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Effects of disturbance on population biology of the rosette species *Eryngium horridum* Malme in grasslands in southern Brazil

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Abstract The Southern Grassland biome in Brazil has long been neglected by the government and by the scientific community as well. Lack of studies about the effects of disturbance (mostly fire and grazing) on plant community and populations are the main hindrances for the future management plans, which complicates the conservation of this rich and unique biome. In this study, the population biology of a rosette species, *Eryngium horridum* (Apiaceae), has been investigated, in order to compare the effects of fire, grazing and abandonment. *E. horridum* is a very common species and many farmers consider it a nuisance. Two different areas were chosen for the study purposes: Morro Santana and the Research Center Pró-Mata. Areas under different types (fire and grazing) and disturbance histories were compared. Populations were analysed in plots of 25 m^2, divided in age-state classes (seedlings, young, adult and reproductive individuals). Both morphological and phenological traits have been investigated. Fire influenced populations in a direct way, whilst grazing showed an indirect effect. Seedlings were found only in areas excluded from disturbance for 3 years on Morro Santana. Due to this, seedling establishment might be more related to environmental conditions than to disturbance regimes. Young individuals were mainly found in recently burned areas, while adult individuals were dominant in areas excluded from disturbance. Additionally, individuals from *E. horridum* showed a great capacity of resprouting after plant damage. Reproductive individuals also showed the capacity of producing new rosettes after the death of the inflorescence axis. This strategy is probably of great importance for the survival of populations in areas excluded from disturbance. Therefore, vegetative reproduction seemed to be the most important strategy for the maintenance and survival of its populations, allowing longer population persistence over time, even in the absence of disturbance.

Keywords Population biology · Fire · Grazing · Rosette species · Grasslands · *Eryngium horridum*

Introduction

Disturbance is any event in time that partially or totally destroys plant biomass (Grime 1979) and thus, opens space in the vegetation (Pickett et al. 1989; Lavorel et al. 1997). It promotes the formation of gaps, enhancing colonization and germination through litter removal (Zedler 1995; Hoffmann 1996; Brewer 2001). Disturbance events also influence

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several abiotic factors (e.g. availability of water and light) (Klinkhamer and de Jong 1988), altering, therefore, habitat conditions for plant populations and communities.

Fire and grazing are common events in many grassland ecosystems (Furley 1999; Nabinger et al. 2000; Bredenkamp et al. 2002), being both used for grassland management. Grazing is the major management activity in temperate and subtropical grasslands with economic and conservation objectives (Pillar and Quadros 1997; Bullock et al. 2001). Fire is also a common tool used for the management of many grassland systems, e.g. tropical savannas (Pivello and Coutinho 1996). Some species die during the burn, since they are incapable to resist heat damage and removal of aboveground biomass. Other species, e.g. in savanna ecosystems, can avoid the effect of fire by a combination of different traits (e.g. thick bark, protected buds) (Gignoux et al. 1997). Such traits are important for the post-disturbance plant community that will be constituted, at least partially, by these surviving individuals.

Different stages of the life cycle can also be affected by fire, e.g. germination, seedling establishment and survival and reproduction of established individuals. Some species exhibit higher fecundity rates and reproductive output after burning (Quintana-Ascencio and Menges 2000; Quintana-Ascencio et al. 2002; Bowen and Pate 2004), whilst others can regrowth after plant damaging (Pfab and Witkowski 1999). For some plant populations, vegetative reproduction stimulated by fire disturbances is more important than sexual reproduction for the population growth rate (Hoffmann 1999).

Grazing significantly influences vegetation communities in their species diversity, life and growth form composition (Sala et al. 1986). Grazed areas are usually characterized by plants with a short and early growing season, a high proportion of flat-rosette growth form, and plants with the capacity for rapid regrowth. Other plants may have developed avoidance mechanisms (Gibson 1988; Noy-Meir et al. 1989; McIntyre et al. 1995). The creation and colonization of gaps is an important consequence of grazing (Bullock et al. 1995), allowing for periodical appearance of open patches in the canopy of dominant plants (Sala et al. 1986). This process permits other less competitive plants to persist (Silvertown et al. 1992; Rambo and Faeth 1999). Thus, grazing influences not only single plant populations, but the entire plant community.

