available at www.sciencedirect.com

ScienceDirect

journal homepage: www.elsevier.com/locate/biocon

Cattle affect early post-fire regeneration in a *Nothofagus dombeyi–Austrocedrus chilensis* mixed forest in northern Patagonia, Argentina

Melisa Blackhall[a,*], Estela Raffaele[a], Thomas T. Veblen[b]

[a]Laboratorio Ecotono, CRUB, Universidad Nacional del Comahue, Quintral 1250, 8400 Bariloche, Argentina
[b]Department of Geography, University of Colorado, Boulder, CO 80309, USA

ARTICLE INFO

Article history:
Received 18 October 2007
Received in revised form
5 June 2008
Accepted 24 June 2008
Available online 9 August 2008

Keywords:
Disturbance
Fire
Herbivory
Livestock
Nothofagus

ABSTRACT

In forest ecosystems where infrequent, severe fires have been an important process in shaping ecosystem structure, understanding the effects of introduced livestock on post-fire recovery of the vegetation is essential for effective forest resource management and preservation. In Nahuel Huapi National Park in northwestern Patagonia, we studied the effects of livestock on the post-fire recovery of a *Nothofagus dombeyi–Austrocedrus chilensis* forest that was burned in 1999. We experimentally excluded cattle by fencing plots and compared the vegetation characteristics of fenced and unfenced control plots over a 5-year period. Although cattle did not significantly reduce total plant cover or total species richness, they did reduce maximum heights of woody species including the dominant tree species. *Chusquea culeou*, a tall understory bamboo, can impede establishment and height growth of the dominant tree species. Although *C. culeou* accounts for the largest percentage of cattle diet, its mean cover and mean maximum height were not strongly affected by cattle. The reduction in the height growth of seedlings of *N. dombeyi* and *Austrocedrus* in the unfenced areas implies that presence of cattle in the recently burned areas may contribute to a post-fire transition from tall forest to bamboo-dominated shrubland that is already widespread in this landscape. Thus, these results provide support for the fencing of recently burned *Nothofagus* and *Austrocedrus* forests in the national parks for periods long enough to allow the dominant tree species to grow to heights at which they are no longer severely inhibited by cattle browsing.

1. Introduction

A major challenge in community ecology is improved understanding of species interactions in the context of fluctuating environmental conditions created by large, severe disturbances (Agrawal et al., 2007). In many ecosystems infrequent, broad-scale natural disturbances are important in driving ecological processes and patterns that persist for decades or centuries (Attiwill, 1994; Perera and Buse, 2004). It is widely recognized that in many temperate forests, severe fires occurring at intervals of many decades or centuries are key natural disturbances that trigger massive tree establishment and allow the development of long-lasting ecological structure. However, in widespread areas of temperate forests in the southern Andes of Argentina and Chile, the introduced large herbivores (livestock and deer) have potentially altered the

* Corresponding author: Tel.: +54 2944428505x503; fax: +54 2944428505.
E-mail addresses: meliblackhall@gmail.com (M. Blackhall), eraffael@crub.uncoma.edu.ar (E. Raffaele), veblen@colorado.edu (T.T. Veblen).
0006-3207/$ - see front matter
doi:10.1016/j.biocon.2008.06.016

early phases of plant community responses to wildfire in forested habitats (Ramirez et al., 1981; Veblen et al., 1989; Raffaele and Veblen, 2001). Although infrequent, severe fires may be an inherent process consistent with preservation of many native forest ecosystems, the effects of introduced animals on post-fire recovery patterns are often uncertain. Thus, where land management goals include preservation or restoration of native forest structures and processes, knowledge of how introduced animals may alter community response to infrequent, severe fires is critical.

In most terrestrial habitats worldwide, fire and large herbivores are major influences on the composition and structure of vegetation through their roles as consumers of plant material. Fire as an abiotic consumer and herbivores (e.g. large mammals) as biotic consumers may create negative feedbacks between these two disturbance types and/or may result in synergistic and more extreme influences on vegetation composition and structure (Bond, 2005). However, the nature of the interactions between these disturbance types and their consequences for plant community composition and structure are highly context specific (Bond, 2005; Agrawal et al., 2007).

In northwestern Patagonia (Argentina), two of the most important disturbances are fire (Kitzberger and Veblen, 1999; Veblen et al., 2003; Alauzis et al., 2004) and herbivory by large introduced mammals, such as livestock and red deer (Martín et al., 1985; Veblen et al., 1989, 1992a,b; De Pietri, 1995; Relva and Veblen, 1998, 2001; Vázquez, 2002). Fire, both natural and human-set, historically has played a major role in creating landscape patterns in northwestern Patagonia along the gradient from dry steppe to wet Andean rain forests (Veblen et al., 2003). The relative importance of fires set by Native Americans prior to European settlement in the late 19th century versus fires ignited by lightning, as well as the effects of fire exclusion during the 20th century, is highly variable according to ecosystem type and location along the gradient from steppe to Andean rainforests (Kitzberger et al., 1997; Veblen et al., 1999, 2003; Kitzberger and Veblen, 2003). The focus of the current study is on the *Nothofagus dombeyi*–*Austrocedrus chilensis* mixed forest type which occupies an intermediate position along the precipitation gradient from xeric Patagonian plains to the wet Andean cordillera. Most stands of *N. dombeyi*–*A. chilensis* originated after widespread fires during the 19th and early 20th centuries ignited either by humans or lightning and associated with exceptional drought (Kitzberger and Veblen, 2003; Veblen et al., 2003). However, following establishment of infrastructure for suppressing fires in the 1940s, the extent of burning in this forest type has been relatively small compared to the extent over the previous 150 years (Veblen et al., 2003).

Overlapping with the reduction of fire occurrence in these forests in the second half of the 20th century has been a major change in the use of the *N. dombeyi*–*A. chilensis* forest type by large mammalian herbivores. Native large mammals in this region include the guanaco (*Lama guanicoe*) and the huemul deer (*Hippocamelus bisulcus*) both of which are believed to have preferred open habitats of the steppe or the alpine timberline (Povilitis, 1978; Caviares and Fajardo, 2005) over dense forests of *N. dombeyi* and *Austrocedrus*. Among native ungulates, the miniature pudu deer (*Pudu pudu*) occurred in dense forests; however, it is not believed to have been abundant and probably did not have a major influence on forest structure (Vázquez, 2002). Thus, the introduction of cattle and several species of Eurasian deer (*Cervus elaphus*, *Dama dama* and *Axis axis*) and their abundance in dense forests, at least locally, is a major departure from the conditions under which the *N. dombeyi* and *A. chilensis*-dominated forests originated. Cattle were present in the steppe of northwestern Patagonia as early as the late 18th century, but were not abundant in forested areas until the phase of intensive European settlement and forest burning of the late 19th and early 20th century (Veblen and Lorenz, 1988). Eurasian deer were introduced as early as 1917 to create a game resource and by the 1940s they were abundant in some areas (Daciuk, 1978; Ramilo, 1985). A survey of the large area of Nahuel Huapi National Park (706,000 ha approximately) in northwestern Patagonia estimated that about 56% of the park's terrestrial surface is affected by cattle to some degree (Lauría Sorge and Romero, 1999). Studies conducted mostly during the 1980s and early 1990s have shown that cattle and cervids have greatly affected the vegetation of the northern Patagonia landscape, including *Nothofagus* and *Austrocedrus* forests (Martín et al., 1985; Veblen et al., 1989, 1992b; Relva and Veblen, 1998). This research has shown that heavy cattle pressure may locally impede or dwarf the regeneration of some arboreal species, shift dominance toward spiny shrubs, favor the abundance of introduced plants, and under some circumstances may shift community structure from tall forests to shrublands (Veblen et al., 1992b, 2003; Relva and Veblen, 1998; Kitzberger et al., 2005). Most studies have examined deer and livestock impacts on mature plant communities with relatively few studies focusing on the earliest and probably most critical stages of vegetation recovery following fire (but see Raffaele and Veblen, 2001).

