Forest Ecology and Management 291 (2013) 300–307

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

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

The effect of altitude and grazing on seedling establishment of woody species in central Argentina

Paula Inés Marcora [a,*], Daniel Renison [b], Ana Inés País-Bosch [c], Marcelo Ruben Cabido [a], Paula Andrea Tecco [a]

[a] Instituto Multidisciplinario de Biología Vegetal, CONICET, F.C.E.F. y N., Universidad Nacional de Córdoba, Avenida Vélez Sarsfield 299, CP 495, 5000 Córdoba, Argentina
[b] Centro de Ecología y Recursos Naturales Renovables – Dr. Ricardo Luti, CONICET, F.C.E.F.y N., Universidad Nacional de Córdoba, Avenida Vélez Sarsfield 299, 5000 Córdoba, Argentina
[c] Facultad de Ciencias Agrarias, Universidad Nacional de Catamarca, Av. Belgrano y Maestro Quiroga, San Fernando del Valle de Catamarca, CP 4700 Catamarca, Argentina

ARTICLE INFO

Article history:
Received 10 October 2012
Received in revised form 19 November 2012
Accepted 20 November 2012
Available online 7 January 2013

Keywords:
Altitudinal gradient
Herbivory
Woodland
Seedling establishment
Central Argentina

ABSTRACT

Understanding the factors that determine altitudinal distribution of species is very important to evaluate the influence of global change. Although climate is the major driver of vegetation distribution, other factors, such as herbivory by livestock, can be more important locally and regionally. Despite its importance, the altitudinal range distribution of species and how it is influenced by climate and livestock are generally unknown. In the Sierras Grandes Mountains of central Argentina, woodlands of lower and upper altitudes are interrupted by an intermediate vegetation belt devoid of forest. Traditionally, this pattern was assumed to be determined by climate, although recent studies suggest that forest distribution would be driven by livestock grazing. However, the potential altitudinal range distribution of the principal woody species of these forests and how it is affected by livestock are still poorly known. In this study, we used an experimental approach to evaluate seedling survival and growth – with and without livestock presence – of the three principal woody species of the mountain woodlands along the entire altitudinal gradient of Sierras Grandes. In January 2009, we planted seedlings of *Polylepis australis*, *Maytenus boaria* and *Escallonia cordobensis* inside and outside livestock exclosures at seven altitudinal sites established every 200–400 m asl, from 940 m asl to 2700 m asl (i.e., maximum altitude of Sierras Grandes). During the three following winters, we evaluated seedling survival and height and measured stocking rates. Although the three species were able to sprout after browsing, livestock markedly reduced seedling survival and height. Inside the exclosure, the three species successfully survived and grew along the entire gradient, including the altitudinal belt devoid of forest. Furthermore, after three growing seasons *P. australis* and *E. cordobensis* flowered inside the exclosure at the altitudes where seedlings reach greater heights (2200 m asl and 1200 and 1600 m asl, respectively). We suggest that under the current high stocking rates, livestock would strongly hinder seedling establishment of the three principal woody species at most altitudes of Sierras Grandes. Our findings are in agreement with the assumption that the present altitudinal belt devoid of forest is not climatically driven; rather, livestock is the major factor of current forest distribution.

1. Introduction

Vegetation patterns along altitudinal gradients are primarily driven by a decrease in temperature with increasing elevation (Crawford, 1989; Körner, 1999; Tranquilini, 1979). Far less attention has been paid to the influence of anthropogenic disturbances such as livestock grazing (Cairns and Moen, 2004; Ellemberg, 1979), despite the importance of livestock rearing in many mountain areas of the world (Hofgaard et al., 2010). Both altitude and livestock can markedly affect several stages of forest development. However, since seedling establishment is foremost sensitive to environmental conditions, this stage can become a bottleneck due to the increasing unfavorable conditions towards the altitudinal limits of distribution (Hofgaard et al., 2009; Cierjacks et al., 2007; Cuevas, 2000; Jump et al., 2009). Additionally, livestock grazing might well prevent tree seedling growth, maintaining grasslands in sites with potential for forest development (Anderson, 1981; Bond, 2005; Vera, 2000). In fact, differences between current and potential climatically determined vegetation show that ecosystems dominated by woody plants would be more extended if climatic conditions were the major constraint and no

---

* Corresponding author. Address: Avenida Vélez Sarsfield 299, 5000, Casilla de correo 495, Córdoba, Argentina. Tel./fax: +54 351 4331056.

E-mail addresses: paulamarcora@hotmail.com (P.I. Marcora), drenison@conicet.gov.ar (D. Renison), aipais@hotmail.com (A.I. País-Bosch), mcabido@imbiv.unc.edu.ar (M.R. Cabido), ptecco@efn.uncor.edu (P.A. Tecco).

0378-1127/$ - see front matter © 2012 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.foreco.2012.11.030

other factors such as fire and livestock were also at play (Bond et al., 2005). However, the influence of livestock grazing on vegetation structure depends on a number of factors. Chief among them are the resistance of woody species to browsing, the ability of recruiting woody seedlings to succeed in the face of the disturbance and competition limitation imposed by herbivores, and the preference of herbivores for tree species over surrounding vegetation (Cairns and Moen, 2004).

