mooney 1995; Jeltsch et al. 1996; Pivello & Coutinho 1996; Liu et al. 1997; Tester et al. 1997), we are unaware of any studies which have actually quantified the interactive effects of episodic *and* chronic disturbances on plant morphology and their implications in plant community physiognomy. In this paper we show how the effects of two kinds of disturbance and their interaction maintain a savanna-like pattern in central Spain.

Species responses to disturbance are governed primarily by their life history and physiological traits and by the characteristics of the disturbance. Species reproductive traits are especially important in determining the potential of species to establish and to persist following disturbance (Chambers 1995).

*Retama sphaerocarpa* (L.) Boiss. is a leafless shrub up to 4 m tall which mostly occurs in the dry regions of North Africa and the Iberian Peninsula. Architecturally, multiple branches hold green, photosynthetic stems (*cladodes*) arising from thick roots that can penetrate into the soil to depths of > 25 m (Haase et al. 1996a). These subterranean parts easily sprout when the aerial biomass is removed. Sexual reproduction is less successful because seedlings die easily due to abiotic factors, herbivory and competition from herbs (Haase et al. 1996b and unpubl. data).

*R. sphaerocarpa* is a xerophytic, N-fixing leguminous shrub which ameliorates climatic conditions in its understorey, thus increasing diversity and productivity of herbaceous species (Moro et al. 1997a, b; Pugnaire et al. 1996). In the Iberian Peninsula it is grazed by domestic and wild herbivores, especially rabbits. It is also a promising species for re-vegetation projects in those sites that satisfy its ecological requirements.

A characteristic of open shrubland and savanna-like formations is the presence of old and scattered individuals of one or a few dominant woody species within a matrix of herbaceous vegetation. The microclimate and soil features under woody canopies differ from those found between individuals, creating heterogeneity in the landscape and acting as ecological islands. *R.*

*sphaerocarpa* shrubland covers large areas of the Iberian Peninsula and it is often the only woody species in this shrubland. The herbaceous flora is primarily annual. We have observed that rabbits can produce both chronic and episodic disturbances in these areas. They normally feed on herbaceous vegetation and rarely browse *R. sphaerocarpa* shrubs. However, they intensively browse the shrubs during periods of drought when herbaceous productivity is abnormally low, and may cause severe damage in a short time.

The main objective of this study is to explore how the joint action of episodic and chronic disturbances may explain the maintenance of savanna-like patterns. The two disturbances were: mechanical cutting – the removal of *R. sphaerocarpa* aerial biomass: an episodic, heavy, short-term disturbance of anthropogenic origin for management purposes and herbivore activity: generally a chronic, weaker (compared to cutting) long-term disturbance.

## Material and Methods

### *Field site*

The study site is a 250-ha shrubland where *R. sphaerocarpa* is the only woody species. The shrubland is located in Fresno del Torote, 30 km NE of Madrid, central Spain, 40°35' N, 3°25' W. The climate is dry, continental Mediterranean, with precipitation of 450 mm/yr and a mean annual temperature of 13.5 °C. The years previous to the field work (1995) were abnormally dry: precipitation figures for 1992, 1993, 1994, and 1995 were 303, 418, 302 and 306 mm, respectively.

At the study site, mechanical cutting of *R. sphaerocarpa* shrubland at ca. 30 cm above the ground is periodically practised to foster game populations and facilitate hunting (new *R. sphaerocarpa* sprouts are more accessible to rabbits). Parts of this shrubland are under different pressure from herbivores (rabbits, hares and sheep) and time since last *R. sphaerocarpa* mechanical cutting varies from 1 to > 10 yr. The impact of rabbits on the shrub canopy is greater than that of hares and sheep: rabbits reach a higher density, and hares and livestock do not feed on *R. sphaerocarpa*. In addition to feeding on *R. sphaerocarpa* when the herb cover is scarce, rabbits dig holes, which mixes soil horizons.