The widespread occurrence of fires during the extreme drought of the late 1990s in forests in northwestern Patagonia (Administración de Parques Nacionales, 1999) provided a rare opportunity to examine the effects of introduced animals on patterns of early post-fire regeneration in the *N. dombeyi*–*A. chilensis* forest type. Our research presents the first experimental results on livestock browsing on early post-fire recovery in this forest type in northwestern Patagonia. Over a 5-year period, we studied the effects of cattle on post-fire vegetation by monitoring exclosures and control plots in a *N. dombeyi* and *Austrocedrus* mixed forest, situated in Nahuel Huapi National Park. The objective of this study is to determine how introduced cattle affect, directly and indirectly, the processes of early post-fire regeneration in a *N. dombeyi*–*Austrocedrus* mixed forest. Because both dominant tree species are obligate seeders that lack the ability to resprout vegetatively (Kitzberger and Veblen, 1999; Veblen et al., 2003), the post-fire recovery of this forest type may be particularly vulnerable to the effects of introduced cattle.

2. Methods

2.1. Study area

The study was conducted in a *N. dombeyi*–*A. chilensis* forest, located on the eastern side of Lago Espejo, in Nahuel Huapi

National Park, Argentina (40°38′S, 71°42′W; c. 850 m above sea level). Physiographically, this area is subdivided from west to east into the main Andean Cordillera, the precordillera foothills and glacial lakes, and the Patagonian plains. Pleistocene glaciers at this latitude retreated 12,000–13,000 years B.P. (Markgraf, 1983). Soils throughout the region are derived from volcanic ash, and in the area studied there are fine sandy loams that are at least 80 cm deep. At this latitude, mean annual precipitation declines steeply from west to east, from over 4000 mm in the Andes to <1000 mm in the Patagonian steppe (Barros et al., 1983). Along this precipitation gradient, mixed evergreen forests co-dominated by the angiosperm *N. dombeyi* and the conifer *A. chilensis* (mean annual precipitation c. 1500–2200 mm) occur at the elevation of the lakes and plains (i.e. at c. 800–850 m).

At the site studied, mean annual precipitation interpolated from nearby climate stations is approximately 2000 mm (Barros et al., 1983); it occurs mainly during autumn and winter months, and summer precipitation is scarce. Mean monthly temperatures range between 2.81 °C in July and 15.15 °C in January (mean, 1996–2006; Bariloche Aerodrome Station, unpublished data).

The unburned forest at our study site is dominated by *N. dombeyi* and *A. chilensis* reaching heights of 40 and 35 m, respectively. Dominant individuals of both species are 1–1.2 m diameter-at-breast height (dbh), and probably originated after the same severe fire in the early part of the 19th century that originated nearby stands (Veblen, 1989). The understory of the unburned forest is dominated by the 3–6 m tall bamboo *Chusquea culeou*. Other common species include the shrubs *Azara lanceolata*, *Desfontainia spinosa* and *Berberis* spp., and a great number of forb species. In the burned area, the shrubs *Aristotelia chilensis* and *Ribes magellanicum*, and the semi-woody climber *Vicia nigricans* are also abundant (Blackhall, 2006). Plant nomenclature follows Correa (1969–1984).

In January 1999, approximately 9 ha of this *N. dombeyi–Austrocedrus* forest was affected by an intense wildfire that killed all trees within the burned area (Administración de Parques Nacionales, 1999). Due to the proximity of the fire to a road, it was quickly suppressed before it could spread further. In this area, cattle are allowed to range freely over extensive areas, and based on our previous observations cattle have long been present at the site of the current study (Veblen et al., 1992b; Lauría Sorge and Romero, 1999).

2.2. Field sampling

In March 2002, eight 25 m × 25 m permanent plots were installed in the burned site to monitor post-fire vegetation changes. The eight plots were located in an area of homogeneous burn severity within the *N. dombeyi–Austrocedrus* forest. Four plots were randomly selected for fencing, while the others were left unfenced as control plots. The barbed-wire fences exclude cattle which is the principal large herbivore in the area. The fences do not exclude small herbivores including native rodents and introduced hare (*Lepus europaeus*). Although some feces of the introduced hare were observed at the study site, they were relatively uncommon in comparison with areas of non-forested vegetation (in the field, cattle and hare bite can easily be distinguished: cattle uproot the vegetal tissues, while hare cut the tissues, leaving bevel shaped apexes). The other introduced large herbivore that is common in some parts of Nahuel Huapi National Park is the red deer (*C. elaphus*), which was not present at the site studied.

In each plot a grid was used to systematically locate 20 permanent subplots of 2 m^2 each for recording vegetation parameters over 5 years in late summer (March, 2002–2006). Data recorded in each subplot were percent cover of all vascular plant species and maximum heights of all woody and climber species. In 2004–2006, the numbers of short tree seedlings (<5 cm tall, including the cotyledon stage), tall tree seedlings (5–200 cm tall), and tree saplings (>200 cm tall but <5 cm dbh) were also counted in each subplot. Seedlings in the cotyledon stage were only abundant during 2006. In each subplot, the degree of browsing by cattle was estimated by observing the number of browsed branches on each woody and climber species and by assigning a browse rating of 3 (heavy, most of the branches browsed), 2 (moderate, more than two branches browsed), 1 (light, one or two branches browsed) or 0 (none, no evidence of browsing) (following Rose and Burrows, 1985).

2.3. Data analyses

Dependent variables analyzed were mean cover (%) of all vascular plants; mean maximum height (cm) of all woody and climber species; mean maximum height (cm) of common woody and climber species; and mean species richness. For some analyses (e.g. comparison of mean cover), plants were grouped into four life-form groups: forbs, graminoids, woody species (including the bamboo *C. culeou*) and semi-woody climbers. To assess tree regeneration we considered mean covers, mean maximum heights and mean number of saplings and seedlings per plot for the two dominant arboreal species: *N. dombeyi* and *Austrocedrus*.

The combined effects of treatments (fenced and unfenced) and time (year, 2002–2006) were analyzed using repeated-measures ANOVA (Gurevitch and Chester, 1986). This test determines if differences between treatments in trends over time in the response variables are statistically significant. For selected variables, one way ANOVAs were performed for identifying statistically significant differences within the same year. Mean cover and mean maximum height of six common woody and climber species were evaluated, including *C. culeou*, *V. nigricans*, *Aristotelia chilensis*, *Berberis darwinii*, *R. magellanicum* and *Buddleja globosa*. Repeated-measures ANOVAs could only be performed for the most abundant species (present in almost all plots). An alternative analysis was used for species that despite their importance in the understory were not very frequent. For these less ubiquitous species, bootstrapped 95% and 99% confidence intervals of the mean differences between treatments (fenced and unfenced) were computed (Manly, 1997). All bootstrapped confidence intervals were estimated from 1000 to 5000 Monte Carlo simulations (i.e. 95% and 99% confidence intervals, respectively; Manly, 1997).

Due to low numbers of tree seedlings and saplings, bootstrapped 95% and 99% confidence intervals of the differences between treatment means (Manly, 1997) were computed to evaluate mean values of cover, maximum height and seedlings, and saplings number of both tree species (*N. dombeyi* and *Austrocedrus*). Means of fenced and unfenced plots were compared for each year (2002–2006). The combined effect of cattle and the indirect effect of the bamboo *C. culeou* on the mean number of seedlings and saplings of *N. dombeyi* in 2006 were tested by using *C. culeou* mean cover (%) as a covariable (Sokal and Rohlf, 1981). These ANCOVA were performed at the scale of the 2 m^2 subplots and compared with fenced and unfenced treatments ($n = 160$). ANCOVAs were performed at a different scale because the aim was to evaluate what was occurring with the establishment of cotyledons and seedlings of the tree species at the scale of microsite (subplot), and not at the scale of stand (plot; as the other variables under study). Cotyledons and seedlings of *N. dombeyi* occur in a patchy distribution and not in a homogeneous way, so, ecologically, cotyledons were studied at microsite scale, and for this purpose the cover of *C. culeou* was analyzed as a descriptor of the microsite conditions. Statistically, the experimental unit was changed because the sampling scale changed. A square-root transformation was applied to densities of seedlings and saplings (Sokal and Rohlf, 1981) to improve homogeneity of variance. *N. dombeyi* seedlings in the cotyledon stage were abundant in only a single year (2006), and consequently they were analyzed separately from category “short seedlings.” ANCOVA was not performed for *Austrocedrus* due to the small numbers of seedlings and saplings of this species. Normality of residuals of all variables was evaluated using Shapiro–Wilk’s test (Shapiro and Wilk, 1965), and homogeneity of variances was analyzed with Levene’s test (Sokal and Rohlf, 1981).

