Original article

Spine production is induced by fire: a natural experiment with three *Berberis* species

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Abstract

Earlier studies indicate that some plant species allocate more mass to produce longer spines in shoots resprouting after browsing. Here we present, for the first time, evidence that fire induces a similar response. Many terrestrial herbivores may benefit from fire through the enhanced availability of fast growing species colonizing or re-sprouting in burned areas. It is less clear whether post-fire plant growth responds to the enhanced risk of herbivory by an increased investment in defensive traits. In this study, we tested whether the production of spines is influenced by the set of environmental conditions that result from fire events. We compared the resource allocation pattern of resprouting shoots from three *Berberis* species growing in two areas that burned 1999 with samples collected from unburned areas within the same plant communities. We divided the shoot into three main components: supporting tissue (twigs), assimilating tissue (leaves) and defensive structures (spines). We found that plants resprouting after fire allocated more mass to spines and leaves but not twigs. This resulted in a higher density of both spines and leaves. Spines were significantly longer in plants resprouting after fire. Leaves were shorter at the apical end of the shoot, but did not show any significant change in size following fire. We suggest that this type of post-fire response may be a general adaptation to pruning and leaf picking by browsing herbivores in arid and semi-arid regions. Changes in the browsing pressure following fire will determine the fitness value of this response.

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1. Introduction

Induced defenses are defined as a plant's responses to herbivore damage that enhance the fitness of the plant by reducing herbivore attack (Karban and Myers, 1989). Temporal and spatial variation in the risk of herbivore attack may select for the production of induced rather than constitutive defenses (Haukioja and Neuvonen, 1985; Åström and Lundberg, 1994; Gomez and Zamora, 2002).

While most studies of induced defenses have focused on the effects of defoliation on the synthesis of specific chemical compounds (e.g., Rhoades, 1983; Bryant et al., 1993; Karban, 1993; Rausher et al., 1993; Stock et al., 1993; Honkanen et al., 1994,1999), some evidence of the role of browsing in inducing changes in physical traits has also been gathered (Young, 1987; Milewski et al., 1991; Myers and Bazely, 1991; Gowda, 1997).

Many terrestrial herbivores may be favored by fire through the enhanced availability of fast growing forage species that colonize or re-sprout in burned areas (Skarpe, 1990; Veblen et al., 1992; Bond and van Wilgren, 1996; Raffaele and Veblen, 2001). However, it is less clear whether plants that re-sprout after fire respond to the increased risk of herbivory by increasing their investments in defensive traits.

In this study, we tested whether the production of spines is influenced by the set of environmental conditions that result from such events. We sought to answer the following questions:

- Does the growth rate of shoots increase following fire? The capacity of plants to compensate for losses in mass may indicate their adaptation to such disturbances. (McNaughton, 1983; Karban and Myers, 1989; Teague, 1989; Du Toit et al., 1990; Whitham et al., 1991; Paige, 1992; Hjälten et al., 1993). Here, we focus only on shoot length and mass, because it is directly associated with the effi-

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ciency of spines as defensive traits (Belovsky et al., 1991; Myers and Bazely, 1991; Gowda, 1996).

- Does the mass and length of spines increase more than that of other tissue types (i.e. leaves and twigs) in shoots resprouting after fire? This has been suggested to be an induced response to pruning by browsing animals (Young, 1987; Milewski et al., 1991; Gowda, 1997; Young et al., 2003).
- Does the portion of the leaf covered by spines vary after fire? Increased spine length may result in a higher protection of the foliage whenever it is not coupled with an increment in the length of leaves (Cooper and Owen-Smith, 1986; Milewski et al., 1991; Gowda, 1996).
- Does spine density increase in new shoots of plants growing after fire, and can this increment be explained by reductions in shoot length as proposed by Myers and Bazely (1991)?
- Are basal spines and leaves larger than apical ones? Basal spines may protect more biomass against pruning, whereas apical leaves may be more exposed to picking (Gowda, 1996).