### *Field sampling*

Our sampling was designed to measure the morphology of *R. sphaerocarpa* and intensity of herbivory. Time since last *R. sphaerocarpa* mechanical cutting was determined by interviewing local land managers. In our field site, there was a mosaic of shrubland patches belonging to four age classes according to time since last cutting: 1, 2, 3 and >10 yr. The first three classes have a low biomass compared to the >10 yr class. We selected seven *R. sphaerocarpa* shrubland patches for sampling based upon time since last mechanical cutting and apparent herbivory. We included in our analyses three patches of 1, 2 or 3 yr since last mechanical cutting (1 patch per time class) and four patches >10 yr since last mechanical cutting. These four patches >10 yr were selected based upon indicators (see below) denoting different intensities of herbivory. A later analysis confirmed significant differences in herbivore disturbance among these four patches.

In the summer of 1995, each shrubland patch was sampled along two parallel 50-m transects at the time of fruit maturity. Every transect included five observation stations at regular intervals. At every observation station the following variables were measured:

1. A 0.5 m × 0.5 m quadrat was sampled for cladodes cut by rabbits, number of rabbit pellets, number of rabbit scrapings and number of *R. sphaerocarpa* seeds.
2. A circle of 5-m radius (ca. 78.5 $m^2$) was sampled for number of rabbit and hare dens or sleeping-places, warrens, burrows, pellet-dropping sites, rabbit scrapings and number of *R. sphaerocarpa* shrubs.
3. The five *R. sphaerocarpa* shrubs closest to the centre of the circles were sampled for their physiognomy, including distance between them and the circle centre (a measure of spread), volume, percentage cover, number of branches, basal diameter of the thickest branch and number of seed pods they contained (by classes): 0, 1 - 10, 11 - 50 and > 50 pods per shrub.

### *Data analysis*

We used two measures of herbivore activity. The first one was the number of cladodes cut by rabbits, a measure of recent herbivory since these cladodes remain recognizable on the ground for only 1 yr. The second was a synthetic variable inferred from a principal component analysis (PCA) performed on a subset of six selected relevant variables indicating herbivore activity. The selected variables were cladodes cut by rabbits and number of beds, warrens, burrows, dropping sites and scrapings. This analysis provided a first PCA axis as an estimate of overall herbivore disturbance (not only herbivory) in the last few years. The axis distinguished sites subject to heavy herbivore disturbance from those with low herbivore disturbance. Disturbances through herbivore activities and mechanical cutting were not correlated ($r_S = 0.17$, $P < 0.2$, $N = 70$). There is a spatial segregation of feeding and resting activities by rabbits that are related to the differences in morphology of shrub patches. There were differences for overall herbivore activity and cladodes cut by rabbits among the four patches of > 10 yr since last mechanical cutting ($F = 45.12$, $P < 0.0001$ and $F = 4.42$, $P < 0.009$, respectively).

We used ANOVAs and Tukey's tests for overall comparison of the various *R. sphaerocarpa* morphology variables among the seven shrubland patches. An additional ANOVA was used to compare *R. sphaerocarpa* morphology in two groups of shrubland patches: recently (1 to 3 yr) cut patches and a patch with clear evidence of having been heavily and recently attacked by rabbits. The morphology of *R. sphaerocarpa* was related to herbivore disturbance and to mechanical cutting disturbance, and their interaction, in a series of general linear models (GLM) performed on an observation station basis. In this analysis, mechanical cutting disturbance was measured as the inverse of time (in years) after last cutting. A non-parametric correlation analysis was used to highlight the relationships between *R. sphaerocarpa* size, seed production and the intensity of disturbances.

## Results

### *Effects of herbivore- and mechanical cutting disturbances on the morphology of R. sphaerocarpa*

There were overall significant differences for all morphology variables among the seven patches (Table 1). However, these differences did not hold for all between-patch comparisons. Fig. 1 and the results of the GLM (Table 2) indicate that herbivore and mechanical cutting disturbances had opposite effects on the morphology of *R. sphaerocarpa*. Thus, figures 1a - f depict relatively well clumped field observations for the various morphology variables according to their values for both types of disturbance. All models in Table 2 were found to be highly significant, and all effects of herbivore and mechanical cutting disturbances and their interaction were significant with only three exceptions out of 18 cases. These three exceptions refer to cover of above-ground biomass and herbivore effects and the interaction effects, and number of branches and mechanical cutting effects. Generally, herbivore disturbance produced shrubland patches with fewer, more scattered, larger shrubs with thicker branches. In contrast, mechanical cutting disturbance produced smaller and closer shrubs, in greater number and with denser aerial biomass due to intense sprouting.

