



Browsing by guanaco (*Lama guanicoe*) on *Nothofagus pumilio* forest gaps in Tierra del Fuego, Chile

Lohengrin A. Cavieres^a, Alex Fajardo^{b,*}

^aECOBIOSIS, Departamento de Botánica, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Casilla 160C, Concepción, Chile

^bCollege of Forestry and Conservation, Science Complex 444, University of Montana, Missoula, MT 59812, USA

Received 25 March 2004; received in revised form 17 September 2004; accepted 17 September 2004

Abstract

The presence of guanaco (*Lama guanicoe*, Muller 1776, Camelidae) in forests of *Nothofagus pumilio* (Poepp. et Endl.) Krasser. (lenga) in Tierra del Fuego has been associated with browsing damage in the regeneration of these forests, but little quantitative data are available. In developing and implementing forest management plans for *N. pumilio* forests, the effects of guanaco browsing are a major source of variation in attaining regeneration and growth goals, however, guanaco is not generally accounted for in management planning in the region. In this study we examined the browsing damage levels of guanaco and introduced livestock on *N. pumilio* regeneration occurring in canopy gaps of forests in Tierra del Fuego, Chile (54°12'S, 68°45'W). Relationships were established between browsing levels and gap characteristics like gap size, gap age and abundance of regeneration. Results indicated that 88.7% of regeneration growing in gaps experienced some degree of damage by browsing, and that the degree of damage was higher in smaller gaps, which might depend on the size of guanaco herds. We also found that the degree of damage was positively related with the abundance of guanacos. However, no relationship was found between gap size and abundance of guanacos.

© 2004 Elsevier B.V. All rights reserved.

Keywords: *Nothofagus pumilio*; Tree fall gaps; Guanaco; Browsing; Tierra Del Fuego

1. Introduction

Browsing by large herbivores can produce important floristic and structural changes in forest ecosystems by shifting the dominance of a tree-species

through the alteration of the regeneration dynamics (Frelich and Lorimer, 1985; Shimoda et al., 1994; Ammer, 1996; Heikkilä and Harkönen, 1996) and by influencing plant productivity and species diversity (Heinen and Sharik, 1990; Mladenoff and Stearns, 1993; Wilkinson and Neilsen, 1995). Even though most research on the effects of browsing on forests has been conducted in temperate forests of the northern hemisphere, significant work has also been initiated in

* Corresponding author. Tel.: +1 406 243 6307; fax: +1 406 243 6656.

E-mail address: alex.fajardo@umontana.edu (A. Fajardo).

forests of the southern hemisphere (Steward and Burrows, 1989; Wilkinson and Neilsen, 1995; Bulinski and McArthur, 1999; Relva and Veblen, 1998), and particularly in *Nothofagus* forests (Raedeke, 1980; Bahamonde et al., 1986; Bonino and Pelliza-Sbriller, 1991; Jane, 1994; Martínez-Pastur et al., 1999; Pulido et al., 2000).

Among the species of the genus *Nothofagus*, *Nothofagus pumilio* is one of the most prominent native species for timber production in Chile, and has been under continuous management in the last decades (Schmidt and Urzúa, 1982; Uriarte and Grosse, 1991; Arroyo et al., 1996). *N. pumilio* (Poepf. et Endl.) Krasser. (lenga) *Nothofagaceae* (syn. *Fagaceae*) (Ramírez et al., 1997) is a widespread deciduous, monoecious tree species that occurs from 35°35'S (Central Chile) to 55°30'S (Cabo de Hornos, Tierra del Fuego) (Donoso, 1993; Veblen et al., 1996). In Tierra del Fuego, it covers an area of near to 33–50% of the island surface (66,000 km²), and it can be found from sea level to 700 m elevation (Arroyo et al., 1996). *N. pumilio* is a shade intolerant species, thus, its regeneration inside the forest depends on the dynamics of forest gap formation (Rebertus and Veblen, 1993; Rebertus et al., 1997; Veblen et al., 1996; Heinemann et al., 2000; Fajardo and de Graaf, 2004).

In the Patagonia region, including Tierra del Fuego Islands, most of the gaps in the *N. pumilio* forests are formed by tree falls due to the strong prevailing winds (Rebertus and Veblen, 1993; Rebertus et al., 1997). The dynamics of *N. pumilio* has been studied with special emphasis on silviculture (e.g. Uriarte and Grosse, 1991; Bava, 1998; López-Bernal et al., 2003), and regeneration dynamics (e.g. Rebertus and Veblen, 1993; Cuevas, 2003; Fajardo and de Graaf, 2004). However, there is a lack of information about the role of large herbivores on regeneration development of *N. pumilio*, and browsing by large herbivores, knowing that both native – guanaco (*Lama guanicoe*, Muller) – and introduced domestic cattle (*Bos taurus*), have been reported in Tierra del Fuego Island (Veblen et al., 1996; Rebertus et al., 1997).

Guanaco is one of the four South American camelid species. In southern Chile, guanaco constitutes a generalist herbivore that uses a wide range of forage types (Raedeke, 1980; Franklin, 1983; Raedeke and Simonetti, 1988; Puig et al., 1997), with grasses and forbs composing between 60% and 90% of guanaco's