Browsing rates were used to compute the following indices (Rose and Burrows, 1985; Veblen et al., 1989, 1992b):

1. Browse index (BI): estimate of the total amount of browsing on a species in the area sampled. $BI = \sum(\text{browse ratings})$.
2. Percentage total browse (%TB): amount of browsing on a species as a proportion of total browsing on all species in the area sampled. $\%TB = 100\ BI/\sum(\text{BI of all species})$.
3. Browse pressure index (BPI): measure of the degree of browsing on a species in relation to the abundance of that species. $BPI = BI/n$, where n is the number of plots in which a species is present.
4. Mean browse index (MBI): summary statistic indicating the intensity of browsing on all species in the area sampled. $MBI = \sum(\text{BI for all species})/N$, where N is the total number of plots in the area.

3. Results

3.1. Cattle effects on post-fire community structure

In 2002, 3 years after the fire, mean cover of all vascular plants was 32.7% ± 3.9 SE in unfenced plots and 31.4% ± 1.2 SE in fenced plots (Table 1). By 2006, 7 years after the fire, plant cover reached 123.6% ± 6.2 SE and 126% ± 3.8 SE in unfenced and fenced plots, respectively. Cattle did not significantly affect mean cover of all vascular plants over time (Cattle × Time: $F_{4,24} = 1.40$, $p = 0.26$).

Among the four life-form classes, forbs and woody species accounted for most of the plant cover during the 5 years of the experiment (2002–2006). Mean cover of forbs in 2002 was 13.2% ± 2.3 SE and 16.6% ± 1.0 SE in unfenced and fenced plots, respectively; in 2006 these values reached 37.6% ± 1.9 SE and 36.4% ± 2.3 SE (Table 1). Mean cover of all woody species at the beginning of the experiment was similar to forbs: 16.7% ± 1.1 SE in unfenced plots and 11.7% ± 0.9 SE in fenced plots (Table 1). However, mean cover of woody species in 2006 was higher than forbs percentages: 57.7% ± 2.8 SE in unfenced plots and 56.6% ± 4.1 SE in fenced plots. Cattle did not significantly affect the mean cover of any life-form group over the full period of the experiment (C × T, forbs: $F_{4,24} = 1.04$, $p = 0.40$; graminoids: $F_{4,24} = 2.06$, $p = 0.12$; woody species: $F_{4,24} = 1.04$, $p = 0.41$; climber species: $F_{4,24} = 2.31$, $p = 0.09$). Nevertheless, mean cover of climber species in 2004 was significantly higher in fenced plots than in unfenced ones (C: $F_{1,6} = 10.02$, $p = 0.019$). Also during 2004 the highest cattle impact was recorded.

Cattle did not significantly affect the mean number of species over the time of the experiment (2002–2006; C × T: $F_{4,24} = 1.66$, $p = 0.19$). Richness values ranged from 21.5 ± 2.5 SE species 2 m^{-2} and 21.2 ± 0.3 SE species 2 m^{-2} in unfenced and fenced plots, respectively, in 2002 to 32.5 ± 1.3 SE species 2 m^{-2} and 27.3 ± 2.7 SE species 2 m^{-2} in unfenced and fenced plots, respectively, in 2006 (Table 2). In 2006, the majority of the species recorded were forbs (17.0 ± 2.2 SE species 2 m^{-2} in unfenced plots and 14.5 ± 1.2 SE species 2 m^{-2} in fenced plots) and woody species (7.5 ± 0.3 SE species 2 m^{-2} in unfenced plots and 7.0 ± 1.5 SE species 2 m^{-2} in fenced plots) (Table 2). Cattle did not significantly affect mean richness of life-form groups over time (C × T, forbs: $F_{4,24} = 1.07$, $p = 0.39$; graminoids: $F_{4,24} = 1.81$, $p = 0.16$; woody species: $F_{4,24} = 0.09$, $p = 0.98$; climber species: $F_{4,24} = 0.27$, $p = 0.84$).

3.2. Cattle effects on woody and climber species post-fire regeneration

Cattle significantly affected the mean maximum height of all woody and climber species as shown by the greater mean heights in fenced plots in the year 2006 (C: $F_{1,6} = 8.22$, $p = 0.03$) and the trend over the period of the experiment (C × T: $F_{4,24} = 5.34$, $p = 0.003$; Fig. 1). In contrast, at the beginning of the experiment, in 2002, there were almost no differences in mean maximum heights of woody and climber species between unfenced and fenced plots (4.4% more height in fenced than in unfenced plots; C: $F_{1,6} = 0.07$, $p = 0.80$). In 2004, the year of the greatest cattle impact, the mean maximum heights in fenced plots were almost twofold greater than the mean maximum height in unfenced plots (73.2% higher in fenced than in unfenced plots; C: $F_{1,6} = 11.91$, $p = 0.01$).

Among woody and climber species, the only species sufficiently abundant to allow analyses of trends over time in mean cover and height using repeated-measures ANOVAs were *C. culeou*, *V. nigricans* and *Aristotelia chilensis*. Other species were not abundant or in some cases were not present

Table 1 – Mean total cover (%) and by life-form class (forbs, graminoids, woody and climber species) ± 1 SE, in unfenced and fenced plots, from 2002 to 2006

Cover	Treatment	2002		2003		2004		2005		2006	
		Mean	±SE	Mean	±SE	Mean	±SE	Mean	±SE	Mean	±SE
Mean total cover	Unfenced	32.70	3.94	108.36	14.32	85.85	9.47	97.84	15.11	123.59	6.24
	Fenced	31.37	1.26	106.93	6.56	124.64	14.36	105.98	19.43	125.97	3.86
Life-form:											
Forbs	Unfenced	13.23	2.29	44.66	7.47	25.74	4.64	29.42	6.50	37.63	1.96
	Fenced	16.65	1.01	42.56	1.91	40.15	6.50	34.23	6.63	36.42	2.27
Graminoids	Unfenced	0.29	0.15	14.60	2.95	11.71	1.17	15.77	3.03	14.46	1.56
	Fenced	1.29	0.37	25.40	5.85	23.96	7.16	15.22	6.02	13.92	5.46
Woody species	Unfenced	16.71	1.13	38.97	3.46	44.02	2.45	43.91	5.64	57.69	2.76
	Fenced	11.66	0.93	28.90	4.00	46.65	3.89	41.80	5.67	56.55	4.11
Climber species	Unfenced	2.46	1.45	10.13	5.05	4.38	2.38	7.75	3.32	13.82	4.70
	Fenced	1.78	0.00	10.06	1.37	13.88	1.83	14.73	3.74	19.07	3.69

Table 2 – Mean total species richness (2 m^{-2}) and by life-form class (forbs, graminoids, woody and climber species) ± 1 SE, in unfenced and fenced plots, from 2002 to 2006

Richness (2 m^{-2})	Treatment	2002		2003		2004		2005		2006	
		Mean	±SE	Mean	±SE	Mean	±SE	Mean	±SE	Mean	±SE
Mean total richness	Unfenced	21.50	2.53	27.25	2.75	25.25	2.69	26.50	3.50	32.50	1.32
	Fenced	24.25	0.25	26.00	1.22	26.75	2.25	25.50	1.04	27.25	2.56
Life-form:											
Forbs	Unfenced	9.75	1.49	15.50	2.66	13.25	2.78	14.75	2.02	17.00	2.16
	Fenced	12.50	1.26	14.50	1.55	13.75	1.25	13.50	0.29	14.50	1.19
Graminoids	Unfenced	3.75	0.48	4.00	0.58	4.00	0.00	4.00	1.22	7.00	0.82
	Fenced	3.50	0.50	3.75	0.25	4.50	0.87	4.25	0.63	4.75	0.63
Woody species	Unfenced	7.00	0.82	6.75	0.48	7.00	0.71	6.75	0.48	7.50	0.29
	Fenced	6.75	1.11	6.50	0.96	7.00	1.29	6.25	1.25	7.00	1.47
Climber species	Unfenced	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00
	Fenced	1.50	0.29	1.25	0.25	1.50	0.29	1.50	0.29	1.00	0.00

in all plots. Cattle did not significantly affect the mean covers of *C. culeou*, *V. nigricans* or *Aristotelia chilensis* over the time from 2002 to 2006 (C × T, *C. culeou*: $F_{4,24} = 0.81$, $p = 0.53$; *V. nigricans*: $F_{4,24} = 2.39$, $p = 0.08$; *Aristotelia chilensis*: $F_{4,24} = 1.81$, $p = 0.16$). However, in 2004 and 2005 the mean cover of *V. nigricans* was higher in fenced plots than in unfenced ones ($p < 0.01$). A similar situation occurred for *R. magellanicum*, the mean cover of which in 2004 and in 2006 was higher in fenced plots than in the unfenced plots ($p < 0.05$). For the other species (*Aristotelia chilensis*, *C. culeou*, *B. darwinii* and *B. globosa*), differences in mean cover between treatments were not observed for any year (2002–2006).