2. Methods

2.1. Study area

In northern Patagonia, Argentina, shrublands (known as matorrales) frequently occur in the ecotone between forest and the steppe (Gallopin, 1978). Matorrales are dense stands of tall (*ca.* 2 m) and low shrubs, combined with herbaceous plants. Matorrales are characterized by species capable of vegetative reproduction: forbs propagate from stolons or rhizomes, grasses tiller, and woody plants sprout from root crowns or trunk bases (Raffaele and Veblen, 1998). Studies of fire history based on tree-ring dating of fire events indicate that the dry forests of the region were subject to high rates of burning (30–40 year intervals) prior to European settlement of the region in the 19th century (Kitzberger and Veblen, 1997; Kitzberger et al., 1997). An increasingly effective fire suppression policy during the 20th century has resulted in a marked increment in fire intervals (Kitzberger and Veblen, 1997).

Fire is also an important disturbance in the western limits of the Patagonian steppe where plant cover is more dense than in the interior of the continent. Near the Andean foothills, plant cover of *c.* 60% corresponds to 700–1100 kg/ha of fine fuels. Here, the steppe consists of a matrix of scattered cushion shrubs (mainly *Mulinum spinosum*) interspersed with tussock grasses (such as *Stipa speciosa* and *Festuca pallescens*) and forbs. Most of these species are flammable, especially during warm and dry summers. Recovery after fire in the steppe is rapid, due to the capacity of nearly all the common shrubs and herbs to resprout from basal buds on stems, root crowns, rhizomes, and other underground organs.

Sampling was conducted in these two plant communities, matorrales and steppe, which are characteristic of the transition between the Andean forest and the Patagonian desert. The matorrales sites have an annual precipitation of 1400 mm, whereas the transitional steppe sites receive an annual precipitation of 600 mm.

Native browsers of significance in the region include *Llama guanicoe*, *Hipppocamelus bisulcus* and *Pudu pudu* (Olrog and Lucero, 1980; Redford and Eisenberg, 1992). Thus, the matorrales have long been subjected to browsing, and more recently non-native herbivores such as *Lepus europeus*, *Cervus elaphus*, and livestock have been added to the vertebrate herbivore community (Raffaele and Veblen, 2001; Veblen et al., 2003).

2.2. Sample collection

The family *Berberidaceae* is composed of 14 genera, distributed in North and South America, Europe, Asia and the north of Africa. *Berberis* is the only genus present in South America. Sixteen species of this genus occur in Patagonia, most of them in the Andean forests, where they are common understory species. All of the *Berberis* species found in the region are shrubs, most of them armed with stipular spines (Bottini, 2000). We sampled three of the most widespread species of Northern Patagonia, *B. buxifolia* Lamark, *B. empetrifolia* Lamark, and *B. heterophylla* Jussieu (in Lamark–Poiret).

B. buxifolia, is a common understory shrub of most Andean forest communities. Plants were sampled in a mixed shrub (Matorral) community that had burned during summer 1999 (Fig. 1). Control (unburned) plants were collected in the same plant community, approx. 2 km west of the burned site (less than 1 km from the fire line).

B. empetrifolia is dwarf shrub characteristic of stony river banks. The plants were sampled along the rocky shore of a river in the same burned area where *B. buxifolia* was collected. Control plants were sampled along the rocky shore of a small stream 2 km east of the burned area.

B. heterophylla is a species characteristic of the Patagonian steppe. The species was sampled in a transitional steppe community that also burned naturally during summer 1999 (Fig. 1). The control plants were collected close to a railroad, 1 km east of the burned area. The railroad had apparently served as a firebreak, protecting approx. 10 ha. of the original plant community from the fire.

Fourteen individuals of each species were randomly sampled from an area of approx. 1 ha. for both the burned and the neighboring unburned control sites. Plants were at least three meters from each other. For each individual, the current annual growth (CAG) of the longest shoot was sampled. All collections took place during the two first weeks of September 2001, approximately 30 days before bud opening.