diet, particularly in Tierra del Fuego (Raedeke, 1980; Bonino and Pelliza-Sbriller, 1991). Guanaco is a steppe species, generally not occurring in dense forests (Veblen et al., 1992) and, although the forest was not considered an important source of forage by Franklin (1983), other studies have reported that guanaco consumes leaves of trees, especially of sapling and seedlings of *N. pumilio* (Raedeke, 1980; Bonino and Pelliza-Sbriller, 1991; Martínez-Pastur et al., 1999), and *N. antarctica* (Bahamonde et al., 1986). Thus, despite their preference for open habitats (Ortega and Franklin, 1988; Marchetti et al., 1992; Puig et al., 1997; Martínez-Pastur et al., 1999), guanaco does move into the forest (Franklin, 1983), potentially impacting *N. pumilio* regeneration (Veblen et al., 1996; Arroyo et al., 1996; Rebertus et al., 1997). Veblen et al. (1996) comment that guanaco browsing can even totally eliminate *N. pumilio* regeneration. It has been also reported that livestock browsing creates serious problems for natural regeneration of *N. pumilio* (Bava and Puig, 1992). In this context, to know the effect that the guanaco browsing could have on the regeneration of *N. pumilio* in forest gaps is especially important on Tierra del Fuego Island, where guanaco populations have increased in recent years (Soto, 1994; Franklin et al., 1997) and the forests are threatened by forest exploitation (Arroyo et al., 1996). In the Argentinean part of Tierra del Fuego, Martínez-Pastur et al. (1999) found that the abundance of guanaco in *N. pumilio* forests was higher in harvested stands (shelterwood cut system), but the highest percentage of damaged plants was found in the old-growth forest, which was not subjected to harvest. Since there is a preference of this species for open habitats and areas with higher availability of resources (seedlings and saplings), once the guanaco is in the forest, we can expect a direct relationship between forest gap size, the abundance of saplings and seedlings, and the intensity of browsing. The age of the gaps could also be an important determinant of the browsing magnitude, since we expect that in older gaps saplings and seedlings might be exposed to browsing for a longer time.

Although, it is already known that guanaco and eventually livestock browse the regeneration of these forests, quantitative data documenting the varying degree and severity of this damage on *N. pumilio* regeneration has been mostly lacking. In this study we

explored relationships between browsing damage levels on regeneration and gap characteristics in *N. pumilio* stands of Tierra del Fuego, Chile. Our main aim was to evaluate the intensity of guanaco browsing on *N. pumilio* regeneration, assessing whether or not the browsing intensity in forest gaps is related to gap size, gap age and the abundance of *N. pumilio* seedling and saplings, as a beginning point for suggestions in management strategies and development of further studies.

2. Methods

2.1. Study site

Sampling was conducted between January and March of 1995 at Estancia Vicuña in the eastern part of Chilean Tierra del Fuego Island (Fig. 1). The climate of this region is characterized by short and cold summers followed by snow and frost in the winter (Soto, 1994). Annual precipitation is ca. 450–500 mm and is evenly distributed over the year. The mean annual temperature is ca. 2.6 °C; with average minimum of –4 and maximum of 9.6 in July and

January, respectively (Arroyo et al., 1996). The study site is located at Estancia area, which is mainly formed by woodlands where *N. pumilio* is the dominant tree species. Since older stands present more gaps than young ones (Franklin et al., 2002), and this may alter the amount of regeneration occurring, only old-growth stands with similar canopy structure were used in the sampling. Woodlands are dominated by pure *N. pumilio*, with different development stages, which present a low density understory mainly composed of the shrubs *Gaultheria mucronata*, *Ribes magellanicum*, *Berberis buxifolia* and the herb *Osmorhiza chilensis*. Species nomenclature follows Marticorena and Quezada (1985).

2.2. Gap sampling and regeneration

Sampling was restricted to an area without any history of logging or recent stand-replacing natural disturbance, which is not hard to find at Estancia Vicuña (Cuevas, 2003). The forest, in general, presents a gentle slope of around 5%. We sampled 35 gaps located in a forest area of ca. 100 ha. We selected gaps non-randomly by covering a full spectrum of sizes and located in different stands on

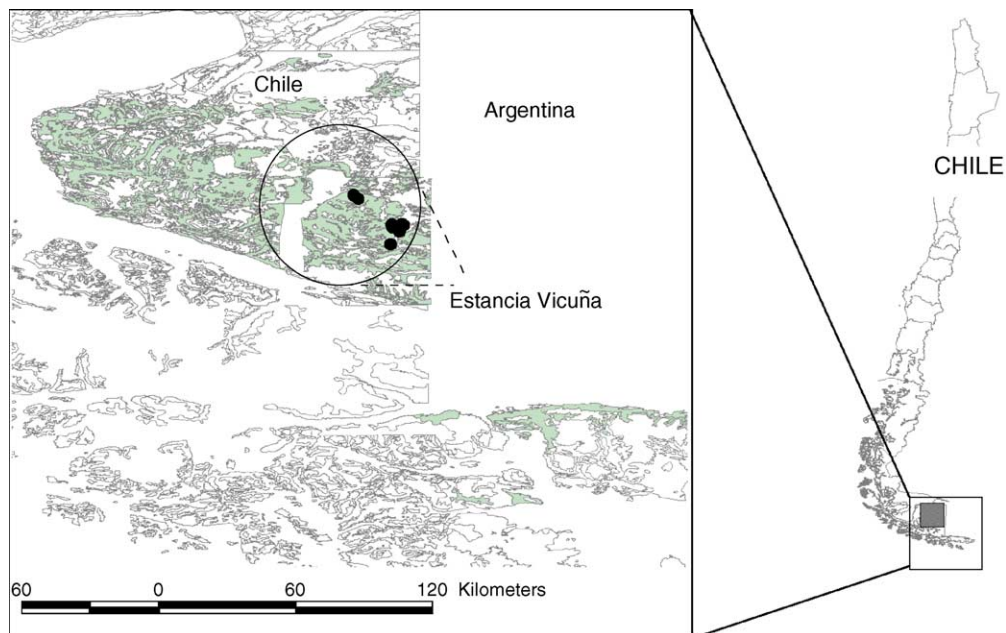


Fig. 1. Location of the study area, Estancia Vicuña, Tierra del Fuego Island, Chile (54°12'S, 68°45'W), showing in bold circles the forest stands sampled. Areas in grey corresponded to forest dominated by *N. pumilio*.

the whole Estancia area (Fig. 1). Only gaps from tree deaths were considered; for example, gaps caused by rock outcrops or swamp vegetation were not included. All the gaps under study were located in the forest matrix and at least 100 m from the steppe ecotone edge. Geographic coordinates at the center of each selected gap were obtained with a portable GPS system (Garmin Co.). We measured expanded gap area, which is defined as the area formed by the canopy gap plus the adjacent area delimited by the stem bases of the canopy trees surrounding the canopy gap (Runkle, 1982). Size of the gap was measured by taking the distance from the center to four stems of the surrounding border trees (the extremes of two perpendicular axes) (Veblen et al., 1989). We assumed an elliptical gap shape and the center of each gap was located subjectively (roughly the geometrical center). Therefore, the formula for the area of a gap is: $A = (\pi LW)/4$, where L is the distance of the longest axis, and W the distance of the shortest axis.