An additional result is that the effects of mechanical cutting on the morphology of *R. sphaerocarpa* were always dominant compared to the effects of herbivore disturbance. This is shown by the greater values of the parameter estimates for mechanical cutting, and the sign of the interaction terms, which always coincided with the sign of this variable (Table 2).

There are general trends shown in Fig. 1 regarding the morphology of *R. sphaerocarpa* and the overall herbivore activity in the equally aged, > 10 yr old, patches. However, the patch with relatively high herbivore activity – indicated by the position on the PCA-axis – and the highest recent herbivory level – measured by the number of cladodes cut by rabbits – (Patch 6 in Table 1) formed noticeable outliers in some cases, particularly in Fig. 1a. The results of the ANOVA used to compare the morphology of *R. sphaerocarpa* in this patch, which was recently heavily attacked by rabbits and in recently (1 - 3 yr) mechanically cut patches, indicated no significant differences for number of shrubs, spread or number of branches (Table 3). Only three morphological variables converged. This suggests that heavy herbivore disturbance can have effects on the morphology of *R. sphaerocarpa* shrubland resembling some of those of mechanical cutting, and that these two types of episodic disturbances did not produce exactly the same shrubland morphology.

**Table 1.** Means and standard deviations of the morphological variables and disturbances by herbivores for the seven *Retama sphaerocarpa* shrubland patches. The table includes the results of the ANOVAs used for overall comparison among patches. All comparisons are significant at $P < 0.0001$ except for number of shrubs ($P < 0.007$), and cladodes cut by rabbits ($P < 0.004$) and the Tukey's test used for between patch comparisons (means with the same superscript are not significantly different at $P < 0.05$).

| Patch label | 4 | 3 | 5 | 1 | 2 | 6 | 7 | $F$ | $R^2$ |
|---|---|---|---|---|---|---|---|---|---|
| Time since last mechanical cutting (years) | 1 | 2 | 3 | >10 | >10 | >10 | >10 | | |
| Disturbances by herbivores | | | | | | | | | |
| Overall herbivore activity | $-0.30 \pm 0.63^{bc}$ | $-1.07 \pm 0.37^{cd}$ | $0.33 \pm 0.81^{b}$ | $-0.34 \pm 0.38^{bc}$ | $2.82 \pm 1.62^{a}$ | $0.26 \pm 0.57^{b}$ | $-1.69 \pm 0.23^{d}$ | 33.01 | 0.76 |
| Cladodes cut by rabbits | $13.6 \pm 12.6^{ab}$ | $13.1 \pm 14.6^{ab}$ | $33.9 \pm 26.8^{ab}$ | $12.2 \pm 15.4^{b}$ | $30.7 \pm 26.4^{cb}$ | $38.8 \pm 16.9^{a}$ | $15.1 \pm 15.3^{ab}$ | 3.63 | 0.26 |
| Morphological variables of *R. sphaerocarpa* | | | | | | | | | |
| Number of shrubs | $63 \pm 20.5^{a}$ | $20.2 \pm 3.9^{b}$ | $47.1 \pm 27.0^{ac}$ | $22.1 \pm 7.32^{bd}$ | $12.8 \pm 5.1^{b}$ | $41.7 \pm 19.4^{ad}$ | $28.5 \pm 10.6^{bcd}$ | 12.21 | 0.54 |
| Shrub spreading (cm) | $147.7 \pm 58.7^{b}$ | $189.2 \pm 52.9^{ab}$ | $145.2 \pm 67.0^{b}$ | $191.5 \pm 46.2^{ab}$ | $251.5 \pm 47.1^{a}$ | $144.8 \pm 50.8^{b}$ | $142.7 \pm 41.5^{b}$ | 5.95 | 0.36 |
| Shrub volume ($m^3$) | $0.52 \pm 0.34^{c}$ | $0.67 \pm 0.34^{c}$ | $0.74 \pm 0.41^{c}$ | $0.78 \pm 0.65^{c}$ | $9.61 \pm 4.08^{a}$ | $3.57 \pm 2.65^{b}$ | $1.14 \pm 0.97^{bc}$ | 30.6 | 0.74 |
| Cover of aerial biomass (%) | $70.4 \pm 5.6^{a}$ | $68.4 \pm 7.9^{a}$ | $64.4 \pm 6.7^{ab}$ | $53.9 \pm 7.9^{c}$ | $52.3 \pm 7.5^{c}$ | $57.4 \pm 5.1^{bc}$ | $51.6 \pm 10.2^{c}$ | 11.15 | 0.51 |
| Number of branches | $9.9 \pm 6.9^{b}$ | $19.9 \pm 11.3^{ab}$ | $16.3 \pm 6.0^{ab}$ | $12.2 \pm 6.4^{ab}$ | $26.6 \pm 24.0^{a}$ | $12.5 \pm 6.6^{ab}$ | $7.6 \pm 5.5^{b}$ | 3.31 | 0.24 |
| Branch thickness (mm) | $8.0 \pm 2.0^{c}$ | $10.1 \pm 2.9^{c}$ | $9.8 \pm 2.5^{c}$ | $11.7 \pm 3.0^{bc}$ | $28.4 \pm 5.6^{a}$ | $16.2 \pm 4.8^{b}$ | $10.5 \pm 3.9^{c}$ | 35.46 | 0.77 |