Samples were oven dried at 40 °C for 72 h, separated into twigs, leaves and spines, and weighed. Shoot length of CAG (apical tip to previous year's scar) was measured and the number of spine rosettes was counted. Because the spines of the three *Berberis* species sampled are produced from the
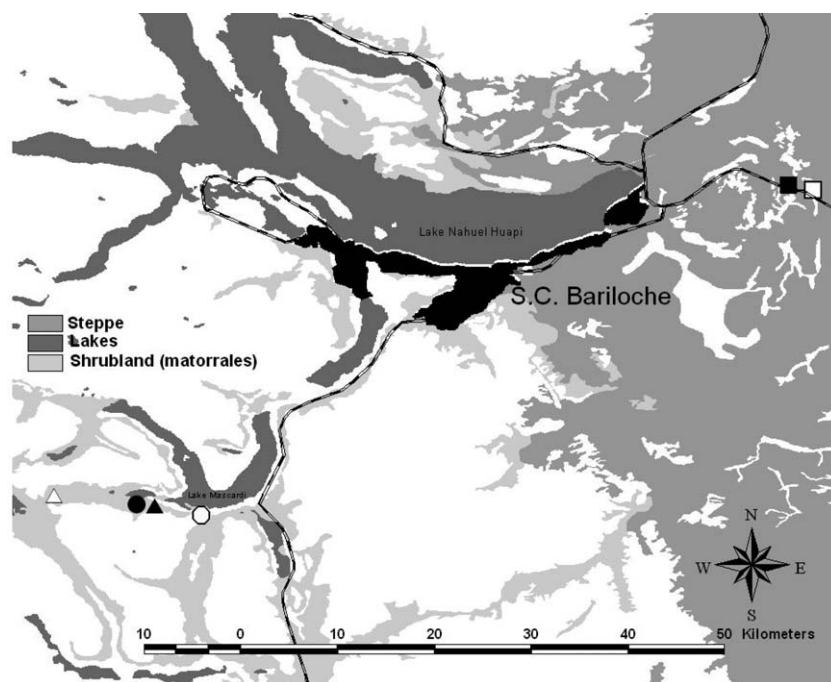
Fig. 1. General view of the collection area. *B. buxifolia* (Δ) and *B. empetrifolia* (O) plants were sampled in a shrubland (Matorral, light grey). *B. heterophylla* (□) plants were sampled at the Western outskirts of the Patagonian steppe. Filled dots represent sites burned year 1999, open dots indicate the areas of collection of control plants.

stipules of opening buds, each spine rosette is associated with a leaf cluster and an active bud that may develop into a new shoot.

To test whether there were differences in the allocation pattern within the shoot, the length of the longest leaves and spines was measured at three consecutive buds at its basal and apical ends (i.e. 4–6th apical buds = apical, 4–6th basal buds = basal). The mean values of the three measurements were used for parwise comparisons between basal and apical ends of the shoot.

2.3. Statistical analyses

The effect of fire on the production of spines in shoots was assessed by comparing the biomass, size and density of spines, and the biomass and size of twigs and leaves of plants between burned and unburned sites. The dependent variables were: spine density, spine and leaf length, and mass of spines, twigs and leaves.

The dependent variables were analyzed by using a two-way ANOVA with a 2×3 factorial arrangement. The factors were: *Fire* (burnt and unburned, and *Species* (three species). The variation in mass of spines was analyzed with an AN-COVA, using mass of twigs and leaves as a covariates to test whether changes in the production of spines was related to these variables (Gowda et al., 2003).

Normality of residuals between observed and predicted values of dependent variables was evaluated by using normal plots (Sokal and Rohlf, 1981). Bonferroni's test was used to adjust the observed significance levels according to the number of comparisons made (Rice, 1989). Pairwise compari-

sons of means were made with a posteriori Tukey's procedure (Sokal and Rohlf, 1981).

Differences in length between apical and basal leaves and spines were tested by Wilcoxon rank signed test. Mann–Whitney test was used to test whether the differences in spine and leaf length found between treatments and species were maintained at the apical and basal shoot ends.

3. Results

There were no significant differences in length or mass of the shoot between plants growing in burned areas and their controls (45.7 cm and 2.4 g versus 40.4 cm and 2.1 g for burned and unburned plants, respectively; Tables 1 and 2). *B. heterophylla* produced significantly shorter twigs than *B. buxifolia* and *B. empetrifolia* irrespective of treatment (Table 2, Tukey test: $n = 40$, $P = 0.005$ and $P = 0.028$, respectively).

The mass of leaves increased significantly in burned areas as compared to their control (1.2 g against 0.8 g for burned and unburned plants respectively; Table 1). *B. buxifolia* had significantly higher leaf mass than *B. heterophylla* and *B. empetrifolia* (Table 1, Tukey-test: $n = 40$, $P = 0.01$ and $P = 0.002$, respectively).