The mean maximum height of *C. culeou* was higher in fenced than in unfenced plots in 2004–2006 ($p < 0.05$; Fig. 1), but significant differences between treatments were not evident for the full period of the experiment (C × T: $F_{4,24} = 1.44$, $p = 0.25$). Cattle significantly affected the mean maximum heights at the end of the experiment of *V. nigricans* and *Aristotelia chilensis* (*V. nigricans*: C: $F_{1,24} = 12.27$, $p = 0.012$; *Aristotelia chilensis*: C: $F_{1,24} = 13.68$, $p = 0.01$) and over time (*V. nigricans*: C × T: $F_{4,24} = 5.05$, $p = 0.004$; *Aristotelia chilensis*: C × T: $F_{4,24} = 6.84$, $p = 0.0008$; Fig. 1). Particularly in 2004, 2005 and 2006, the mean maximum height was higher in fenced than in unfenced plots ($p < 0.01$) for both species and also in 2003 for *V. nigricans* ($p < 0.05$). In 2004, the year of the highest cattle impact, the mean maximum height of *Aristotelia chilensis* in fenced plots was almost threefold greater than that in unfenced plots (176% higher in fenced than in unfenced plots; Fig. 1). Similarly, in the same year, the mean maximum height measured on *V. nigricans* was more than twofold greater in fenced plots than in unfenced ones (132% higher in fenced than in unfenced plots; Fig. 1). The mean maximum height of *B. globosa* was significantly greater in fenced plots from 2003 to 2006 (2003: $p < 0.05$; 2004–2006: $p < 0.01$; Fig. 1) than in unfenced plots. Overall, the mean maximum height of *B. globosa* and *Aristotelia chilensis* was the most affected by cattle among the woody species.

Cattle did not significantly affect the mean maximum heights of the broad-leaved shrub *R. magellanicum* or of the spiny shrub *B. darwinii* (2002–2006: $p < 0.05$; Fig. 1). Few *R.*

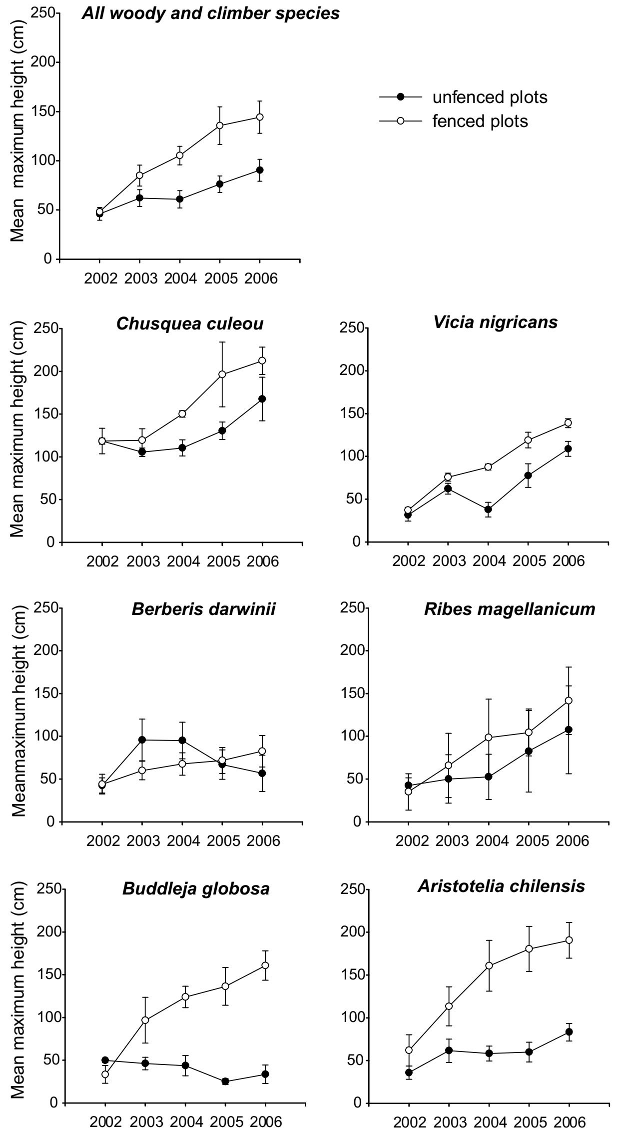

Fig. 1 – Mean maximum height (cm) ± 1 SE of all woody and climber species, and the six most common woody and climber species in unfenced and fenced plots over time (2002–2006).

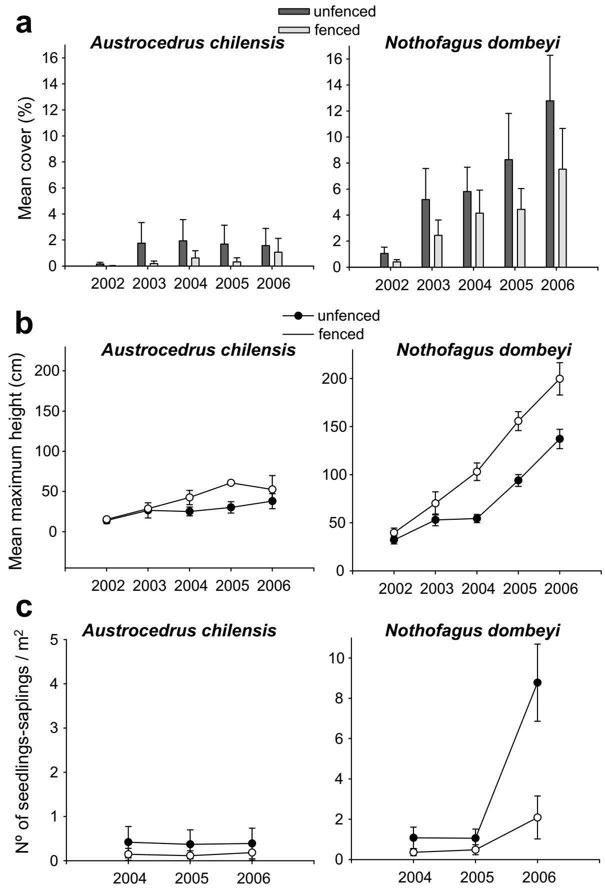

Fig. 2 – (a) Mean cover (%) ± 1 SE, (b) mean maximum height (cm) ± 1 SE and (c) mean number of seedlings and saplings (/m^2) ± 1 SE of *Austrocedrus* and *N. dombeyi* in unfenced and fenced plots over time (2002–2006).

magellanicum saplings were found in unfenced plots, and most of them were located in almost inaccessible sites for cattle (mostly between deadwood forming natural refugia).

3.3. *Cattle effects on regeneration of tree and bamboo species*

Mean cover of *N. dombeyi* was not influenced by cattle over the period from 2002 to 2006 (C × T: $F_{4,24} = 0.87$, $p = 0.49$), but a significant difference in mean cover was detected in 2003 ($p < 0.05$), 2005 ($p < 0.05$) and in 2006 ($p < 0.01$). In these 3 years, mean cover was unexpectedly higher in unfenced than in fenced plots (Fig. 2a). In contrast, mean maximum height of *N. dombeyi* was lower in unfenced plots when the full experimental period was considered (C × T: $F_{4,24} = 6.8$, $p = 0.0008$; Fig. 2b). Individual years for which the mean maximum height of *N. dombeyi* was higher in fenced than in unfenced plots included 2004–2006 ($p < 0.01$).