The Southern Grassland biome in Brazil is rich in species (estimations about 3000 plant species, Boldrini 1997). However, this biome has been neglected by both Brazilian government and scientific community (Overbeck et al. 2006). There is a lack of studies on diversity of these grasslands, and almost no studies exist about population biology of single species. Such studies would be helpful for conservation biologists to evaluate endangerment status of target species and to elaborate management plans for the conservation of these unique grasslands. The use of target species that show clear responses to management practices has been widely reported in the literature (e.g. Bowers 1997; Bowen and Pate 2004; Fensham et al. 2002; Hegland et al. 2001; Klinkhamer and de Jong 1988). On the other hand, while allowing for biodiversity conservation, management should also allow for efficient and sustainable use of the forage produced, and should aim at keeping a low proportion of undesirable species with bad forage value or high-competitive abilities that may have negative effects on pasture quality and plant diversity (Gonçalves and Girardi-Deiro 1986; Pillar and Quadros 1997; Nabinger et al, 2000). *Eryngium horridum* is such a species: where fire and grazing are intense, its individuals become a nuisance plant, invading great areas and decreasing the quality of pastures (Mathias et al. 1972). *E. horridum* is a common species in grasslands in southern Brazil (Rambo 1957; Mathias et al. 1972; Irgang 1974). It belongs to the Apiaceae botanical family and is a rosette plant with thorny, fibrous leaves. Its rosette has thick rhizomes, shows clonal growth (Graf et al. 1998) and the ability to resprout quickly after disturbances, exhibiting thus, an important role in post-disturbance dynamics of the plant community. The inflorescence axis can reach up to 3 m, with numerous inflorescences and flowers bearing wind-dispersed seeds (Mathias et al. 1972; Irgang 1974). After flowering, the main rosette dies and other rosettes can grow from the same rhizome. Only young individuals and the softer leaves in the centre of the rosette are browsed by cattle. Therefore, farmers usually burn or plough their pastures in order to destroy its populations. Another management strategy frequently applied by farmers is the cutting of the inflorescence axis before the flowers are mature. Nonetheless, only the destruction of the entire plant (including rhizome) is effective. In abandoned grasslands excluded from grazing and fire, this rosette plant seems to facilitate the establishment of short forbs within the dense grass layer, playing an important role on the maintenance of plant diversity (Fidelis et al., in preparation).

E. horridum has xeromorphic characteristics (e.g. scleromorphous leaves, presence of a sclerenchymatic hypodermis, and presence of stomata only in the abaxial face of the leaves) (Oliveira, pers. comm.). In paleoecological studies, pollen of *Eryngium* species were found in peat profiles, thus confirming the presence of the species under past drier climatic conditions in the early Holocene, when grasslands were the dominant vegetation formation (Behling et al. 1997, 2004; Behling 2002).

In this study, we analyse the effects of fire, grazing and abandonment on population biology of *Eryngium horridum*. An analysis of population structure, morphological and phenological traits was carried out in order to establish management strategies in view of this species. We hypothesized that its populations are favoured by fire and grazing, principally by increasing vegetative reproduction through resprouting after the removal of aboveground biomass.

Material and methods

Study area

The study was carried out in two regions in southern Brazil, on Morro Santana (near Porto Alegre, 30°02′ S to 30°04′ S and 51°06′ W to 51°09′ W, 311 m a.s.l.) and at the Research Center Pró-Mata (on the southern Brazilian Araucaria Plateau, 29°27′ to 29°35′ S and 50°08′ to 50°15′ W, 900 m a.s.l.). The climate in the Porto Alegre region is subtropical humid (Köppen classification Cfa), with a mean temperature of 22°C (Livi 1999). The soils are characterized by a horizon A rich in clay; Acrisol is the predominant soil type (Streck et al. 2002). Grasslands undergo frequent disturbances, principally by anthropogenic fires, which occur in intervals of 3–5 years, and are not being grazed. Recent studies showed that these grasslands are rich in species (450–500 plant species in a grassland area of 220 ha; with high fine-scale diversity; Overbeck et al. 2006) and fire may be crucial for the maintenance of species diversity (Overbeck et al. 2005). The grassland is composed by a matrix of caespitose grasses (e.g. *Elionurus muticus*, *Aristida flaccida* and *Andropogon lateralis*) and a large number of small forbs (mainly from Asteraceae, Leguminosae and Rubiaceae). *Eryngium horridum* is among the herb species with the highest relative cover values in these areas (Overbeck et al. 2006), dominating large parts of the grasslands physiognomically.

The Research Center Pró-Mata exhibits a Cfb climate, with mean temperatures of the warmest month not higher than 22°C, and with a well distributed annual precipitation higher than 2000 mm, with no dry season (Bertoletti and Teixeira 1995). Soils are usually acid, not hydromorphic, with a horizon B rich in organic matter (Bertoletti and Teixeira 1995). Three vegetation formations can be observed at the Research Center Pró-Mata: Araucaria Forest, Atlantic Rainforest and grasslands. Since establishment of the Research Center in 1994, fire and grazing have been excluded from the grassland areas (Bertoletti and Teixeira 1995). The grassland structure differs from that one on Morro Santana: the grass layer is higher and denser due to 10 years of abandonment. Additionally, forest encroachment processes are under way (Oliveira and Pillar 2004; Overbeck et al. 2005). Diversity in these abandoned areas are strongly reduced by the dominance of a few caespitose grasses and accumulation of litter (Overbeck et al. 2005). An area of 25 ha was burned in 1999 at the border of the Research Center next to an adjacent farm. The pastures of this farm, grazed by cattle and burned every two to three winters, were also included in this study, in order to investigate the influence of fire and grazing and only grazing (with last burn more than 3 years back) on populations of *Eryngium horridum*.

Field work

Four areas with different disturbance types and histories were chosen on Morro Santana (B0- recently burned (in August 2003), B1 – burned 1 year before, B2 – burned 2 years before, and B+ – burned at least 3 years before) and at the Research Center Pró-Mata (FG – farm, recently burned and grazed, G – farm, grazed, P1 – Research Center Pró-Mata, excluded from disturbance since 1999, and P2 – Research Center Pró-Mata, excluded from disturbance since 1994). The two excluded areas at the Research Center Pró-Mata differed from each other with respect to vegetation structure. Area P1 showed a tall and dense grass cover, whilst area P2 (probably a secondary grassland) was characterized by shrubland (dominance of *Baccharis uncinella).* Area FG was burned in August 2003 and area G has not been burned since at least 3 years.