Gap age was estimated by extracting cores from each one of the four trees in the edges at 1.4 m height, approximately, to check for major changes in rates of radial increment and synchronous releases (Lorimer, 1985). To determine major changes in rates of radial increment, tree cores were dried and mounted in grooved wooden boards and sanded with successively finer grades of sand paper to reveal annual rings (Schweingruber, 1996). Ring widths were measured to the nearest 0.1 mm using a binocular microscope. Finally, gap ages were determined from coincident dates of release where at least a two and a half fold change in mean ring width occurred in adjacent groups of five or more rings (Veblen et al., 1989; Rebertus and Veblen, 1993).

To assess abundance and height of regeneration in gaps, we counted all seedlings (less than 10 cm tall) and little saplings (between 10 and 100 cm tall) of *N. pumilio* in a 1 m wide transect, which was staked out in one of the longest radii (between the center and one of the border trees). Three individuals were chosen for height measurements every meter along the transect.

2.3. Browsing characterization

Pulido et al. (2000) reported that in the understory of old-growth forest while the cover of grasses and

forbs is similar to the seedlings of *N. pumilio* (ca. 14%), gaps are completely dominated by the latter. Indeed, there is a dearth of other shrub species (e.g. *Berberis microphylla*), which are the usual food source of these animals out of the forest (Raedeke, 1980; Franklin, 1983). It is known that guanaco only browse leaves, leaving branches intact (Arroyo et al., 1996). The degree of browsing was estimated by a browse-rating index (BRI), proposed by Veblen et al. (1989). The BRI was calculated for every sapling located on the perimeter of the transect in each gap. This index is based on simple categories, visually established by percentage of browsing damage in the foliage of an observed individual. We considered the following BRI categories: 0 = no damage (0%); 1 = low (1–25%); 2 = moderate (26–50%); 3 = high (51–75%); 4 = very high (76–100%); and 5 = death due to browsing. For the latest case, we considered a dead sapling due to browsing when the morphology of that sapling indicated that browsing was intense and sustained over time. Saplings under these conditions lose their apical dominance and only grow in width, with clear deformations in the position of branches (Martínez-Pastur et al., 1999). With the values of BRI we computed the browsing mean index (BMI) for each gap, which corresponds to the BRI mean for all the individuals of such a gap.

2.4. Guanaco and livestock abundance

The dung piles of guanaco can be localized at both the open steppe and in the forest. The forest is often used as a sleeping place (Franklin, 1983). The sleeping place is marked (through the dung piles) and defended by the dominant male of the group (Franklin, 1982). Based in this relation (dung piles and guanaco presence), we estimated the relative abundance of guanaco in each gap by counting dung piles in four 100 m × 4 m lineal transects, located parallel to and from the longest axis in the gap. The transects were located in both gaps and beneath canopy forest. Since not all guanacos produce or make dung piles (Franklin, 1983), we also counted small groups of feces on the transects, which are usually deposited by females and chulengos (baby guanacos). We considered only dung piles with clear evidence of feces deposited during recent times, otherwise guanaco abundance could be overestimated. Recent dung piles

can be distinguished from abandoned ones because of the presence of small pioneer herbs recruiting in the latter (Franklin, 1983). Livestock abundance was estimated in the same way as for guanacos.

2.5. Spatial autocorrelation analysis: Moran's *I*

Moran's *I* index was used to measure the degree of spatial autocorrelation displayed by a quantitative variable (gap size), and to test the null hypothesis that there is no significant spatial autocorrelation for gap size (Fortin et al., 1989), to say gap size is spatially distributed at random. In this case, gap

size (z) is attached to the coordinates of the gap center (x, y in UTM) and each gap is considered to represent its surrounding portion of space (Upton and Fingleton, 1985; Skálová et al., 1999). Moran's *I* index ranges from -1 to $+1$, with zero being the null hypothesis of no spatial autocorrelation for the variable (Mast and Veblen, 1999). The statistical significance and confidence intervals are computed with respect to distance classes showing significant positive or negative spatial autocorrelation when the values of the variable are spatially dependent (Legendre and Fortin, 1989). Significances of autocorrelation were tested by Monte Carlo permu-

Table 1

Variables estimated in 35 gaps of *N. pumilio* forests in Tierra del Fuego, Chile. MBI is mean browse index (see methods).

Gap	Age (years)	MBI	Gap area (m ²)	<i>N. pumilio</i> regeneration (ind./m ²)	Guanaco abundance (dung piles/m ²)	Livestock abundance (dung piles/m ²)
1	57	2.26	626.7	19.0	0.02	0.00
2	26	1.57	1130.9	5.5	0.03	0.00
3	30	2.84	201.5	13.2	0.01	0.00
4	62	3.76	159	16.8	0.02	0.00
5	25	1.68	794.8	3.7	0.02	0.00
6		3.17	157.8	22.4	0.05	0.06
7	19	2.78	1114.5	13.4	0.05	0.02
8	22	3.10	141.4	56.0	0.08	0.04
9	36	2.73	315.7	24.5	0.03	0.07
10		2.59	146.9	52.4	0.06	0.04
11	45	0.88	184.3	10.9	0.04	0.03
12	35	4.21	125.7	22.0	0.07	0.01
13	68	2.57	646.8	33.3	0.07	0.02
14	36	2.50	133.9	78.9	0.07	0.03
15	37	1.33	1500.3	33.5	0.07	0.03
16		2.13	586.9	13.4	0.13	0.00
17	35	3.01	731.99	34.0	0.03	0.00
18	60	4.62	323.1	5.4	0.01	0.00
19	62	4.19	684.8	9.9	0.06	0.01
20	65	3.68	520.7	19.6	0.06	0.01
21	45	3.33	659.7	19.4	0.06	0.00
22	29	5.06	150.8	6.1	0.09	0.01
23	100	3.42	204.2	32.8	0.08	0.00
24	80	4.09	161.6	5.2	0.07	0.00
25	40	2.02	440.7	4.2	0.00	0.00
26		2.01	379.3	6.4	0.01	0.00
27	17	2.67	387.2	10.4	0.01	0.00
28	44	2.62	464.96	8.7	0.03	0.00
29	38	2.49	453.96	21.1	0.04	0.00
30		1.95	517.8	4.6	0.03	0.00
31	44	2.63	397.9	17.1	0.03	0.00
32	27	2.70	1036.7	14.1	0.02	0.00
33	70	3.19	765.8	10.4	0.05	0.00
34	39	4.67	306.4	27.2	0.17	0.00
35	30	4.86	707.6	5.9	0.15	0.01

tations (1000) for the gap size data. More detailed descriptions of the ways of computing and testing this index can be found in Cliff and Ord (1981). Moran's I was calculated using the spatial module in S-PLUS (S-PLUS, 2002).