The mean number of seedlings and saplings of *N. dombeyi* was also affected by cattle (C: $F_{1,12} = 6.95$, $p = 0.04$) and over time (C × T: $F_{2,12} = 10.43$, $p = 0.002$; Fig. 2c). Each year (2004–2006), the mean number of seedlings and saplings was greater in unfenced than in fenced plots ($p < 0.01$). In 2006, on average, 8.8 saplings and seedlings/m^2 in unfenced plots and 2.1 saplings and seedlings/m^2 in fenced plots were recorded. However, more than 70% of these seedlings and saplings were cotyledon seedlings, recording 7.7/m^2 and 1.5/m^2 cotyledons in unfenced and fenced plots, respectively. This increment of seedlings in the last year indicates a new *N. dombeyi* seedling bank.

In general, mean cover, mean maximum height and mean number of seedlings and saplings were considerably greater for *N. dombeyi* than for *Austrocedrus* (Fig. 2). Abundance and cover parameters for *Austrocedrus* were not analyzed with repeated-measures ANOVAs because this species was not present in all plots. However, bootstrapped analysis showed that the mean cover of *Austrocedrus* was significantly greater in unfenced than in fenced plots from 2003 to 2005 (2003 and 2005: $p < 0.01$; 2004: $p < 0.05$; Fig. 2a). Cattle significantly affected the mean maximum height of *Austrocedrus*; from 2004 to 2006 the mean maximum height was greater in fenced than in unfenced plots ($p < 0.01$; Fig. 2b). In 2005, the mean maximum height of seedlings and saplings in fenced plots was twofold greater than that in unfenced plots (100.7% higher in fenced than in unfenced plots). And finally, from 2004 to 2006, the mean number of seedlings and saplings of *Austrocedrus* was higher in unfenced than in fenced plots ($p < 0.05$; Fig. 2c). In 2006, on average, 0.4 saplings and seedlings/m^2 in unfenced plots and 0.2 saplings and seedlings/m^2 in fenced plots were recorded.

There is a negative relationship between the density of *N. dombeyi* juveniles and the cover of bamboo (*C. culeou*) as shown by linear regression. In 2006, a significant negative regression ($F_{1,157} = 16.82$, $p = 0.00006$) of the bamboo mean cover (*X*) on the number of *N. dombeyi* seedlings and saplings (*Y*), at the scale of 2 m^2 subplots, was recorded (Fig. 3a). ANCOVA results evidenced a significant effect of cattle on the number of seedlings and saplings of *N. dombeyi* corrected for the effect of *C. culeou* mean cover, as a covariable ($F_{1,157} = 8.59$, $p = 0.004$). These results also showed a higher number of *N. dombeyi* seedlings and saplings in unfenced than in fenced plots (Fig. 3a). On the other hand, in 2006 the number of cotyledons of *N. dombeyi* was significantly affected by the interaction of herbivory and *C. culeou* mean cover (C × *C. culeou* mean cover: $F_{1,156} = 4.15$, $p = 0.043$; Fig. 3b). At a low mean cover of *C. culeou*, the number of cotyledons was higher in unfenced than in fenced plots; while at a high mean cover of *C. culeou*, the number of cotyledons was fewer, and similar in both types of treatments. Given that the relationship between 2006 cotyledons of *N. dombeyi* and mean cover of *C. culeou* in fenced and unfenced plots was not parallel (test of homogeneity of slopes model; Mead, 1994), it was not possible to evaluate the covariable-corrected main effects of herbivory.

3.4. *Browsing patterns*

The highest cattle impact was recorded for 2004 (mean browse index (MBI) = 4.7; Table 3). The species that provided the largest percentages of the diet of browsing animals were *C. culeou*, *N. dombeyi*, *Aristotelia chilensis*, *V. nigricans* and *Austrocedrus* (Table 3). Despite the fact that *C. culeou* was the main woody food species in the study area (mean percentage of total browse (%TB) for the 3 years = 30.1), it was not the most heavily browsed species in relation to its availability; moreover, its large %TB was directly related to its great percentage.

On the other hand, the two tree species, *N. dombeyi* and *Austrocedrus*, were moderately to heavily browsed in relation to their abundance. Although these species did not have high cover values, they accounted for high percentages of TB (Table 3). *Aristotelia chilensis* was the species that presented the highest %TB in relation to its cover. Together with *R. magellanicum*, browse pressure indexes (BPI) of *Aristotelia chilensis* were the highest. BPI of *Aristotelia chilensis* remained similar over the period from 2004 to 2006 in contrast to the declining pattern for other species as shown by the lower MBI in 2006. Other species such as *B. darwinii* and *Solanum brevidens* showed light or no evidence of browsing, especially after the MBI decreased.

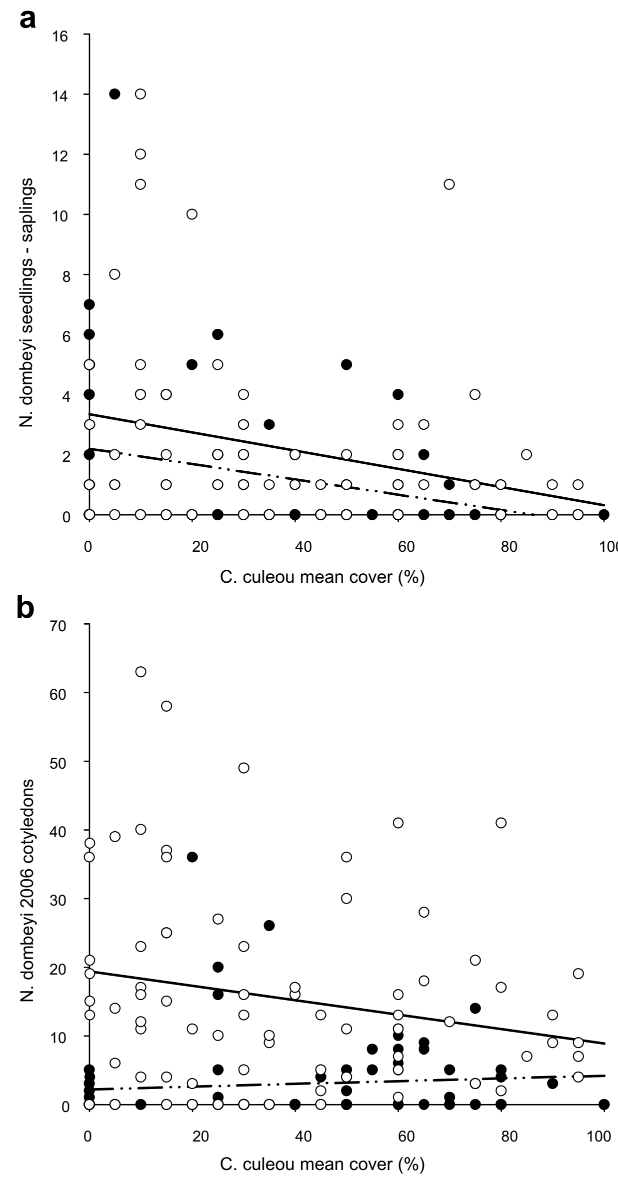

Fig. 3 – Plots of (a) numbers of seedlings and saplings (excluding cotyledons) versus mean cover of *C. culeou* in 2006 and (b) numbers of cotyledons of *N. dombeyi* in 2006 versus mean cover of *C. culeou*. Regression lines are shown for fenced (solid circles/dashed line) and unfenced (empty circles/solid line) micro-plots.