In each of these areas, sites with the presence of *E. horridum* were chosen and three plots (25 m^2 each) were randomly established per area in October of 2004. All individuals of *Eryngium horridum* in each plot were considered a population for the purpose of this study. Since *Eryngium horridum* shows clonal growth, the differentiation of individuals in the field was very difficult. An individual may either consist of several ramets (rosettes, which form one genet, but each possessing their own rhizome and being able to survive after separation) or be multi-stemmed, i.e. possess rosettes, which are growing from the same rhizome, but cannot be considered physiologically independent. For this study, each rosette was considered an individual. Since it is not easy to evaluate the age of individuals in the field, the concept of age state classes (see Gatsuk et al. 1980; Oostermeijer et al. 1994; Hegland et al. 2001) was adopted for characterization of populations. All individuals present in each plot were grouped into the following classes: seedlings, young individuals (rosette diameter <25 cm), adult individuals (rosette diameter $\geq$25 cm), and reproductive individuals (rosette with inflorescence axis).

For the evaluation of the effects of fire and grazing on populations, morphological and phenological traits were examined. The chosen traits were: rosette diameter (d), rosette height (h), percentage of dead biomass/individual (db), average number of leaves/individual/area (nl), average leaf width (lw), average leaf length (ll), inflorescence axis height (hi), average diameter of inflorescences (di), average number of inflorescence/individual (ni), average number of flowers/individual (fi), percentage of buds and flowers (bf) and percentage of flowers and fruits (ff). The three first traits were measured for all individuals in each population. The leaf traits measurements were carried out for 10 individuals/class (except for seedlings) in each area and the phenological traits, for 12 individuals/area (random selection of individuals). Leaf area was calculated by multiplying leaf width and leaf length. For the total leaf area/individual, this value was multiplied by the total number of leaves/individual.

Further, vegetation cover and cover of bare soil, rock and litter were estimated for each plot, using a modified Braun-Blanquet (1964) scale (1: $\leq$ 1%, 2: 1–10%, 3: 10–25%, 4: 26–50%, 5: 51–75%, and 6: 76–100%). Cover classes were transformed into average values correspondent to the intervals for data analysis (1: 0.5%; 2: 5%; 3: 17.5%; 4: 37.5%; 5: 62.5%; 6: 87.5%).

Clipping experiments were conducted in order to investigate the resprouting capacity of individuals from the different age state classes after disturbance. The experiments were carried out with selected single parts from both study areas (area B1 on Santana Hill and area P2 at the Research Center Pró-Mata), using 10 individuals from each class (except for seedlings). All aboveground biomass was removed and observations of resprouting capacity were carried out after one and two weeks.

Statistical analysis

An analysis of variance with randomization tests were used to determine differences between populations under different disturbance types (separately for each area) concerning their morphological and phenological traits, as well as the demographic composition (ρ = 0.05). In order to analyse the relation between the vegetation cover and populations, Pearsońs correlation analyses were performed between demographic structure and structural attributes of vegetation, separately for the two study areas. Additionally, Principal Coordinate Analysis (PCoA) was performed for separate analysis of population in the two areas, using demographic, morphological and phenological data, and testing stability of axes by bootstrap resampling (Pillar 1998, 1999). The resemblance measure used for all analysis was Euclidean distance (Podani 2000). In both randomization test and bootstrap resampling, 1000 iterations were calculated. All statistical analyses were performed by the program MULTIV 2.2.7 (Pillar 2004).

Results

Population structure

On Morro Santana, 981 individuals were recorded in a total area of 75 m^2. Most of the individuals were adults (46.5%), distributed almost regularly throughout the different study areas (Fig. 1A). Seedlings were not found in the recently burned area (B0), but were abundant in area B+ (78.8% of all seedlings). On the other hand, reproductive individuals were predominantly found in area B1.

At the Research Center Pró-Mata, most of the 990-recorded individuals were young individuals (60%), mostly found in the burned and grazed areas (62%; Fig. 1B). Using space-for-time substitution, an evident decrease in number of young individuals was observed with increasing time since last disturbance. The number of adult individuals showed the opposite distribution pattern. No seedlings could be found in any of these areas, and only 1.2% of the total number of individuals exhibited inflorescence axes.

Since few seedlings were found concentrated in one area from Morro Santana, they were not considered in the further statistical analysis of morphological data.

Morphological and phenological traits

Rosette diameter differed significantly between all areas ($p = 0.001$), except between areas B1 and B+ (Fig. 2A). Smaller individuals were found in area B0 and the larger ones in area B1 and B+. Rosette height showed the same pattern, with the tallest individuals in areas B1 and B+ and the shortest in B0 ($p = 0.001$). The percentage of dead biomass estimated in this area was also higher ($p = 0.001$).

Young and adult individuals revealed no significant differences for rosette height between areas B0 and B2, and for rosette diameter between areas B1 and B+. Young individuals also did not differ significantly for rosette height between B2 and B+. No significant differences could be observed for rosette height in reproductive individuals between areas B1 and B+ and B2 and B+. Between areas B2 and B+, the same could be observed for both rosette diameter and dead biomass.