The mass of spines increased significantly in burned areas, being correlated with twig but not leaf mass (0.27 g against 0.15 g for burned and unburned plants respectively; Table 1). *B. buxifolia* had significantly lower spine mass than *B. heterophylla* and *B. empetrifolia* (Tukey test: $n = 40$, $P = 0.009$ and 0.002, respectively).

Table 1
Differences in mass of shoot components of three *Berberis* species between recently burned and unburned areas. The species studied were *B. heterophylla*, *B. buxifolia*, and *B. empetrifolia*. Factors of the two way ANCOVA´s: species (SPP) and fire (F). **Bold** values are significant after correction by Bonferroni test

	Df	MS	F	*P*-level
		Twig biomass (g)		
SPP	2	179	0.42	0.659
F	1	279	1.31	0.257
SPP × F	2	481	1.13	0.330
Error	75	213		
		Leaf biomass (g)		
Twig biomass [a]	**1**	**1005**	**83.1**	**0.001**
SPP	**2**	**317**	**13.1**	**0.001**
F	**1**	**147**	**12.2**	**0.001**
SPP × F	2	60	2.48	0.091
Error	74	12.1		
		Spine biomass (g)		
Twig biomass [a]	**1**	**8.9**	**7.14**	**0.009**
Leaf biomass [a]	1	1.8	1.45	0.225
SPP	**2**	**11.1**	**8.84**	**0.001**
F	**1**	**18.1**	**14.84**	**0.001**
SPP × F	2	1.9	1.56	0.214
Error	73	1.23		
		Number of spine and leaf rosettes		
Twig length [a]	**1**	**3991.9**	**134.5**	**0.001**
SPP	**2**	**1841.8**	**61.5**	**0.001**
F	**1**	**652.7**	**20.8**	**0.001**
SPP × F	2	13.97	0.52	0.598
Error	74	29.3		

[a] Covariate.

Table 2
Differences in length of shoot components of three common *Berberis* species between recently burned and unburned areas. The species studied were *B. heterophylla*, *B. buxifolia*, and *B. empetrifolia*. Factors of the two way ANCOVA's: species (SPP) and fire (F). **Bold** values are significant after correction by Bonferroni test

	df	MS	F	*P*-level
		Length of twig (cm)		
SPP	**2**	**1668**	**6.53**	**0.002**
F	1	807	3.05	0.072
SPP × F	2	348	1.29	0.243
Error	76	242		
		Length of leaves (mm)		
SPP	2	8.79	1.046	0.356
F	1	0.054	0.006	0.936
SPP × F	2	4.12	0.490	0.615
Error	76	8.40		
		Length of spines (mm)		
Leaf Length [a] (mm)	1	11.89	2.45	0.112
SPP	**2**	**114**	**23.6**	**0.001**
F	**1**	**271**	**55.9**	**0.001**
SPP × F	2	3.5	1	0.695
Error	75	4.86		

[a] Covariate.

The number of spines and leaf rosettes showed a significant increase for plants growing in burned areas as compared to their controls (36 against 28 per shoot, or 0.81 against 0.74

per cm for burned and unburned plants, respectively; Table 1). *B. empetrifolia* had a significantly higher number of spines and leaf rosettes than the other two species (Table 1, Tukey test: $n = 80$, $P < 0.001$ for both species), and showed the most significant increment following fire (Tukey test, $n = 28$, $P = 0.009$). Number of spines and leaf rosettes showed a significant and positive covariation with twig length (Table 1).

There were no significant changes in leaf length between species or following fire for any of the species studied (Table 2). Irrespective of species or treatment, leaves produced at the basal end of the shoots were significantly longer than those produced at the apical end (Table 3).

The length of spines showed a significant increase in plants growing in burned areas as compared to their controls (Tables 2 and 3; Fig. 1). *B. heterophylla* had significantly longer spines than the other two species. Basal spines were significantly longer than apical ones only for unburned plants of *B. heterophylla* and burned plants of *B. buxifolia* (Table 3).

The combination of longer spines after fire with no elongation of leaves in burned plants resulted in a significantly higher portion of the foliage protected by the spines (Fig. 3).