2.6. Data analysis

The relationship between BMI (dependent variable) and the rest of independent variables, gap size and age, density of regeneration, the presence of livestock and guanacos, and the distance to the forest edge was carried out through multivariate comparisons (Sokal and Rohlf, 1995; Husheer et al., 2003), using general linear models in SYSTAT (SPSS, 2000). The data were normalized by a logarithmic transformation before statistical analysis. In addition, the variables for this model were checked for orthogonality (no-colinearity among the variables considered).

3. Results

3.1. Gap and regeneration characteristics

The density of seedlings and saplings was not significantly related to gap size or gap age ($P > 0.05$;

$F_{1,33} = 0.935$). The regeneration abundance showed a high variation, with a range of densities from 2.7 to 78.8 individuals m^{-2} (27,000–780,000 individuals ha^{-1} , Table 1). The range of gap sizes in the study area was between 127 and 1500 m^2 . We found no spatial autocorrelation for gap size ($P > 0.05$, Fig. 2). More than 50% of the gaps were $< 400 m^2$, representing more than 50% of the size range (Fig. 3a). Gaps were age estimated to range from 17 to 100 years old, where more than 50% were younger than 40 years, 40% were between 40 and 70 years, and only 10% were older than 80 years (Fig. 3b). For analysis purposes, we determined that there was no relationship between gap size and gap age ($P > 0.05$; $F_{1,33} = 1.579$); the general model was orthogonal between them.

3.2. Guanacos and livestock abundance and gap regeneration

The density of dung piles was neither significantly related to gap size ($P > 0.05$; $F_{1,33} = 0.87$ for guanacos, and $P > 0.05$; $F_{1,33} = 3.84$ for livestock) nor to gap age ($P > 0.05$; $F_{1,33} = 0.665$ for guanacos, and $P > 0.05$; $F_{1,33} = 1.524$ for livestock). The relative abundance of guanaco's dung piles ranged from 0.01 to 0.17 dung piles m^{-2} (100–1700 dung piles ha^{-1}), and from 0 to 0.07 dung piles m^{-2} (0–700 dung piles ha^{-1}) for livestock.

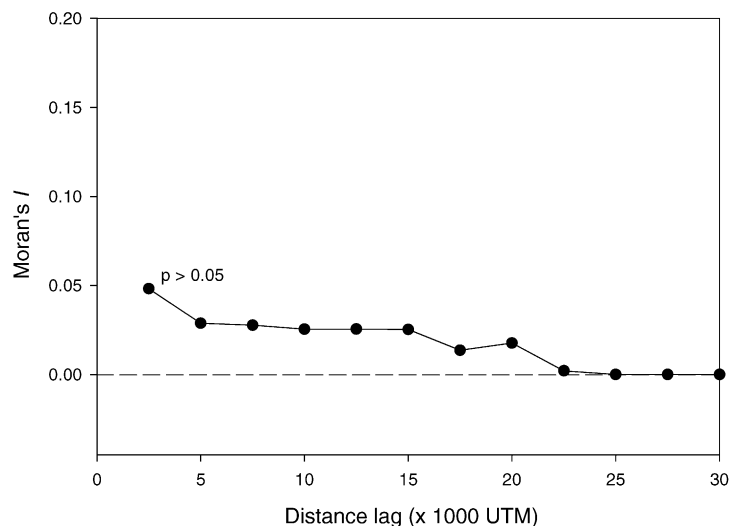


Fig. 2. Moran's I index for gap size as a function of lag-distance between gap centers in Estancia Vicuña, Tierra del Fuego, Chile. Broken line indicates the expectation of Moran's I under no spatial association.

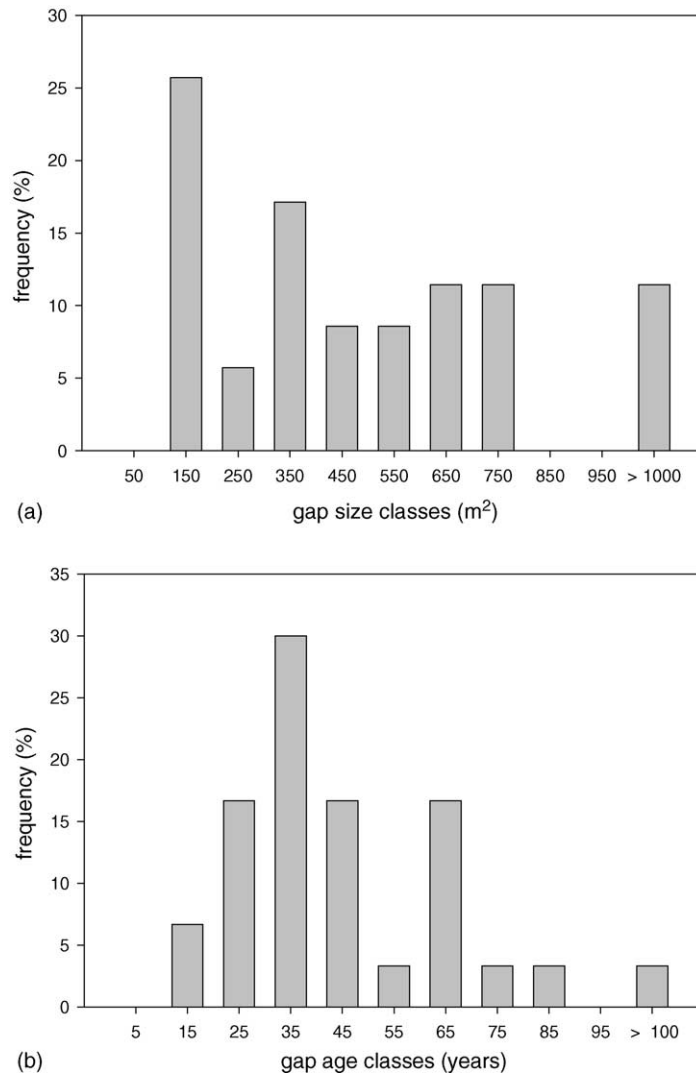


Fig. 3. Size (a) and age (b) distribution of *N. pumilio* forest gaps in the area of Estancia Vicuña, Tierra del Fuego, Chile.