At the Research Center Pró-Mata, populations in areas under fire and grazing and under grazing (FG and G) showed smaller individuals (height and diameter) in comparison to areas with exclusion of fire and grazing (P1 and P2) (Fig. 2B). The highest values for dead biomass were found in the area FG. Rosette height and dead biomass differed significantly between all areas ($p \leq 0.05$). Rosette diameter exhibited the same results, except for populations in areas P1 and P2 (no significant differences).

Rosette height differed significantly between all areas for adult individuals ($p = 0.001$), as well as

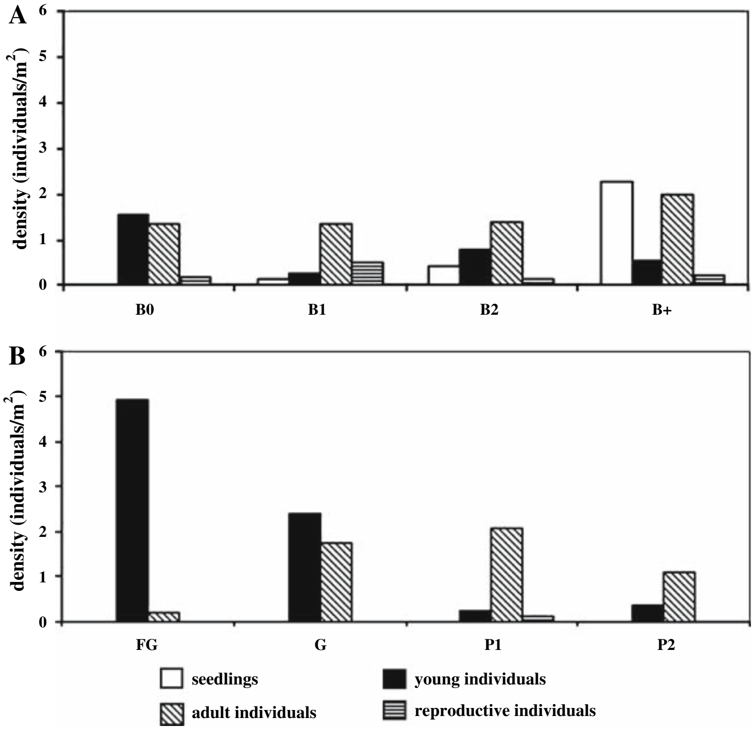

Fig. 1 Density of individuals from both study sites. **A** – on Morro Santana (B0 – recently burned, B1 – burned 1 year ago, B2 – burned 2 years ago, and B+ – not burned since 3 years) and **B** – at the Research Center Pró-Mata (FG – campo under fire and grazing, G – campo under grazing, P1 – campo excluded from disturbance since 1999, and P2 – campo excluded from disturbance since 1994)

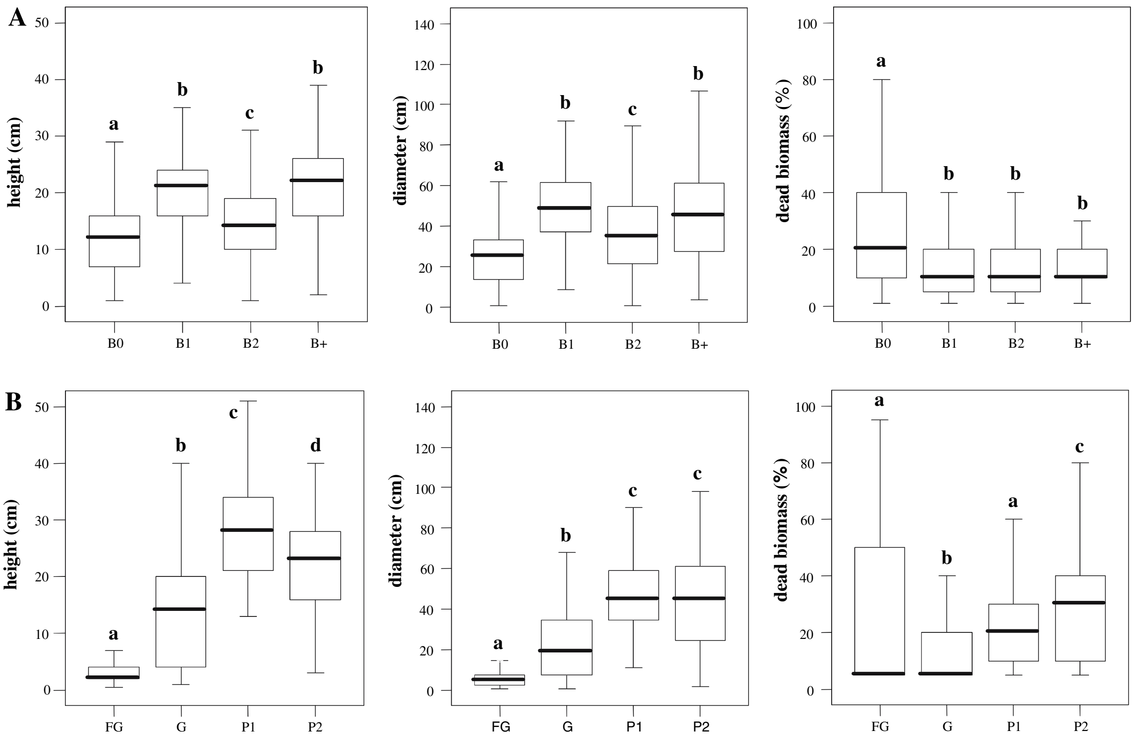

Fig. 2 Differences in morphological traits (rosette height, rosette diameter and percentage of dead biomass/individual) from populations of *Eryngium horridum* in the different study areas, across different age states. **A** – Morro Santana (B0 – recently burned, B1 – burned 1 year ago, B2 – burned 2 years ago, and B+ – not burned since 3 years). **B** – Research Center Pró-Mata (FG – campo under fire and grazing, G – campo under grazing, P1 – campo excluded from disturbance since 1999, and P2 – campo excluded from disturbance since 1994). Randomization tests used Euclidian distances and 1000 iterations. Different letters mean significant differences ($p \leq 0.05$). The line between the boxes represents the median, boxes 25%-interquartils, and the *t*-shaped lines the maximum and minimum values