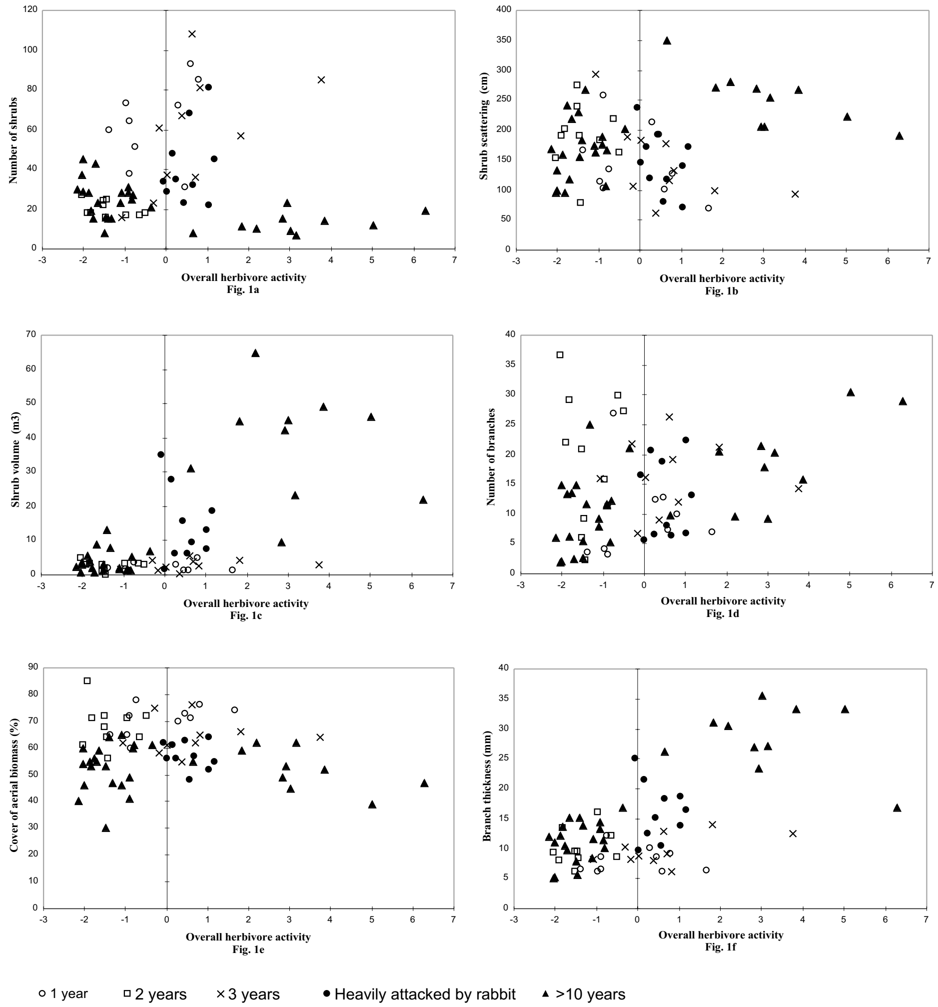


**Fig. 1.** Relationships between the morphological variables of *Retama sphaerocarpa* shrubland and the intensity of herbivore disturbance, measured by a PC axis. The symbols refer to time since last mechanical cutting and to the shrubland patch heavily attacked by rabbits.

*Effects of herbivores and mechanical cutting on the seed production of Retama sphaerocarpa*

Increasing time since last mechanical cutting and the size of *R. sphaerocarpa* (measured as volume) were significantly related to greater seed production ($r_S$ = 0.44 and 0.6, respectively, $P < 0.0001$, $n = 70$). There was also a high correlation between number of seeds counted on the ground and shrub size ($r_S = 0.55$, $P < 0.0001$, $n = 70$). Thus, the absence of mechanical cut-

**Table 2.** Results of the multiple regression of *Retama sphaerocarpa* morphology variables on overall herbivore and cutting disturbances.

| | Parameter estimated and *P*-values (in parentheses) | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Morphology variable | Herbivore effects | | Mechanical cutting effects | | Interaction | | $R^2$ | *P*-value |
| Number of shrubs | – 5.9 | (0.004) | 54.1 | (0.0001) | 43.6 | (0.0001) | 0.41 | 0.0001 |
| Shrub spreading (cm) | 21.8 | (0.001) | – 50.2 | (0.05) | – 77.2 | (0.009) | 0.17 | 0.005 |