We did not find any significant correlation between density of dung piles and regeneration (seedling and sapling) density in the gaps ($P > 0.05$; $F_{1,33} = 2.14$ for guanacos, and $P > 0.05$; $F_{1,33} = 1.44$ for livestock). When all gaps were considered, only 495 saplings, out of 4148 were unbrowsed. Therefore, we found that 88.7% of the saplings experienced some degree of damage by browsing. The browsing mean index (BMI) ranged from 0.8 to 4.7. We also found that BMI was not correlated with the distance to the forest edge ($P > 0.05$; $F_{1,30} = 2.78$). Finally, the multiple regression model indicated that gap size (negatively related;

Fig. 4) and guanaco's dung pile density (positively related; Fig. 5) were the only variables significantly related to BMI (Table 2). The partial regression coefficients from this analysis showed that the density of guanaco's dung piles is the most important variable in accounting for browsing damage (Table 2).

4. Discussion

For our study area we found that gap size was negatively related with browsing intensity, which

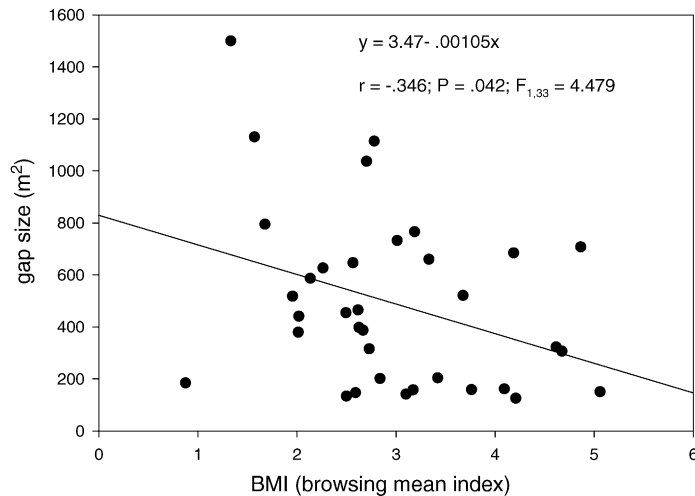


Fig. 4. Scatter plot of gap size versus BMI in 34 gaps found in a *N. pumilio* forest in Estancia Vicuña, Tierra del Fuego, Chile.

suggests that regeneration was most affected by herbivores in smaller gaps of *N. pumilio* forests. This is in agreement with Rebertus et al. (1997) who also found a negative relationship between guanaco browsing and the blowdown area in *N. pumilio* forests. However, they found that browsing only affected saplings located in the periphery of these blowdown areas, while in forest gaps we observed damage in seedling and sapling throughout the gap.

The negative relationship between gap size and browsing intensity might mean that guanacos pre-

ferentially feed in smaller gaps. However, it is important to note that guanaco density was not correlated with gap size, which contrasts with what Martínez-Pastur et al. (1999) reported; the larger the harvested area (in comparison with un-harvested forest) the larger the abundance of guanaco. Although we did not account for guanaco's herd size, we believe this variable can certainly have an effect on the degree of damage for a determined gap size, explaining the negative relationship between gap size and browsing intensity. Guanacos usually live in small herds, and

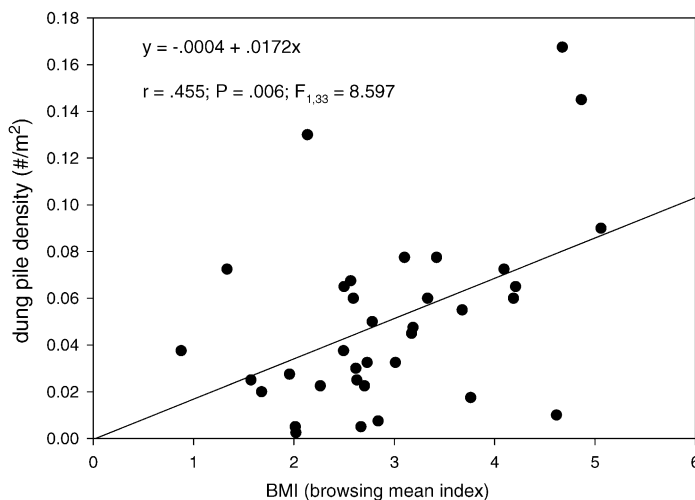


Fig. 5. Scatter plot of dung pile density vs. BMI in 35 gaps found in a *N. pumilio* forest in Estancia Vicuña, Tierra del Fuego, Chile.

Table 2

Multiple regression results between large herbivores browse intensity (MBI) and structural variables of forest-gaps in *N. pumilio* forest en Tierra del Fuego, Chile

Source of variation	S.S.	d.f.	M.S.	F-ratio	P
Regression	16.787	5	3.358	5.15	0.002**
Residual	15.635	24	0.651		

Variable	β -Coefficient	Partial regression coefficient	P
Gap age	0.004	0.1249	0.599
Gap area	-0.538	-0.466	0.013*
Abundance of			
<i>N. pumilio</i> regeneration	-0.018	-0.320	0.103
Guanacos	16.161	0.6292	0.001**
Livestock	-11.815	-0.249	0.209

$R = 0.72$; adjusted $R^2 = 0.62$; $F(5,24) = 5.16$; $P < 0.0024$, $SEE = 0.8071$; * $P < 0.05$, ** $P < 0.01$.

when a herd is in a smaller gap, they are certainly going to be at higher density than in a larger gap, causing larger impacts on the regeneration.