rosette diameter, except between areas FG and G. Young individuals also revealed significant differences in relation to their rosette height and diameter between areas ($p \leq 0.05$).

Traits related to leaf morphology in populations on Morro Santana showed no clear pattern between the areas. Individuals from area B1 showed the highest number of leaves, and individuals from areas B2 and B+ showed high values for total leaf area/individual (Fig. 3A) At Pró-Mata (Fig. 3B), leaf areas were the highest in area P1.

Although most of the reproductive individuals on Morro Santana were present in area B1, individuals from area B0 exhibited the greatest number of inflorescences ($p = 0.001$) and flowers (no significant differences) (Table 1). The highest inflorescence axes were found in area B+ (Fig. 4A). In the recently burned area (B0), the reproductive individuals had a delayed flowering time in comparison to the other areas. On Pró-Mata different results were obtained. Reproductive individuals from the burned and grazed area (FG) showed the lowest values for all phenological traits (inflorescence axis, inflorescence number, inflorescence diameter, and total number of flowers). Individuals from areas G and P1 had the highest inflorescence axis, the greatest inflorescence diameters, and number of flowers (Fig. 4B). Additionally, times of flowering differed between areas, with flowering taking place earlier in areas FG and G.

As shown by the Principal Coordinate Analysis (Fig. 5A), populations from area B0 formed a distinct group from the other areas on Morro Santana. The number of young individuals correlated negatively to the axis 1 ($r = -0.86$), as well as the percentage of dead biomass ($r = -0.83$). Number of adult individuals, rosette height and diameter correlated negatively to the axis 2 ($r = -0.66$, 0.56, and

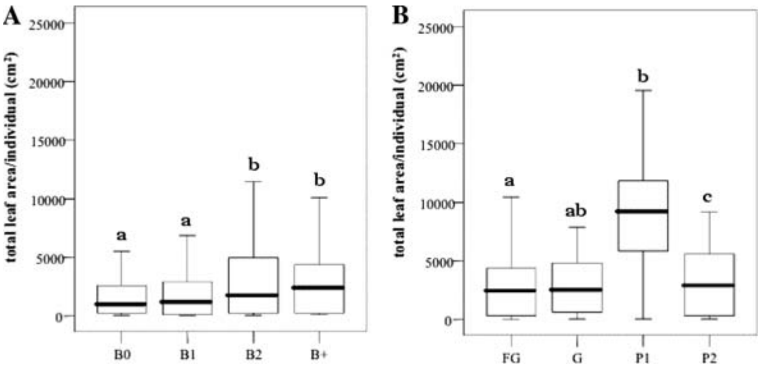

Fig. 3 Differences on the total leaf area/individual (cm^2) between the study areas. **A** – Morro Santana (B0 – recently burned, B1 – burned 1 year ago, B2 – burned 2 years ago, and B+ – not burned since 3 years) and **B** – Research Center Pró-Mata (FG – campo under fire and grazing, G – campo under grazing, P1 – campo excluded from disturbance since 1999, and P2 – campo excluded from disturbance since 1994). Randomization tests used Euclidian distances and 1000 iterations. Different letters mean significant differences ($p \leq 0.05$). The line between the boxes represents the median, boxes 25%-interquartils, and the t-shaped lines the maximum and minimum values

Table 1 Phenological traits from populations of *Eryngium horridum* on Morro Santana (B0, B1, B2, and B+) and at the Research Center Pró-Mata (FG, G, P1, and P2)

Area	Plot	di	ni	fi	bf
Morro Santana	B0	1.04 ± 0.12	134.3 ± 50.40	15956.82 ± 6472.53	56.67 ± 40.30
	B1	1.01 ± 0.1	101 ± 55.76	11779.51 ± 6552.76	0 ± 0
	B2	0.99 ± 0.13	93.5 ± 89.80	11111.31 ± 11142.46	0 ± 0
	B+	1.09 ± 0.08	105.83 ± 54.45	13025.76 ± 7131.69	0 ± 0
Pró-Mata	FG	0.94 ± 0.07	56.5 ± 24.23	6333.44 ± 2904.41	93.75 ± 6.41
	G	1.14 ± 0.16	144.42 ± 60.77	18312.34 ± 8391.62	96.67 ± 3.89
	P1	1.1 ± 0.11	129.33 ± 60.16	15828.93 ± 7537.09	73.75 ± 36
	P2	1.03 ± 0.09	87.33 ± 30.86	10401.21 ± 4127.19	58.33 ± 33.29

Average values and standard errors of diameter of inflorescence/individual (di), number of inflorescence/individual (ni), number of flowers/individual (fi), and percentage of buds and flowers/individual (bf)

−0.66, respectively). All areas separated clearly in the ordination from populations from the Research Center Pró-Mata (Fig. 5B). Young individuals correlated negatively to the first axis ($r = -0.91$), whereas adult individuals, rosette height and diameter correlated positively to this axis ($r = 0.84$, 0.95, and 0.92, respectively). Dead biomass correlated negatively to axis 2 ($r = -0.89$).