4. Discussion

4.1. *Cattle effects on post-fire community structure*

Experimental exclosure of cattle from 2002 to 2006 revealed that in general, following the burning of this *N. dombeyi*–*Austrocedrus* forest in 1999, heights of shrubs and juveniles of the dominant tree species were significantly affected by livestock. Nevertheless, mean cover and mean number of vascular plant species were not altered by cattle. However, when different life-form groups were considered, it was evident that climber species were vulnerable to cattle-induced

Table 3 – Mean cover, percentage of total browse (%TB) and browse pressure index (BPI) of woody and climber species from 2004 to 2006

Species	2004			2005			2006		
	Cover	%TB	BPI	Cover	%TB	BPI	Cover	%TB	BPI
Austrocedrus chilensis	4.01	8.82	1.57	3.28	11.37	1.95	2.20	8.33	0.73
Nothofagus dombeyi	12.01	24.33	1.69	15.99	22.16	1.49	17.88	13.02	0.34
Aristotelia chilensis	5.18	15.51	2.07	4.73	21.28	2.61	4.55	33.85	2.10
Berberis darwinii	0.91	1.34	1.00	0.97	0.29	0.20	0.96	0.00	0.00
Buddleja globosa	0.91	3.74	2.33	0.12	0.58	1.00	0.53	1.04	0.25
Chusquea culeou	66.64	31.55	1.66	58.81	30.61	1.42	53.41	28.13	0.69
Ribes magellanicum	0.13	1.07	2.00	0.12	1.46	2.50	0.18	1.04	0.67
Solanum brevidens	0.65	1.34	1.00	0.49	0.00	0.00	0.35	0.00	0.00
Vicia nigricans	9.04	10.96	1.46	15.00	11.66	1.38	19.33	14.06	0.50
MBI		4.67			4.29			2.40	

Mean browse index (MBI) is indicated for each year (2004–2006). Species with frequencies not >2.5% for each of the 3 years are not shown. For definitions of %TB, BPI and MBI see the text.

reductions in abundance and cover. Yet, the vulnerability of the climber life-form varied with the degree of cattle pressure. Cattle pressure in the year of peak browsing (2004) strongly reduced the mean cover of climber species, but during the years of less browsing pressure there were no significant reductions in the mean cover of this life-form. Despite the strong effect in 2004, no subsequent effects of cattle on the mean cover of climbers were evident because these are annual species. Similarly, in a nearby study of cattle impacts on a recently burned tall shrubland, abundance and cover of climber species were significantly reduced by heavy browsing (Raffaele and Veblen, 2001).

Our results did not show a significant influence of cattle on total species richness in this recently burned forest. Over this 5-year study, the mean number of species remained similar between fenced and unfenced burned sites, suggesting that cattle do not affect species richness at these sites. In contrast with our results, studies in other ecosystem types have shown large differences in species richness in relation to livestock pressure. For example, grazing increased species richness in seasonally flooded grasslands in the pampas of Argentina (Rusch and Oesterheld, 1997), in German-managed grasslands (Klimek et al., 2007), in grazed pastures of southwest Sweden (Gustavsson et al., 2007), and in short-grass prairies in Oklahoma, USA (Collins, 1987), where species richness increased with increasing intensity of disturbance by fire and grazing. Overall, our results showed no differences in the number of vascular plant species between fenced and unfenced plots. However, the number of species in the burned area was greater than those in the unburned *N. dombeyi*–*Austrocedrus* forest that was also subject to browsing and grazing by livestock (Blackhall, 2006). Thus, as expected, severe disturbance by fire appears to increase species richness.

4.2. *Cattle effects on post-fire regeneration of woody shrubs and climber species*

The variable that showed the greatest differences between fencing treatments and controls was mean maximum height for woody and climber species. The mean maximum height for almost all woody and climber species was significantly higher inside the exclosures than in unfenced plots. In addition, many woody species were strongly affected by cattle browsing (e.g. *Aristotelia chilensis*, *B. globosa*, and *N. dombeyi*). Analogous to other studies conducted in *N. dombeyi*–*Austrocedrus* forests in Patagonia and in *Nothofagus* forests in New Zealand, the most severe impacts of introduced mammals (deer) were on subcanopy tree and shrub species (Veblen and Stewart, 1982; Veblen et al., 1989).

Under cattle pressure, each woody species presented a particular response. During the years with highest MBI, the mean cover of *R. magellanicum* was reduced by cattle, while its mean maximum height was not affected. Although *R. magellanicum* plants showed evidence of browsing, most of these plants, particularly in unfenced plots, were situated in piles of fallen trees that were almost inaccessible to livestock. A similar observation has been made for the highly palatable *Aristotelia chilensis* under deer pressure in the nearby *N. dombeyi* forests and *Austrocedrus* forests (Barrios García Moar, 2005; López Westernholm and Relva, 2005). It has been reported in *Pinus* spp. forests in Sweden, that dead woody aggregations formed after fire and windthrow can work as physical and visual obstructions, allowing seedlings and saplings to grow in an area relatively free of browsing (de Chantal and Granström, 2007). Similar results were found for Aspen (*Populus tremuloides*) after 1988 fires in Yellowstone National Park, Wyoming, USA, where post-fire coarse woody debris created “safe zones” free of elk browsing (Turner et al., 2003).

Cattle did not affect either the mean cover or mean maximum height of *B. darwinii*. Browsing patterns indicated that *B. darwinii*, together with *S. brevidens*, were not preferred by cattle, since they presented scarcely any browsing when MBI decreased. It is known that species from these two taxonomic families, Berberidaceae and Solanaceae, present either physical or chemical defenses against herbivores (Gowda and Raffaele, 2004; Cipollini and Levey, 1997).

Field observations suggest that *Aristotelia chilensis* was one of the most affected woody species under cattle pressure. The BPI of this palatable subcanopy tree was high, including in 2006, when all the other species presented light or no evidence of browsing. The relative decline in browsing in 2006 probably reflects post-fire recovery of the vegetation to the degree that it physically impeded access by cattle. Other studies in northwest Patagonian forests have also recorded high herbivore pressure on *Aristotelia chilensis*, mainly due to exotic deer and domestic cattle (Veblen et al., 1989; Veblen et al., 1992b). Furthermore, it has been noted that in *N. dombeyi* and *Austrocedrus* forests under heavy deer pressure, this palatable species grows mainly inside natural refugia (e.g. deadwood aggregations) (Barrios García Moar, 2005).

Despite the fact that the bamboo *C. culeou* was the species that provided the largest percentage of the diet of browsing animals (%TB), its mean cover and its mean maximum height over time were not strongly affected by cattle. Similarly, its BPI showed only moderate to light browsing. All these results imply that *C. culeou* is an essential species in cattle diet, but it is not preferred as other woody species that evidenced higher BPI values and lower %TB (e.g. *Aristotelia chilensis*, *R. magellanicum*, *N. dombeyi*, and *Austrocedrus*). It is well known that *Chusquea* bamboos are keystone species in southern Chilean and Argentinean temperate forests, principally due to their dominance in forest understories, their importance as fuels and their ability to inhibit tree regeneration and other woody species (Veblen, 1982, 2003; Pearson et al., 1994; González et al., 2002; Raffaele et al., 2007). In this study, the relatively moderate impact of livestock on the cover and height of *C. culeou* implies that it will continue to play an inhibitory role on tree regeneration following fire when the site is exposed to livestock grazing and browsing.

4.3. Cattle effects on regeneration of dominant tree species and bamboos

In general, the mean cover of *N. dombeyi* and *Austrocedrus* seedlings and saplings was higher outside exclosures than inside them. However, field observations indicated that cattle browsing turned saplings and seedlings into dwarfed and misshapen trees. This is also reflected in the lower mean maximum heights of both species in unfenced than in fenced plots. Similar results were found in the previous studies, which evaluated exotic deer and livestock effects on tree regeneration in *N. dombeyi* and *Austrocedrus* forests (Veblen et al., 1989; Relva and Veblen, 1998). In this study, *N. dombeyi* seedlings and saplings grew substantially in height in 2003 and 2004 in fenced but not in unfenced plots. These results are consistent with browsing indexes showing the highest values in 2004. A reduction in browsing impact could release vegetation growth, as was recorded in the field (e.g. *N. dombeyi*, *V. nigricans*, and *R. magellanicum*; see periods 2004–2005).

Numbers of seedlings and saplings of both *N. dombeyi* and *Austrocedrus* were unexpectedly greater in unfenced than in fenced plots. Potentially, reduced competition from highly palatable woody species in unfenced areas indirectly resulted in increased seedling establishment of the two dominant tree species. By increasing the area of bare mineral soil and reducing the shade produced by palatable understory plants, cattle may improve conditions for tree seedlings establishment. Similar results have been recorded for *N. dombeyi* under deer impact, where near elimination of the subcanopy tree *Aristotelia chilensis* by deer browsing benefited *N. dombeyi* seedlings establishment (Veblen et al., 1989). Likewise, Tercero-Bucardo et al. (2007) recorded in more xeric post-fire forests than in our study area a higher rate of survival of *N. dombeyi* and *Austrocedrus* seedlings under livestock impact than without it over a 2-year period.