Gap size was not related to seedling and sapling density, which is in accordance with another study, conducted in *N. pumilio* forests in Coyhaique (Patagonia) and Central-Chile (Fajardo and de Graaf, 2004).

Contrary to our initial expectation, guanacos are not confined to gaps closer to the forest edge only, but also explore and browse in gaps distributed throughout the forest matrix. Guanacos neither showed any particular preference for gap size, and since gap size was not spatially correlated, we might conclude that guanacos fully explore the forest no matter the size of the gap is or how distant the gap is from the edge. Nonetheless, additional studies would be necessary to elucidate if, in a landscape context, size and shape of forest stands may have a role on this spatial browsing pattern.

The relationship between the browsing effects by large mammals and the development of young cohorts, particularly in these *Nothofagus* forests, is considered important for both forestry and successful management (Gill, 1992). We found that the abundance of guanaco is the most important variable in explaining the variability of browsing intensity. This result is in accordance with other studies, which have found that the abundance of herbivores is the key factor to explain browsing intensity in temperate forests (e.g., Bergquist and Orlander, 1998; Bulinski and McArthur, 2003; Weisberg and Bugmann, 2003).

Although we found that 88.7% of the seedlings and saplings experienced browsing, this does not eliminate the regeneration, but we believe that rather affects in an irreversible way its shape and growth rate, which certainly has important management consequences. We did not measure reduction in growth rates, however other studies have documented that guanaco browsing significantly diminishes the growth rate of *N. pumilio* regeneration (Dodds, 1997; Martínez-Pastur et al., 1999; Pulido et al., 2000). Hence, browsing of guanaco becomes a limiting factor on initial growth of *N. pumilio* seedlings and saplings, but we cannot anticipate what the effects of such a browsing would be on the long-term for those seedlings/saplings, and, particularly, on the dynamics gap replacement.

In developing and implementing forest management plans for *N. pumilio* forests, the effects of guanaco and introduced livestock browsing are a major source of uncertainty in attaining regeneration and growth goals, however this factor has not been taken into account so far in management planning in the region (Martínez-Pastur et al., 1999). According to our results, it is likely that the most important variable to consider in management programs is the abundance of guanaco within the forest, particularly in gaps. Nevertheless, guanaco prefers open areas like humid steppe, alpine vegetation and the forest-steppe and forest-peatland ecotones (Raedeke, 1982; Franklin, 1982, 1983; Soto, 1994), where they feed mainly on grasses and shrubs. Tree species browsing only

constitute between 15 and 20% of its diet, although the importance of these species may increase in winter (Raedeke, 1980; Ortega and Franklin, 1988; Bonino and Pelliza-Sbriller, 1991). These studies also reported that guanaco would make use of the forest as a feeding place due to a competitive displacement steppe-to-forest, by introduced livestock mainly involving sheep. They also suggested and predicted that if livestock (sheep) is removed from the steppe, then guanaco could come back and make use of its natural habitat. Raedeke (1982) and Puig et al. (1997) confirmed this prediction and reported that when introduced sheep was excluded from the steppe a successful guanaco re-colonization occurred. Nonetheless, forest may be still used either as a refuge and sleeping area, or also as a passing corridor, especially for those migratory populations coming down from alpine to lowland areas (Raedeke, 1978). These displacements also depend on the sheep movements during the different seasons of the year. During summer, when the interaction with sheep is higher, guanacos utilize the forest and the alpine vegetation at higher elevations to feed, coming down to the steppe during winter (Raedeke, 1978).

Even though, the presence of introduced large herbivores has been considered as one of the main factors involved in the successful establishment of regeneration in temperate forests of the southern Hemisphere (Relva and Veblen, 1998; Husheer et al., 2003), in our study the abundance of domestic cattle was not significantly related with browsing intensity. It is thought that domestic cattle browse in the forest occasionally, mostly when some individuals are strayed. While leaves of *N. pumilio* regeneration are part of guanaco's diet, domestic cattle mostly browse grasses and regeneration leaves only constitute a low proportion of its diet (Arroyo et al., 1996).

Although we found a relation between abundance of guanacos and browsing intensity, we did not find any significant relation between the abundance of guanacos and the regeneration density, which is in contrast to other studies (e.g., Heikkilä and Harkönen, 1996). Hence, browsing of regeneration of *N. pumilio* by guanaco seems to be an opportunistic event, not influenced by the density of regeneration. Finally, although we are aware of the correlative nature of our study, and that dung pile is not the best surrogate of guanacos abundance, we have found that smaller gap

regeneration is more vulnerable to guanaco browsing. This result calls for a note of caution for forest regeneration because small gaps are more frequent than larger ones. According to the information available we can anticipate that only by decreasing the amount of livestock in the Patagonic prairies, the harmful effect of guanaco in the *N. pumilio* regeneration may be avoided.

Acknowledgements

To Jorge Mella, Ana María Humaña, Leonora Rojas, Héctor Jiménez and Alejandro Peñaloza who assisted in the field. We thank P. Alaback and M. Gundale and two anonymous reviewers for useful comments and improvements to this manuscript. Fieldwork was funded by Río Córdor Project-Forestal Trillium, Ltd. Data analyses and preparation of the manuscript was supported by MECESUP UCO 9906 Travel Fellowship to L.A.C. This paper forms part of the research activities of the Millennium Center for Advanced Studies in Ecology and Research on Biodiversity supported by Grant No. P02-051-F ICM.

References

- Ammer, C., 1996. Impact of ungulates on structure and dynamics of natural regeneration of mixed mountain forest in Bavarian Alps. *For. Ecol. Manage.* 88, 43–53.
- Arroyo, M.T.K., Donoso, C., Murúa, R., Pisano, E., Schlatter, R., Serey, I., 1996. Toward an ecologically sustainable forestry project. concepts, analysis and recommendations. *Protecting Biodiversity and Ecosystem Processes in the Rio Condor Project—Tierra del Fuego*, Departamento de Investigacion y Desarrollo, Universidad de Chile, 253 pp.
- Bahamonde, N., Martin, S., Pelliza-Sbriller, A., 1986. Diet of guanaco and red deer in Neuquen Province, Argentina. *J. Range Manage.* 39 (1), 22–24.
- Bava, J., 1998. Los bosques de lenga en Argentina. In: Donoso, C., Lara, A. (Eds.), *Silvicultura de los bosques nativos de Chile*. Editorial Universitaria, Chile, pp. 273–296.
- Bava, J., Puig, C., 1992. Regeneración natural de Lenga, análisis de algunos factores involucrados. *Actas Seminario Manejo Forestal de la Lenga y aspectos ecológicos relacionados* 85–110.
- Bergquist, J., Örlander, G., 1998. Browsing damage by roe deer on Norway spruce seedling planted on clearcuts of different ages. 1. Effect of slash removal, vegetation development, and roe deer density. *For. Ecol. Manage.* 105, 283–293.