| Shrub volume ($m^3$) | $8.1 \times 10^6$ | (0.0001) | $-14.8 \times 10^6$ | (0.0004) | $-12.2 \times 10^6$ | (0.01) | 0.59 | 0.0001 |
| Cover of aerial biomass (%) | – 0.8 | (0.4) | 20.7 | (0.0001) | 2.0 | (0.6) | 0.41 | 0.0001 |
| Number of branches | 4.2 | (0.0005) | – 1.0 | (0.3) | – 2.2 | (0.03) | 0.23 | 0.0007 |
| Branch thickness (mm) | 4.1 | (0.0001) | – 9.6 | (0.0001) | – 6.1 | (0.0001) | 0.65 | 0.0001 |

**Table 3.** Means and standard deviations of the morphological variables for two groups of *Retama sphaerocarpa* shrubland patches: (1) a patch heavily and recently attacked by rabbits and (2) recently (3 years or less) mechanically cut patches. The table includes the results of the ANOVAs used for the comparisons.

| | Heavily attacked patches | Recently cut patches | *F* | $R^2$ | *P* |
|---|---|---|---|---|---|
| Number of shrubs | 42.8 ± 26.1 | 0.01 | 0 | 0.9 | |
| Shrub spreading (cm) | 144.8 ± 50.8 | 160.7 ± 61.3 | 0.54 | 0.01 | < 0.5 |
| Shrub volume ($m^3$) | 3.57 ± 2.65 | 0.64 ± 0.36 | 36.4 | 0.49 | < 0.0001 |
| Cover of aerial biomass (%) | 57.4 ± 5.1 | 67.7 ± 70.2 | 18.3 | 0.32 | < 0.0001 |
| Number of branches | 12.5 ± 6.6 | 15.3 ± 9.2 | 0.81 | 0.02 | < 0.4 |
| Branch thickness (mm) | 16.2 ± 4.8 | 9.3 ± 2.6 | 33.4 | 0.47 | < 0.0001 |

ting and high levels of herbivore disturbance resulted in larger shrubs that produced higher numbers of seeds, whereas mechanical cutting pushed *R. sphaerocarpa* towards vegetative propagation.