A probable explanation for the association of higher tree seedling densities with livestock presence is the indirect effects of cattle mediated through their reduction in the understory dominance by the bamboo *C. culeou*. *Chusquea* bamboos can impede the regeneration of shade-intolerant species, such as *Nothofagus*, that dominate most of the forests in Patagonia and the southern Andes (Veblen, 1982; González et al., 2002; Raffaele et al., 2007). In our study, it is likely that the competitive influences of *C. culeou* on tree seedling abundance in areas free of cattle outweigh the inhibitory effects of cattle on tree seedling establishment. Similarly, Raffaele et al. (2007) found, in a *N. dombeyi* forest where a massive die-off of *C. culeou* had occurred, that tree seedlings were considerably more heavily browsed in the absence of live bamboo. On the other hand, *C. culeou*, as a rapidly growing resprouter capable of forming a dense understory cover, may impede the growth of *Nothofagus* seedlings through shading and perhaps inhibit new seedling establishment by creating a deep and continuous litter layer (Veblen, 1982; González et al., 2002). Thus, at sites of recently burned forests of both obligate seeders, *N. dombeyi* and *Austrocedrus*, regenerating populations of *C. culeou* can have complex, both positive and negative, effects on tree regeneration that are contingent upon the intensity of herbivory from cattle and time since the fire. Inhibition of the development of a dense bamboo cover and exposure of bare mineral soil under heavy cattle pressure may be favorable for initial establishment of seedlings of the dominant tree species as appears to be the case in this study. However, lower height growth rates of seedlings and saplings in our unfenced plots imply that the probability of tree juveniles attaining the main canopy is low due to inhibition by both cattle and bamboo. Similar results were found in conifer forests in the Bhutan Himalayas, where a bamboo species (*Yushania microphylla*) apparently reduced the maximum possible recruitment of conifer seedlings on the forest floor, mainly due to light availability (Darabant et al., 2007). Nevertheless, despite the large number of seedlings established outside the exclosures, continual cattle browsing impeded the recruitment of these small seedlings into larger size-classes, similar to the findings of this study.

5. Concluding remarks

Our experimental results clearly show that cattle affect early post-fire regeneration of a *N. dombeyi–Austrocedrus* mixed forest. Continuous browsing in recently burned areas, particularly for a long period, may lengthen the time required for tall tree species to regain dominance and potentially can shift dominance towards shrub and bamboo species. Thus, this synergism between introduced livestock and fire in mesic *N. dombeyi–Austrocedrus* mixed forests may result in the development and maintenance of shrublands dominated by the bamboo *C. culeou*. Such bamboo-dominated shrublands are common in the mesic tall forest district of the northwestern Patagonia and potentially may have originated from the burning of tall forests followed by prolonged, intensive pressure from livestock.

Although both dominant tree species were negatively affected by cattle, the regeneration of *Austrocedrus* may be more vulnerable than that of *N. dombeyi*. In the rainfall range represented by our study, the height and diameter growth of *Austrocedrus* is substantially less than that of *N. dombeyi*, and at post-fire sites *Austrocedrus* is typically represented by smaller numbers of seedlings (Veblen and Lorenz, 1987). Due to its smaller population of seedlings and slower growth rates, *Austrocedrus* is less likely to successfully attain canopy tree size than its more prolific and rapidly growing associate, *N. dombeyi*. Clearly, the greater the size and intensity of the burn and the greater the subsequent pressure from livestock, the slower the recovery will be to a forest dominated by these two species. In general in the national park studied, the overall management objective following fire is to assure that exotic herbivores do not impede tree regeneration and recovery of the vegetation to its pre-burn species composition. Thus, the results of this study and other studies provide support for the exclusion of cattle from the recently burned *Nothofagus* and *Austrocedrus* forests in the national parks for periods long enough to allow the dominant tree species to grow to heights at which they are no longer severely inhibited by cattle browsing.

Acknowledgements

This study was supported by the National Science Foundation of the USA (Award 0117366), the National Geographic Society (Grant 7155-01), the Universidad Nacional del Comahue (B103), and UNC-PICT (Grant 01-07320). For field assistance we thank N. Tercero, J. Paritsis, and numerous others. For critically commenting on the manuscript we thank M. Albright and J. Paritsis. We also thank the Administración de Parques Nacionales for permission to perform the research. MB is a CONICET doctoral fellow and ER is a researcher for CONICET (Consejo Nacional de Investigaciones Científicas y Tecnológicas, Argentina).

REFERENCES

Administración de Parques Nacionales, 1999. Informe sobre las consecuencias ecológicas de los incendios forestales – Temporada 1998–1999. Parque Nacional Nahuel Huapi. Unpublished Report, San Carlos de Bariloche, Argentina.

Agrawal, A.A., Ackerly, D.D., Adler, F., Arnold, A.E., Cáceres, C., Doak, D.F., Post, E., Hudson, P.J., Maron, J., Mooney, K.A., Power, M., Schemske, D., Stachowicz, J., Strauss, S., Turner, M.G., Werner, E., 2007. Filling key gaps in population and community ecology. Frontiers in Ecology and the Environment 5, 145–152.

Alauzis, M.V., Mazzarino, M.J., Raffaele, E., Roselli, L., 2004. Wildfires in NW Patagonia: long-term effects on a *Nothofagus* forest soil. Forest Ecology and Management 192, 131–142.

Attiwill, P.J., 1994. The disturbance of forest ecosystems: the ecological basis for conservation and Management. Forest Ecology and Management 63, 247–300.

Barrios García Moar, N., 2005. Patrones de daño, uso actual y tendencia histórica de la abundancia de ciervos introducidos en bosques nativos de la Isla Victoria, Patagonia, Argentina. Unpublished Licenciatura Thesis, Centro Regional Universitario Bariloche, Universidad Nacional del Comahue, Bariloche, Río Negro, Argentina.

Barros, V., Cordon, V., Moyano, C., Mendez, R., Forquera, J., Pizzio, O., 1983. Cartas de precipitación de la Zona Oeste de las Provincias de Río Negro y Neuquén, Primera Contribución. Facultad de Ciencias Agrarias, Universidad Nacional del Comahue, Cinco Saltos.

Blackhall, M., 2006. Efecto del ganado sobre la regeneración temprana post-fuego de un bosque mixto de *Nothofagus dombeyi* y *Austrocedrus chilensis*. Unpublished Licenciatura Thesis, Centro Regional Universitario Bariloche, Universidad Nacional del Comahue, Bariloche, Río Negro, Argentina.

Bond, W.J., 2005. Large parts of the world are brown or black: a different view on the "Green World" hypothesis. Journal of Vegetation Science 16, 261–266.

Caviares, L.A., Fajardo, A., 2005. Browsing by guanaco (*Lama guanicoe*) on *Nothofagus* pumilio forest gaps in Tierra del Fuego, Chile. Forest Ecology and Management 204, 237–248.

Cipollini, M.L., Levey, D.J., 1997. Why are some fruits toxic? Glycoalkaloids in *Solanum* and fruit choice by vertebrates. Ecology 78, 782–798.

Collins, S.L., 1987. Interaction of disturbances in tallgrass prairie: a field experiment. Ecology 68, 1243–1250.

Correa, M.N., 1969–1984. Flora Patagónica, vol. 4. Instituto Nacional de Tecnología Agropecuaria, Buenos Aires.

Daciuk, J., 1978. Notas faunísticas y bioecológicas de Península Valdés y Patagonia. IV. Estado actual de las especies de mamíferos introducidos en la subregión araucana (Rep. Argentina) y del grado de coacción ejercidos en el ecosistema. Anales de Parques Nacionales 14, 105–130.

Darabant, A., Rai, P.B., Tenzin, K., Roder, W., Gratzer, G., 2007. Cattle grazing facilitates tree regeneration in a conifer forest with palatable bamboo understory. Forest Ecology and Management 252, 73–83.

de Chantal, M., Granström, A., 2007. Aggregations of dead wood after wildfire act as browsing refugia for seedlings of *Populus tremula* and *Salix caprea*. Forest Ecology Management 250, 3–8.

De Pietri, D.E., 1995. The spatial configuration of vegetation as an indicator of landscape degradation due to livestock enterprises in Argentina. Journal of Applied Ecology 32, 857–865.