The Sierras Grandes Mountains in central Argentina provide a suitable scenario to address the combined effect of both factors, altitude and livestock grazing, on the distribution pattern of tree species. In this system, the distribution of lower (400–1300 m asl) and higher (1700–2800 m asl) mountain forest belts is currently interrupted by an intermediate altitudinal belt devoid of forests, occupied by a mosaic of mountain grasslands and shrublands (1300–1700 m asl) (Giorgis, 2011; Luti et al., 1979). Continuous forests along the altitudinal gradient are only present in large ravines; outside ravines, the forests of the higher zone, dominated by *Polylepis australis,* are often restricted to rocky outcrops (Cingolani et al., 2004; Renison et al., 2002). This vegetation pattern has been traditionally assumed to be the consequence of more favorable climatic conditions in ravines and outcrops and, secondly, to a lower human disturbance in the rough relief of the ravines and in rocky outcrops (Cabido, 1985; Cingolani et al., 2003; Luti et al., 1979). However, recent studies challenge that assumption. Increasing evidence suggests that human activities, such as logging, fire management and livestock grazing, are the major drivers of the present forest distribution. These anthropogenic activities reduce *P. australis* growth and survival (Giorgis et al., 2010; Renison et al., 2002; Teich et al., 2005); forest remnants are far from the influence of humans, and topography *per se* cannot fully explain the present distribution of mountain forests (Cingolani et al., 2008). On the other hand, according to global patterns defined by Körner and Paulsen (2004) there should not be a climatic treeline explaining the lack of forests at certain altitudes in the Sierras Grandes. Treelines in mountains all throughout the world are expected to be determined by the isotherm of 6–7 °C of mean ground temperature during the growing season (Körner and Paulsen, 2004). Considering that at 6–7 °C, air and soil temperature are similar (Körner and Paulsen, 2004), the Sierras Grandes would not surpass this isotherm since the annual average air temperature at the maximum altitude (i.e., 2800 m asl) is 7.4 °C (Marcora et al., 2008). Accordingly, individuals of *P. australis* growing at these maximum altitudes can exhibit tree habit (Marcora et al., 2008).

Despite this sound evidence of the effects of both livestock grazing and climate on *P. australis* forests, no studies have still addressed the combined influence of both factors to explore the relative influence of each driver on forest distribution in Sierras Grandes. Furthermore, the potential altitudinal distribution of tree species still remains unknown, particularly for *Maytenus boaria* and *Escalonia cordobensis*, other representative trees frequently associated with *Polylepis* woodlands. Whether tree species present inside ravines can be established on more unfavorable high topographic positions, particularly between 1300 and 1700 m asl, also remains to be elucidated.

In this study we evaluate the combined effect of livestock grazing and altitude on the survival and growth of seedlings of three tree species occurring in the Sierras Grandes using a manipulative experimental approach. Unlike most previous studies that have focused only on *P. australis*, our study also provides basic information of *M. boaria* and the endemic species *E. cordobensis*. We hypothesize that the combined effects of livestock grazing and harsh weather conditions prevailing at the altitudinal limits of distribution could greatly retard or completely inhibit forest establishment.

2. Materials and methods

2.1. Study area

The study was conducted in the Sierras Grandes Mountains, Córdoba, central Argentina. The experimental plots were placed on the eastern slope which is more accessible than the western slope, and along an altitudinal gradient that ranging from 900 m asl up to the highest altitude of the mountain range, at 2700 m asl (Linderos road, 32°5′S, 64°9′W). The whole gradient comprises the following vegetation belts described by Cabrera (1976) for the Mountain Chaco District: (1) the upper portion of Chaco mountain forest, which is distributed between 400 and 1300 m asl; (2) an intermediate belt devoid of forest currently occupied by mountain grasslands and shrublands (1300–1700 m asl; Giorgis, 2011); and (3) a mosaic of high mountain grasslands and *P. australis* woodlands (above 1700 m asl). Along the gradient, mean annual temperature varies between 15.7 °C at 900 m asl and 7.4 °C at 2700 m asl (Marcora et al., 2008) and annual precipitation at 2100 m asl is about 840 mm (Cabido, 1985). The main economic activity is livestock rearing that began in the early 17th century and had completely replaced the native herbivores (*Lama guanicoe*) by the beginning of the 20th century (Díaz et al., 1994).