Bare soil showed a positive correlation to the number of young individuals in both study areas (Table 2) and a negative correlation to the number of adult individuals. Seedlings found on Morro Santana correlated significantly to litter ($r = 0.49$*) and cover of dead grass ($r = 0.45$**). Higher percentages of bare soil were found in the disturbed areas (areas B0 and FG), whilst a higher accumulation of litter was found in the areas B1, B+ and P2. Forb cover was higher in the grazed area in comparison to the other areas at the Pró-Mata. However, on Morro Santana, no significant differences could be found.

Resprouting capacity

In both study regions, individuals of *Eryngium horridum* showed a great capacity to resprout, regardless of initial size. Some adult and reproductive individuals exhibited more than one new resprout (Table 3). At the Research Center Pró-Mata, reproductive individuals showed an average number of 6.1 new resprouts per rhizome.

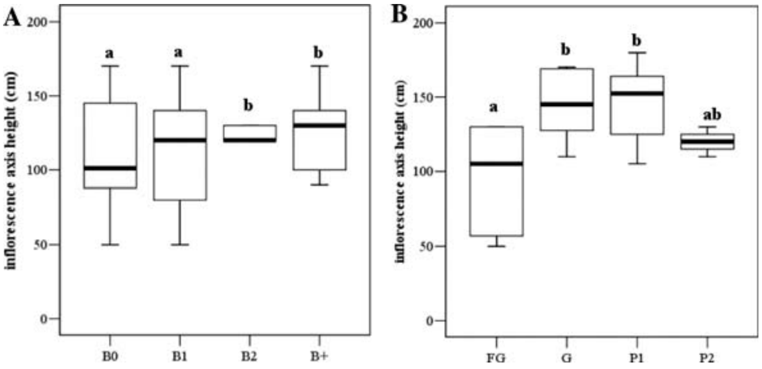

Fig. 4 Differences on the inflorescence axes height (cm) between the study areas. **A** – Morro Santana (B0 – recently burned, B1 – burned 1 year ago, B2 – burned 2 years ago, and B+ – not burned since 3 years) and **B** – Research Center Pró-Mata (FG – campo under fire and grazing, G – campo under grazing, P1 – campo excluded from disturbance since 1999, and P2 – campo excluded from disturbance since 1994). Randomization tests used Euclidean distances and 1000 iterations. Different letters mean significant differences ($p \leq 0.05$). The line between the boxes represents the median, boxes 25%-interquartils, and the *t*-shaped lines the maximum and minimum values

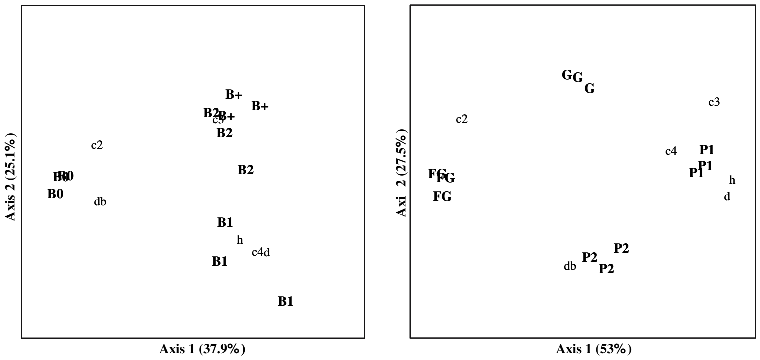

Fig. 5 Ordination of the population data (c2 – number of young individuals, c3 – number of adult individuals, c4 – number of reproductive individuals, d – rosette diameter, h – rosette height, and db – % of dead biomass) from the different study areas. **A** – Morro Santana (B0 – recently burned, B1 – burned 1 year ago, B2 – burned 2 years ago, and B+ – not burned since 3 years) and **B** – Research Center Pró-Mata (FG – campo under fire and grazing, G – campo under grazing, P1 – campo excluded from disturbance since 1999, and P2 – campo excluded from disturbance since 1994). The ordination method is principal coordinate analysis (PCoA), applied to Euclidian distance between sampling units. Bootstrap resampling analysis showed no stability of the axes from ordination A and stability for axis 1 and 2 from ordination B ($p = 0.07$)

Discussion

Effects of disturbance on the morphological and phenological traits

Plastic responses of morphological traits could be observed in *Eryngium horridum* populations in areas with longer intervals since the last disturbance. The Pró-Mata area P1 (excluded from disturbance since 1999) had the densest and tallest vegetation cover, mostly formed by tall tussock grasses. *E. horridum* individuals in this area were the tallest, showing the highest number of leaves and the highest values for total leaf area/individual. In area P2, also excluded from fire and grazing since 10 years, vegetation cover was not as dense as in P1, but dominated by tall shrubs from *Baccharis uncinella*, presenting patches of bare soil between tussock grasses and shrubs. Population in this area showed individual rosettes as large as the ones from the area P1 concerning their diameter, but not as tall. Presumably, competition for light was not as critical as in area P1 with its dense grass canopy. In the disturbed areas, morphological traits principally reflected the recent biomass