4. Discussion

The ability of species to resprout following fire and browsing may be a good indicator of their adaptation to such events (McNaughton, 1983,1984). In this study, there were no significant differences in mass or length of the shoot between plants growing in burned areas and their controls, indicating that plants were not overcompensating for the loss of burned tissue by producing longer shoots. Further tests of the ability of *Berberis* species to compensate for tissue loss should focus on the number of shoots produced, as well as on changes in the activity of root rhizomes.

Our results indicate that plants resprouting after fire allocated significantly more shoot mass to assimilating and defensive tissue. Whereas increments in leaf mass and density are generally associated with higher assimilation, the functional importance of increments in spine mass is less obvious.

Increasing densities of spines resulted in lower foraging rates by free ranging goats and a reduction of the twig biomass consumed (Gowda, 1996). We may therefore expect a reduction of twig pruning and foraging efficiency of vertebrates browsing on spiny *Berberis* species resprouting after fire. Myers and Bazely (1991) proposed that increments in spine density following damage may be an indirect effect of reduced twig growth. Our results show that shoots growing after fire are slightly longer than their controls. The increments in spine density documented here should therefore be considered an induced response triggered by fire.

Spine length has often been related to the protection of leaves (Cooper and Owen-Smith, 1986; Milewski et al., 1991), and increments in spine length are assumed to be an

Table 3
Differences in length between apical and basal leaves and spines of three *Berberis* species in burned and unburned areas. Leaves were significantly longer at the basal end of the twig, independently of treatment, spines were significantly longer in burned areas independently of shoot part

		Differences between basal and apical shoot ends							
		Leaf length				Spine length			
				Wilcoxon signed ranks					
Species	Shoot part	Mean	S.D.	Sign test	Z and P	Mean	S.D.	Sign test	Z and P
				Burned plants					
Berberis buxifolia	Basal	16.2	3.3	14	*3.296*	11.2	2.8	10	*1.854*
	Apical	12.3	1.8	0	**0.001**	9.3	2.1	4	0.062
B. mpetrifolia	Basal	14.8	3.0	11	*2,794*	11.4	2.0	8	*1.099*
	Apical	12.2	2.0	3	**0.005**	10.7	1.7	6	0.272
B. heterophylla	Basal	15.8	2.3	12	*2.417*	15.7	4.0	10	*2.166*
	Apical	12.6	3.2	2	**0.016**	12.9	2.9	4	**0.030**
				Unburned plants					
B. buxifolia	Basal	17.0	6.1	12	*3.110*	7.9	1.6	9	*2.201*
	Apical	13.3	3.9	1	**0.002**	6.4	1.6	4	**0.028**
B. empetrifolia	Basal	13.8	2.4	9	*1.036*	6.6	1.8	6	*–0.596*
	Apical	13.5	2.3	5	0.300	7.4	1.9	8	0.551
B. heterophylla	Basal	14.6	3.4	9	*2.046*	11.0	3.0	4	*–0.628*
	Apical	12.5	2.2	3	**0.041**	11.7	1.6	8	0.530
		Differences between burned and unburned plants by shoot part							
		Leaf length				Spine length			
				Mann–Whitney test					
		Burned n	Unburned n	U-test	P	Burned n	Unburned n	U-test	P
B. buxifolia	Basal	14	14	104.5	0.790	14	14	166	**0.002**
	Apical	14	13	80.5	0.610	14	13	158	**0.001**
B. empetrifolia	Basal	14	14	114.5	0.448	14	14	192	**0.001**
	Apical	14	14	65	0.123	14	14	182	**0.001**
B. heterophylla	Basal	14	12	110	0.181	14	12	136	**0.007**
	Apical	14	12	78.5	0.777	14	12	103	0.316