- Bonino, N., Pelliza-Sbriller, A., 1991. Composición botánica de la dieta del guanaco (*Lama guanicoe*) en dos ambientes contrastantes en Tierra del Fuego, Argentina. *Ecol. Aust.* 1, 97–102.
- Bulinski, J., McArthur, C., 1999. An experimental field study of the effects of mammalian herbivore damage on *Eucalyptus nitens* seedlings. *For. Ecol. Manage.* 113, 241–249.
- Bulinski, J., McArthur, C., 2003. Identifying factors related to the severity of mammalian browsing damage in eucalypt plantations. *For. Ecol. Manage.* 183 (1/3), 239–247.
- Cliff, A.D., Ord, J.K., 1981. *Spatial Processes: Models and Applications*. Pion Limited, London.
- Cuevas, J.G., 2003. Gap characteristics in relation to forest structure and implications for southern beech forest dynamics. *Can. J. For. Res.* 33 (10), 1915–1922.
- Dodds, P., 1997. Efecto del ramoneo de guanaco sobre la regeneración de lenga (*Nothofagus pumilio*) en Russfin, Tierra del Fuego. Tesis de Ingeniero Forestal. Facultad de Ciencias Forestales, Universidad de Chile, p. 58.
- Donoso, C., 1993. Bosques templados de Chile y Argentina: Variación, estructura y dinámica, Tercera edición, Editorial Universitaria, Santiago de Chile.
- Fajardo, A., de Graaf, R., 2004. Tree dynamics in canopy gaps in old-growth forests of *Nothofagus pumilio* in Southern Chile. *Plant Ecol.* 173 (1), 95–105.
- Fortin, M.J., Drapeau, P., Legendre, P., 1989. Spatial autocorrelation and sampling design in plant ecology. *Vegetatio* 83, 209–222.
- Franklin, J.F., Spies, T.A., van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., Chen, J., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *For. Ecol. Manage.* 155, 399–423.
- Franklin, W.L., 1982. Biology, ecology and relationship to man of the South American camelids. In: Mares, M.A., Genoways, H.H. (Eds.), *Mammalian Biology in South America Special Publications Series*, vol. 6. Pymatuning Laboratory of Ecology and University of Pittsburgh, Pittsburgh, pp. 457–489.
- Franklin, W.L., 1983. Contrasting socioecologies of South America's wild camelids: the vicuña and the guanaco. In: Eisenberg, J.F., Kleiman, D. (Eds.), *Advances in the Study of Mammalian Behavior*. Special Publications No. 7. American Society of Mammalogist, Shippensburg, pp. 573–629.
- Franklin, W.L., Bas, F., Bonacic, C.F., Cunazza, C., Soto, N., 1997. Striving to manage Patagonia guanacos for sustained use in the grazing agroecosystems of southern Chile. *Wildlife Soc. Bull.* 25, 65–73.
- Frelich, L.E., Lorimer, C.G., 1985. Current and predicted long-term effects of deer browsing in hemlock forests in Michigan, USA. *Biol. Conserv.* 34, 99–120.
- Gill, R.M.A., 1992. A review of damage by mammals in north temperate forests. 3. Impact on trees and forests. *Forestry* 65 (4), 363–388.
- Heikkilä, R., Harkönen, S., 1996. Moose browsing in young Scots pine stands in relation to forest management. *For. Ecol. Manage.* 88, 179–186.
- Heinemann, K., Kitzberger, T., Veblen, T.T., 2000. Influences of gap microheterogeneity on the regeneration of *Nothofagus pumilio* in a xeric old-growth forest of northwestern Patagonia Argentina. *Can. J. For. Res.* 30, 25–31.
- Heinen, J.T., Sharik, T.L., 1990. The influence of mammalian browsing on tree growth and mortality in the pigeon river state forest Michigan. *Am. Midland Nat.* 123, 202–206.
- Husheer, S.W., Coomes, D.A., Robertson, A.W., 2003. Long-term influences of introduced deer on the composition and structure of New Zealand *Nothofagus* forests. *For. Ecol. Manage.* 181, 99–117.
- Jane, G.T., 1994. The impact of browsing animals on the stand dynamics of monotypic mountain beech (*Nothofagus solandri*) forest in Canterbury New Zealand. *Aust. J. Bot.* 42, 113–124.
- Legendre, P., Fortin, M.-J., 1989. Spatial pattern and ecological analysis. *Vegetatio* 80, 107–138.
- López-Bernal, P.M., Bava, J.O., Antequera, S.H., 2003. Regeneración en un bosque de lenga (*Nothofagus pumilio* (Poepp. et Endl.) Krasser) sometido a un manejo de selección en grupos. *Bosque* 24 (2), 13–21.
- Lorimer, C.G., 1985. Methodological considerations in the analysis of forest disturbance history. *Can. J. For. Res.* 15, 200–213.
- Marchetti, B., Oltremari, J., Peters, H., 1992. Estrategias para el manejo y aprovechamiento racional del guanaco (*Lama guanicoe*). Proyecto FAO/PNUMA sobre manejo de Areas Silvestres, Areas Protegidas y Vida silvestre en América Latina y el Caribe. Documento Tecnico # 9, Santiago, Chile, 162 pp.
- Marticorena, C., Quezada, M., 1985. Catálogo de la flora vascular de Chile. *Gayana* 42, 1–157.
- Martínez-Pastur, G., Peri, P.L., Fernández, M.C., Staffieri, G., Rodríguez, D., 1999. Desarrollo de la regeneración a lo largo del ciclo del manejo forestal de un bosque de *Nothofagus pumilio*: 2 Incidencia del ramoneo de *Lama guanicoe*. *Bosque* 20, 47–53.
- Mast, J.N., Veblen, T.T., 1999. Tree spatial patterns and stand development along the pine-grassland ecotone in the Colorado Front Range. *Can. J. For. Res.* 29, 575–584.
- Mladenoff, D.J., Stearns, F., 1993. Eastern hemlock regeneration and deer browsing in the northern Great Lakes region: a re-examination and model simulation. *Conserv. Biol.* 7, 889–900.
- Ortega, I., Franklin, W., 1988. Feeding habitat utilization and preference by guanaco male groups in the Chilean Patagonia. *Revista Chilena de Historia Natural* 61, 209–216.
- Puig, S., Videla, F., Cona, M., 1997. Diet and abundance of the guanaco (*Lama guanicoe*) in four habitats of northern Patagonia, Argentina. *J. Arid Environ.* 36, 343–357.
- Pulido, F.J., Díaz, B., Martínez-Pastur, G., 2000. Incidencia del ramoneo del guanaco (*Lama guanicoe* Muller) sobre la regeneración temprana en bosques de lenga (*Nothofagus pumilio* (Poepp et Endl) Krasser) de Tierra del Fuego Argentina. *Investigación Agraria de Sistemas y Recursos Forestales* 9, 381–394.
- Raedeke, K., 1978. El Guanaco en Magallanes, Chile. Su Distribución y Biología. Santiago, Chile, CONAF, Publicacion Tecnica # 4, 182 pp.
- Raedeke, K., 1980. Food habits of the guanaco (*Lama guanicoe*) of Tierra del Fuego, Chile. *Turrialba* 30, 177–181.
- Raedeke, K., 1982. Habitat uses by guanaco and sheep on common range, Tierra del Fuego, Chile. *Turrialba* 32, 309–314.