González, M.E., Veblen, T.T., Donoso, C., Valeria, L., 2002. Tree regeneration responses in a lowland *Nothofagus* dominated forest alter bamboo dieback in South Central Chile. Plant Ecology 161, 59–73.

Gowda, J., Raffaele, E., 2004. Spine production is induced by fire: a natural experiment with three *Berberis* species. Acta Oecologica 26, 239–245.

Gurevitch, J., Chester, S.T.Jr., 1986. Analysis of repeated measures experiments. Ecology 67, 251–255.

Gustavsson, E., Lennartsson, T., Emanuelsson, M., 2007. Land use more than 200 years ago explains current grassland plant diversity in a Swedish agricultural landscape. Biological Conservation 138, 47–59.

Kitzberger, T., Veblen, T.T., 1999. Fire-induced changes in northern Patagonian landscapes. Landscape Ecology 14, 1–15.

Kitzberger, T., Veblen, T.T., 2003. Influences of climate on fire in northern Patagonia, Argentina. In: Veblen, T.T., Baker, W.L., Montenegro, G., Swetnam, T.W. (Eds.), Fire Regimes and Climatic Change in Temperate Ecosystems of the Western Americas. Springer-Verlag, New York, pp. 296–321.

Kitzberger, T., Veblen, T.T., Villalba, R., 1997. Climatic influences on fire regimes along a rainforest-to-xeric woodland gradient

in northern Patagonia, Argentina. Journal of Biogeography 24, 35–47.
Kitzberger, T., Raffaele, E., Veblen, T.T., 2005. Variable community responses to herbivory in fire-altered landscapes of northern Patagonia, Argentina. African Journal of Range and Forage Science 22, 85–91.
Klimek, S., Ritcher gen Kemmermann, A., Hofmann, M., Isselstein, J., 2007. Plant species richness and composition in managed grasslands: the relative importance of field management and environmental factors. Biological Conservation 134, 559–570.
Lauría Sorge, R.M., Romero, C.A., 1999. La ganadería doméstica de los pobladores con permiso de ocupación y pastaje (P.P.O.P.) en tierras fiscales del Parque Nacional Nahuel Huapi. Administración de Parques Nacionales, Intendencia Parque Nacional Nahuel Huapi. Unpublished Report, San Carlos de Bariloche, Argentina.
López Westernholm, C., Relva, M.A., 2005. Extracción de árboles muertos por "Mal del Ciprés": efecto sobre la sucesión vegetal y el uso animal. In: Proceedings of "I Reunión sobre ecología, conservación y uso de los bosques de ciprés de la cordillera", Ciefap, Esquel, Chubut, Argentina, p. 51.
Manly, B.F., 1997. Randomization Bootstrap and Monte Carlo Methods in Biology, second ed. Chapman & Hall, London.
Markgraf, V., 1983. Late and postglacial vegetational and paleoclimatic changes in subantarctic, temperate, and arid environments in Argentina. Palynology 7, 43–70.
Martín, C., Mermoz, M., Gallopín, G., 1985. Impacto de la ganadería en la cuenca del Río Manso Superior. Parte I: Bosque de Ñire con Laura. Report, Administración de Parques Nacionales, Buenos Aires, Argentina.
Mead, R., 1994. The Design of Experiments. Cambridge University Press, Great Britain.
Pearson, A.K., Pearson, O.P., Gomez, I.A., 1994. Biology of the bamboo *Chusquea culeou* (Paceae: Bambusoideae) in southern Argentina. Plant Ecology 111, 93–126.
Perera, A.H., Buse, L.J., 2004. Emulating natural disturbance in forest management: an overview. In: Perera, A.H., Buse, J.L., Weber, M.G. (Eds.), Emulating Natural Forest Landscape Disturbances. Columbia University Press, New York, pp. 3–7.
Povilitis, A., 1978. The Chilean Huemul project (1975–76): Huemul ecology and conservation. Ph.D. dissertation, Colorado State University, Fort Collins, Colorado, USA.
Raffaele, E., Veblen, T.T., 2001. Effects of cattle grazing on early postfire regeneration of matorral in northwest Patagonia, Argentina. Natural Areas Journal 21, 243–249.
Raffaele, E., Kitzberger, T., Veblen, T., 2007. Interactive effects of introduced herbivores and post-flowering die-off of bamboos in Patagonian *Nothofagus* forests. Journal of Vegetation Science 18, 371–378.
Ramilo, E., 1985. Situación y manejo del ciervo colorado en los Parques Nacionales Lanín y Nahuel Huapi. Report, Administración de Parques Nacionales, Buenos Aires, Argentina.
Ramirez, C., Godoy, R., Eldridge, W., Pacheco, N., 1981. Impacto ecológico del ciervo rojo sobre el bosque de olivillo en Osorno, Chile. Anales del Museo de Historia Natural de Valparaiso 14, 195–210.
Relva, M.A., Veblen, T.T., 1998. Impacts of introduced large herbivores on *Austrocedrus chilensis* forests in northern Patagonia, Argentina. Forest Ecology and Management 108, 27–40.
Rose, A.B., Burrows, L.E., 1985. The impact of ungulates on the vegetation. In: Davis, M.R., Orwin, J. (Eds.), Report on a Survey of the Proposed Waipiti Area, West Nelson. Forest Research Institute, Christchusch, New Zealand, pp. 210–234.
Rusch, G.M., Oesterheld, M., 1997. Relationship between productivity, and species and functional group diversity in grazed and non-grazed pampas grasslands. Oikos 78, 519–526.
Shapiro, S.S., Wilk, M.B., 1965. An analysis of variance test for normality (complete samples). Biometrika 52, 591–611.
Sokal, R.R., Rohlf, F.J., 1981. Biometry, second ed. Freeman, San Francisco, CA.
Tercero-Bucardo, N., Kitzberger, T., Veblen, T.T., Raffaele, E., 2007. A field experiment on climatic and herbivore impacts on post-fire tree regeneration in north-western Patagonia. Journal of Ecology 95, 771–779.
Turner, M.G., Romme, W.H., Tinker, D.B., 2003. Surprises and lessons from the 1988 Yellowstone fires. Frontiers in Ecology and the Environment 1, 351–358.
Vázquez, D.P., 2002. Multiple effects of introduced mammalian herbivores in a temperate forest. Biological Invasions 4, 175–191.
Veblen, T.T., 1982. Growth patterns of *Chusquea* bamboos in the understory of Chilean *Nothofagus* forests and their influences in forest dynamics. Bulletin of the Torrey Botanical Club 109, 474–487.
Veblen, T.T., 1989. *Nothofagus* regeneration in treefall gaps in northern Patagonia. Canadian Journal of Forest Research 19, 365–371.
Veblen, T.T., Lorenz, D.C., 1987. Post-fire stand development of *Austrocedrus–Nothofagus* forests in northern Patagonia. Vegetatio 71, 113–126.
Veblen, T.T., Lorenz, D.C., 1988. Recent vegetation changes along the forest/steppe ecotone in northern Patagonia. Annals of the Association of American Geographers 78, 93–111.
Veblen, T.T., Stewart, G.H., 1982. The effects of introduced wild animals on New Zealand forests. Annals of the Association of American Geographers 72, 372–397.
Veblen, T.T., Mermoz, M., Martin, C., Ramilo, E., 1989. Effects of exotic deer on forest regeneration and composition in northern Patagonia. Journal of Applied Ecology 26, 711–724.
Veblen, T.T., Kitzberger, T., Lara, A., 1992a. Disturbance and forest dynamics along a transect from Andean rain forest to Patagonian shrubland. Journal of Vegetation Science 3, 507–520.
Veblen, T.T., Mermoz, M., Martin, C., Kitzberger, T., 1992b. Ecological impacts of introduced animals in Nahuel Huapi National Park, Argentina. Conservation Biology 6, 71–83.
Veblen, T.T., Kitzberger, T., Villalba, R., Donnegan, J., 1999. Fire history in northern Patagonia: the roles of humans and climatic variation. Ecological Monographs 69, 47–67.
Veblen, T.T., Kitzberger, T., Raffaele, E., Lorenz, D.C., 2003. Fire history and vegetation changes in northern Patagonia, Argentina. In: Veblen, T.T., Baker, W.L., Montenegro, G., Swetnam, T.W. (Eds.), Fire and Climatic Change in Temperate Ecosystems of the Western Americas. Springer-Verlag, New York, pp. 265–293.