Table 2 Correlation coefficient (*r*) between vegetation cover (bare soil, rock, litter, forb, live grass, dead grass, live shrub, and dead shrub) and the individuals from class 1 (seedlings), class 2 (young individuals), class 3 (adult individuals), and class 4 (reproductive individuals) on Morro Santana and Research Center Pró-Mata

Cover	All individuals	class 1	class 2	class 3	class 4
Morro Santana					
Bare soil	−0.09	−0.21	0.44*	−0.42*	0.52**
Rock	−0.49**	−0.23	−0.29	−0.42*	0.12
Litter	0.34	0.49*	−0.49*	0.41*	−0.14
Forb	−0.15	0.02	−0.41*	0.08	−0.14
Live grass	−0.29	−0.12	−0.31	0.08	−0.54**
Dead grass	0.18	0.45**	−0.56**	0.2	−0.17
Live shrub	−0.08	0.10	−0.39	0.07	−0.12
Dead shrub	−0.03	−0.06	0.08	0.12	−0.41**
Pró-Mata					
Bare soil	0.57**	–	0.74***	−0.59**	−0.2
Rock	0.34	–	0.38	−0.21	−0.16
Litter	−0.35	–	−0.35	0.17	−0.05
Forb	0.41*	–	0.32	0.06	−0.14
Live grass	0.51**	–	0.53**	−0.28	0.01
Dead grass	−0.68***	–	−0.77***	0.48*	0.12
Live shrub	−0.64***	–	−0.55**	0.12	−0.25
Dead shrub	−0.42*	–	−0.42*	0.21	−0.13

Randomization tests were performed to evaluate the significance of the correlation (1000 iterations)

*$p \leq 0.05$

**$p \leq 0.01$

***$p \leq 0.001$

Table 3 Average number of rosettes, and rosette diameter (cm) after the clipping experiment on Morro Santana (1 week after) and at the Research Center Pró-Mata (2 weeks after), showing the resprouting capacity from the different age-state classes (%, class 1—seedlings, class 2—young individuals, class 3—adult individuals, and class 4—reproductive individuals)

Area	Classes	Number of rosettes	Resprout capacity (%)	Diameter (cm)
Morro Santana	2	1	100	1 ± 0.24
	3	1	80	1.93 ± 1.35
	4	2.2	50	0.6 ± 0.72
Pró-Mata	2	1	60	2.55 ± 1.00
	3	1.6	100	3.84 ± 0.76
	4	6.1	100	2.45 ± 0.32

Ten individuals for each class were measured in each area

removal, resulting in significantly shorter leaves and smaller rosettes. Since *E. horridum* is largely rejected by cattle, this effect was less pronounced in plots that had only been grazed, but not recently burned.

In general, flowering can be influenced by grazing and fire. Some authors showed that plants in burned areas tended to show a greater proportion of flowering individuals (Brewer and Platt 1994; Menges and Quintana-Ascencio 2004). Grazing is known to delay flowering time, due to a general decreased reproductive output that reduces growth and flowering (Ehrlén 1997; del Val and Crawley 2004). In our study we observed that areas recently burned (B0) and burned 1 year before showed the highest number of reproductive individuals in comparison to the other areas (B2 and B+). Despite the removal of biomass caused by fire, plants could still develop inflorescence axis and flowers. On the other hand, at the Research Center Pró-Mata, under fire and grazing influences, few reproductive individuals could be observed. Many of the reproductive *E. horridum* individuals showed few or no inflorescences, due to damages caused by insects, fruit and seed development was greatly impeded by the insect larvae, which damaged the interior part of the inflorescence axes of many attacked reproductive individuals in both study areas (pers. obs.). Consequently, these inflorescence axes died, sometimes before the complete development of flowers. At the Research Center Pró-Mata, about 50% of all reproductive individuals showed their inflorescences damaged or killed by the larvae (pers. obs). The presence of taller inflorescence axes in populations in areas where vegetation cover was also higher and denser (for example, B2, B+ on Morro Santana), agrees with the results found for species from Apiaceae by Jongejans and Telenius (2001). On the other hand, height of inflorescence axes in the disturbed areas might be attributed to the removal of aboveground biomass by disturbance and the consequently high effort of the plant dedicated to resprouting.

Effects of disturbance on the population structure of *Eryngium horridum*

The distribution of age state classes differed between the areas under different types and time since last disturbance. Seedlings could only be found on Morro Santana, where the presence of seedlings showed a positive correlation to litter (mostly in the area B+). Litter can have both positive and negative effects on seedling establishment. Xiong and Nilsson (1999) stated that plant litter has a negative impact on both germination and establishment. At Research Center Pró-Mata, no seedlings were recorded, neither on protected nor on disturbed sites. This may be due to either the lack of seeds, low germination rates, and high-seedling mortality. Considering that percentage of reproductive individuals in the year of the study was very low, we assume that in the year before, which most likely was responsible for the seedlings found, generative propagation also had not been very pronounced. These results suggest that populations of *E. horridum* in the protected areas on Pró-Mata, with mostly old individuals, already are in a senile phase (Oostermeijer et al. 1994; Hegland et al. 2001). Those of the few seeds that may have successfully germinated in the abandoned areas probably suffered from unsuitable environmental conditions in the extremely dense grass layer, with severe light restrictions (at least in the P1 site). Fungal attack, a severe problem for seedlings in very moist climates (Moles and Westoby 2004a, b) may have further increased seedling mortality. While litter may favour seed germination and establishment, as shown on Morro Santana, too high values for litter and grass densities might cause difficulties to this process. In the grazed areas on Pró-Mata, the absence of sexually reproductive individuals and seedlings is difficult to interpret and would require further studies for a conclusive statement. A possible explanation is that cattle, in general rejecting the spiny rosettes of *E. horridum*, will browse the softer hearts of the rosettes, thus damaging exactly those parts of the plants that would give rise to an inflorescence axis. Such behaviour should indirectly favour vegetative reproduction, since the resources not used for sexual reproduction could be designated for expansion of rhizomes and sprouting of new ramets.