induced response to pruning by browsing ungulates (Young, 1987; Karban and Myers, 1989; Bryant et al., 1991; Milewski et al., 1991; Young et al., 2003). An increment of spine length will only lead to a higher protection of leaves whenever it is not coupled with an elongation of the associated foliage. Resprouting *Berberis* showed a significant increment in spine length (Fig. 2, Table 3), coupled with no changes in leaf length (Table 3), which resulted in a reduction
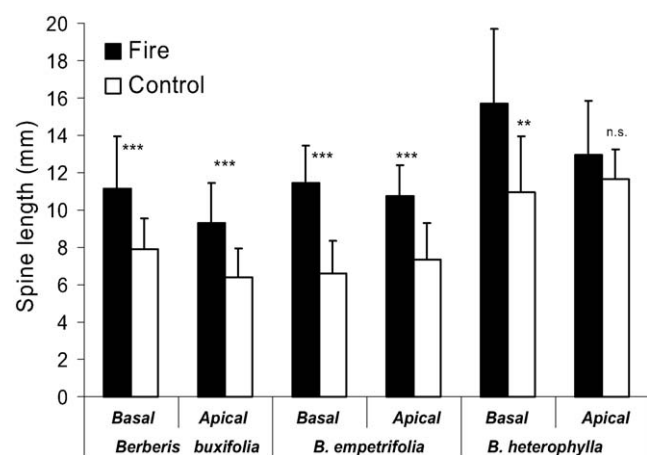
in the length of leaf tips exposed (Fig. 3), indicating that the leaves of all the studied species are more protected following fire. Apical leaves were significantly shorter than basal ones (Table 3), leaving a shorter tip not protected by the spine (Fig. 3).

We expected plants with no apical dominance (most shrubs and the studied *Berberis* species), to produce longer basal spines than apical ones because basal spines not only
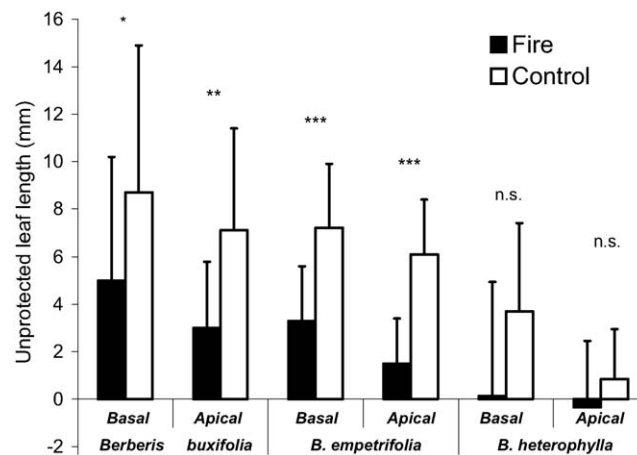

Fig. 2. Individuals of three species of *Berberis* produced significantly longer spines when resprouting after fire than in control areas. *P*-level for individual comparisons (Mann–Whitney test): * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Fig. 3. The increment in spine length following fire results in a significant reduction in unprotected leaf length. *P*-level for individual comparisons (Mann–Whitney test): *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

protect a larger portion of the shoot, but also the buds that will develop into future growing points. We found no support for this hypothesis (Table 3).

Fire induced spine production may be a common feature in semi-arid plant communities, where fire and herbivory are believed to interact in conditioning the dynamics of the plant community (Pellew, 1983; McNaughton, 1984; Mwalyosi, 1990; Skarpe, 1992; Prins et al., 1994). In these systems, where plants and plant parts exposed to herbivory usually respond to browsing by increments in spine length (Young, 1987; Milewski et al., 1991; Gowda and Palo, 2003; Young et al., 2003), studies on the interaction between fire, herbivores and resprouting plants may help us further in understanding the regulation of inducible defensive traits.

In Northern Patagonia, where spiny shrubs are a common feature, few browsing ungulates were living in the forest ecosystems before the colonization by Europeans (Redford and Eisenberg, 1992; Olrog and Lucero, 1980). Frequent fires along the ecotone between forests and steppe for hunting *Llama guanicoe, Hippocamelus bisulcus*, and rheas (Cox, 1863; Musters, 1871) may have maintained a very dynamic system, dominated by resprouting matorral and steppe communities. Post fire matorral communities are today the most favorable feeding habitat for *Hippocamelus bisulcus* (Alejandro Vila, pers. com.), while cattle, sheep, *Lamma guanicoe*, *Lepus timidus* and *Cervus elaphus* are attracted by post fire communities in the steppe.

During the past 100 years an increment in fire intervals, coupled with a displacement of native browsers by introduced mammalian grazers, has strongly influenced the dynamics of the plant community of the region (Kitzberger and Veblen, 1997; Veblen et al., 2003), making it difficult to assess the ecological importance of spines and other defensive of Northern Patagonia.

Acknowledgements

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