## Discussion

Terrestrial plants often live in environments in which above-ground organs are removed by disturbances. Our results show that the morphology of a *R. sphaerocarpa* shrubland depends upon the conflicting effects of episodic and chronic disturbances. More importantly, the interaction of the two types of disturbance had a significant effect on the morphology of this shrubland. Disturbance by herbivores produced *R. sphaerocarpa* patches with fewer, more scattered, thicker branched and larger shrubs, i.e. an open shrubland or savanna-type structure. In contrast, mechanical cutting produced smaller and denser shrubs with greater canopy biomass and cover, i.e. a closed-shrubland morphology. However, herbivore activities may also imply episodic disturbance, when the climate is abnormally dry – because they feed on shrubs when herbaceous cover is scarce. Episodic disturbances such as wildfires and severe droughts are frequent but unpredictable in dry Mediterranean environments. We hypothesize that mechanical cutting of shrubs in this plant community mimics natural high-intensity disturbances such as fires or intense browsing, and the observed pattern of morphology is the product of episodic and chronic disturbances. *Dehesas* (Mediterranean man-made oak savannas) represent an analogy of the system under study at a different scale. Medium and large size domestic and wild herbivores are responsible for the existence of some old, scattered *Quercus* trees in a matrix of predominantly herbaceous communities by killing or stunting small woody plants (Marañón 1988). Oak management in dry periods includes heavy trimming which makes soft tissues available to cattle.

Other theoretical and empirical studies have also documented the role of various types of disturbance (anthropogenic and natural, catastrophic and mild) as being partly responsible for spatial patterns of woody vegetation in other ecosystems of the world. Intense sprouting of woody species after catastrophic disturbances, mostly fire and cutting, is well documented (Perelevotsky & Haimov 1991; Frelich & Reich 1995; Vilá & Terradas 1995). Studies on the effects of herbivore activities, including digging, on the morphology of woody vegetation have produced comparable results when the intensity of the disturbance is taken into account (Bullock 1991; Swihart & Picone 1991; Dinerstein 1992; Dolman & Sutherland 1992; Manning et al. 1996).

The differences in seed production under the two types of disturbance may have implications for the propagation of *R. sphaerocarpa*. Less recent mechanical cutting and herbivore activity produced larger shrubs which had greater seed production. In contrast, cutting stimulated vegetative propagation in *R. sphaerocarpa*. In shrubland under these two types of disturbance we find an alternation of patches resulting from vegetative propagation and patches consisting of seed producers selected by herbivores. Several studies have shown that the preference of animals is negatively correlated to the occurrence of chemical and physical defence mechanisms in plants (Stock et al. 1993; Milton 1995; Woodward & Coppock 1995). Thus, *R. sphaerocarpa* adopts a propagation strategy that depends upon active disturbance: (1) intense sprouting as a response to episodic disturbance and (2) generation of thick branches producing flowers in response to chronic disturbance by herbivores.

We conclude that disturbance history is a major factor controlling local variation in community structure. Passive recovery by woody vegetation is constrained by both climatic and biological factors. Unfavourable weather conditions, occurring at random, result in unusually heavy episodic disturbance (Iwasa & Kubo 1995). Our data illustrate how transitions from closed shrubland to open shrubland and to savanna-like vegetation can be mediated by herbivores. Herbivores probably maintain grassland, open shrubland and savannas by preventing woody species such as *R. sphaerocarpa* from establishing or attaining dominance. In Mediterranean environments, management of vegetation has led to the extension of savanna-type ecosystems. Investigations of environmental constraints on the distribution of vegetation and the abundance of its species should take into account the historical role of herbivores in shaping present systems (Weltzin et al. 1997). To mimic natural disturbances, mechanical removal of biomass may be a suitable ecosystem management practice, where burning is impractical.

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