- Raedeke, K., Simonetti, J.A., 1988. Food habits of *Lama guanicoe* in the Atacama desert in northern Chile. *J. Mammal.* 69, 198–201.
- Ramírez, C., San Martín, C., Oyarzún, A., Figueroa, H., 1997. Morpho-ecological study on the South American species of the genus *Nothofagus*. *Plant Ecol.* 130, 101–109.
- Rebertus, A.J., Veblen, T.T., 1993. Structure and tree-fall gap dynamics of old-growth *Nothofagus* forests in Tierra del Fuego, Argentina. *J. Veg. Sci.* 4, 641–654.
- Rebertus, A.J., Kitzberger, T., Veblen, T.T., Roovers, L.M., 1997. Blowdown history and landscape patterns in the Andes of Tierra del Fuego, Argentina. *Ecology* 78, 678–692.
- Relva, M.A., Veblen, T.T., 1998. Impacts of introduced large herbivores on *Austrocedrus chilensis* forest in northern Patagonia Argentina. *For. Ecol. Manage.* 108, 27–40.
- Runkle, J.R., 1982. Patterns of disturbance in some old-growth mesic forests of the eastern North America. *Ecology* 63, 1533–1546.
- Schmidt, H., Urzúa, A., 1982. Transformación y manejo de los bosques de lenga en Magallanes. *Ciencias Agrícolas* No. 11, CONAF-Universidad de Chile.
- Schweingruber, F.H., 1996. *Tree Rings and Environment Dendrology*. Berne Publishers, 609 pp.
- Shimoda, K., Kimura, K., Kanzaki, M., Yoda, K., 1994. The regeneration of pioneer tree species under browsing pressure of Sika deer in evergreen oak forest. *Ecol. Res.* 9, 85–92.
- Skálová, H., Krahulec, F., Düring, H.J., Hadincova, V., Pechackova, H., Herben, T., 1999. Grassland canopy composition and spatial heterogeneity in the light quality. *Plan. Ecol.* 143 (2), 129–139.
- Sokal, R.R., Rohlf, F.J., 1995. *Biometry*, 3rd ed. Freeman, New York, 887 pp.
- Soto, N., 1994. Proyecto Conservación y Manejo del Guanaco *Lama guanicoe* en Isla Tierra del Fuego. Estimación poblacional-1993. Corporación Nacional Forestal (CONAF) Punta Arenas.
- S-PLUS, 2002. Version 6.1. Insightful Corporation, Seattle, USA.
- SPSS, 2000. SYSTAT 10.0. SPSS Inc., Chicago, USA.
- Steward, G.H., Burrows, L.E., 1989. The impact of white-tailed deer *Odocoileus virginianus* on regeneration in the coastal forests of Stewart Island New Zealand. *Biol. Conserv.* 49, 275–293.
- Upton, G.J.G., Fingleton, B., 1985. *Spatial Data Analysis by Example. Point Pattern and Quantitative Data*, vol. 1. Wiley.
- Uriarte, A., Grosse, H., 1991. Los bosques de lenga. Una orientación para su manejo (recopilación bibliográfica). Instituto Forestal. Informe técnico 126. Concepción, Chile.
- Veblen, T.T., Mermoz, M., Martin, C., Ramillo, E., 1989. Effects of exotic deer on forest regeneration and composition in northern Patagonia. *J. Appl. Ecol.* 26, 711–724.
- Veblen, T.T., Mermoz, M., Martin, C., Kitzberger, T., 1992. Ecological impacts of introduced animals in Nahuel Huapi National Park, Argentina. *Conserv. Biol.* 6, 71–90.
- Veblen, T.T., Donoso, C., Kitzberger, T., Rebertus, A.J., 1996. Ecology of southern Chilean and Argentinean *Nothofagus* forests. In: Veblen, T.T., Hill, R.S., Read, J. (Eds.), *The Ecology and Biogeography of Nothofagus Forests*. Yale University Press, New Haven, pp. 293–353.
- Weisberg, P.J., Bugmann, H., 2003. Forest dynamics and ungulate herbivory: from leaf to landscape. *For. Ecol. Manage.* 181, 1–12.
- Wilkinson, G.R., Neilsen, W.A., 1995. Implications of early browsing damage on the long term productivity of eucalypt forests. *For. Ecol. Manage.* 74 (1-3), 117–124.