Clonal plants often exhibit infrequent seedling recruitment and vegetative reproduction may thus, play an important role for maintenance of populations (Grubb 1977; Eriksson 1989). The same has been shown in our study. At some rhizomes exposed after fire, large numbers of resprouts (in one case 12 resprouts stemming from one rhizome) could be observed. The clipping experiments showed the high resprouting capacity of *Eryngium horridum*, regardless of initial size of clipped individuals. This enables regeneration of existing populations without dependence on suitable microsite conditions for seed germination and seedling establishment, favouring competition for space in sites opened by disturbance. Moreover, establishment success of vegetative resprouts should be higher than that of seedlings, due to a greater maternal investment of resources and initial physiological dependency of ramets (Grime 1979; Cook 1985; Sebens and Thorne 1985). Resprouting, however, was not restricted to disturbance. After flowering and subsequent death of an inflorescence axis, the original rosette also died and new rosettes resprouted at its base, stemming from the same rhizome. This strategy might guarantee the successful survival of *Eryngium horridum* populations once established, both in disturbed and not disturbed grasslands. However, the number of new ramets is clearly lower than in populations in disturbed areas.

Plant population structure can be defined as ‘‘invasive’’ (high proportion of seedlings and young plants in relation to adult and generative ones), ‘‘normal’’ (higher proportions of adult and reproductive individuals), and ‘‘senile’’ (no seedlings and young individuals, only adult plants) (Oostermeijer et al. 1994; Hegland et al. 2001). In both study sites, recently disturbed areas were characterized by invasive populations, although these populations showed no seedlings, but large numbers of young individuals, as discussed above. Populations from the areas B1, B2 (Morro Santana), G, P1, and P2 (Pró-Mata) could be defined as normal populations. The area B+ presented populations with a high percentage of seedlings and adult individuals in relation to other age state classes, being difficult to be classified. Likewise, even though individuals from area P2 seemed to be very old (with high percentage of dead biomass and adult individuals), these populations could not be defined as senile, due to the presence of young individuals.

Therefore, even in the absence of disturbance (e.g. in the areas excluded from disturbance at the Research Center Pró-Mata), individuals of *Eryngium horridum* are still able to reproduce (vegetatively and in lower rates, in this case) and guarantee the survival of the population by producing new rosettes after the generative phase. In regularly burned populations (e.g. on Morro Santana), we assume that resprouting will always be stimulated by disturbance (see above), although its rates would decrease in the absence of disturbance events. Despite the apparent relation between litter and seedling occurrence, sexual reproduction could not be closely linked to the disturbance regime, and may depend primarily on environmental conditions, e.g. climatic differences between years.

Grazing and fire: distinct effects of different disturbances

Fire affects both young and adult individuals. A greater number of young individuals could be found in recently burned areas, whilst adult individuals were often found in abandoned areas without fire. These results reinforce the hypothesis that fire might enhance regeneration by resprouting after plant damage (Pfab and Witkowski 1999). When burns are frequent, vegetative reproduction will occur at high rates. Destruction of a rosette usually leads to development of several rosettes, and therefore, to a denser population structure and lateral expansion of populations. Indirectly, however, this dense population structure may contribute greatly to population growth: if, in any given year, a high-generative reproductive output, i.e. high seed-production, coincides with good germination conditions, chances for mass recruitment are good. It would possibly affect areas in larger distance from the seed-source, as seeds are easily dispersed by wind. Grazing, on the other hand, acted a lot more selectively, as only young individuals and the centre of adult rosettes were grazed by cattle, with thus markedly less effects on long-term population structure, unless—as hypothesized above—this does in fact affect sexual reproduction. Nonetheless, in the face of the two disturbances fire and grazing, *E. horridum* showed to be disturbance-specialist (Lavorel et al. 1997). Fire clearly increased vegetative reproduction and led to population growth. Grazing, favoured the species passively, since it was principally rejected by cattle. In addition, it managed to sustain its populations and to expand them vegetatively. In the absence of disturbance, the species can maintain its populations due to long-lived rhizomes and regeneration by producing new rosettes within the leaves of the old rosette. However, on the long term, populations in abandoned areas should suffer from increased competition, which might impede both sexual and vegetative reproduction.

Our results show that farmers, who frequently burn their lands in order to improve forage quality and avoid the invasion of undesirable plants should re-evaluate their management practices. In fact they are stimulating vegetative propagation of *E. horridum* populations, not destroying them. Therefore, the use of fire with these purposes should be reviewed and new management approaches should be offered if the objective is to avoid this species in these grasslands.

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