2.2. Study species

We selected three native woody species that grow along the altitudinal range. *E. cordobensis* (KUNTZE) HOSSEUS (Escalloniaceae) is an endemic shrub of mountains of central Argentina that grows in both low and highland mountain forest and can reach up to 5 m in height, whereas *M. boaria* MOLINA (Celastraceae) and *P. australis* BITT. (Rosaceae) are tree species that form forests at higher altitudes, but may be found as isolated individuals at lower levels, where other woody species dominate the forests. The best performance of *P. australis* (i.e. vitality of adults individuals, tree-ring growth, seed mass, seed productivity and seed germination) in the Sierras Grandes is observed at about 1900 m asl, where the largest forest areas currently occur (Cingolani et al., 2008; Marcora et al., 2008). To the best of our knowledge, no studies regarding the effect of altitude on distribution patterns of *E. cordobensis* and *M. boaria* have been conducted. Cattle browse a high proportion of *P. australis* stems, even under low stocking rates (Giorgis et al., 2010; Teich et al., 2005). *M. boaria* is also browsed by livestock (Donoso and Wendler, 1985). There are no reports about the response of *E. cordobensis* to livestock; however, browsed individuals have been observed (pers. obs.).

2.3. Experimental design

Seven sites were selected along the altitudinal gradient, placed at intervals of about 200–400 m asl (963, 1243, 1600, 1803, 2248, 2458 and 2685 m asl). All sites were established on ridges with similar gentle slopes and high solar insolation (Table 1). Soil characteristics of each site are summarized in Table 1 (Tecco P.A., unpublished data). At each altitudinal site, a 20 × 20 m exclosure was built to exclude domestic livestock. In January 2009, at each site we planted 50, 34 and 36 seedlings of *E. cordobensis*, *M. boaria* and *P. australis*, respectively. Half of the seedlings were planted inside the exclosure, whereas the other half were planted outside, in a plot adjacent to the exclosure, i.e., exposed to livestock grazing. Seedlings had been grown in a greenhouse using seeds from over 30 parent trees per species collected from the study area at altitudes from 1400 to 1900 m asl. At the moment of transplanting in the field, average seedling height was 14.80(±5.69) cm for *P.*

Table 1
Summary of soil conditions of the seven study sites (means (SE)) from Tecco et al., unpublished data. Means of samples measured inside and outside the exclosures.

Altitude (m asl)	Slope orientation	Slope (%)	Soil depth (cm)	Organic matter (%)	*C* (%)	*N* (%)	*P* (ppm)
963	S	5	36.2(7.6)	3.9(0.3)	2.3(0.2)	0.19(0.01)	3.3(1.6)
1243	E-NE	8	48.2(6.1)	5.5(0.4)	3.2(0.2)	0.26(0.02)	7.7(2.1)
1600	NE	13	35.2(6.2)	3.7(0.9)	2.2(0.5)	0.19(0.04)	1.7(0.2)
1803	N-NE	5	17.2(3.5)	10.3(0.6)	6(0.4)	0.50(0.04)	7.5(0.7)
2248	NE	12	55.4(2.8)	9.6(0.3)	5.6(0.3)	0.45(0.01)	2.1(0.1)
2458	E	5	68.9(1.8)	16.1(1)	9.3(0.6)	0.76(0.06)	1.3(0.4)
2685	W-SW	5	66(1.9)	15(1)	8.7(0.6)	0.73(0.05)	2(0.5)

australis, 17.51(±8.87) for *M. boaria*, and 17.38(±6.25) for *E. cordobensis*. Seedlings were randomly assigned to both treatments and all seedlings were watered immediately after transplanting, but received no additional irrigation. We protected planted seedlings with three rocks 10 cm in height and identified the site with a metal tag. Every winter (May–August) we recorded seedling survival and total height per individual (at 6, 18 and 33 months after planting) to estimate growth throughout the growing season (approximately from December to April). We considered seedlings to be dead when the aboveground biomass was dry or had disappeared. To characterize the areas surrounding the exclosure in terms of stocking rates, at each visit we recorded the number of dung present in 30 randomly placed 30 × 30 cm squares (following Cingolani et al., 2003 and von Müller et al., in press).

2.4. Data analyses

We analyzed two response variables for each species and growing season: (1) proportion of live seedlings and (2) seedling height. Both response variables were analyzed with univariate General Linear Models (GLMs). Livestock exclosure was included as a fixed categorical factor and altitude as a continuous variable. We also added the term 'squared altitude' as another term to determine whether variables had an optimum at intermediate altitudes. We included main effects and the interaction between exclosure and altitude. We performed manual backward selection to eliminate non-statistically significant variables and terms from the models. When necessary, we applied $\log_{10}$ transformations to meet assumptions of homoscedasticity and normality, which were checked with Levene and Kruskal Wallis tests, respectively. We analyzed variables of the three years separately because the assumptions of Repeated Measures GLMs were not met. Since seedling survival in plots outside the exclosure was achieved in less than three sites, we did not include the 'altitude × exclosure' interaction in the case of seedling height of *P. australis* and *M. boaria* after the second and third growing seasons and for *E. cordobensis* after the third growing season. The exclosure factor was not included in the analysis of seedling height of *M. boaria* after the third growing season.

3. Results

For the three species, both seedling survival (Table 2) and height (Table 3) were significantly affected by altitude, livestock grazing and/or the interaction of both factors. The response of seedling survival and height to altitude differed between species. By contrast, seedling survival and height of the three species were significantly lower at most sites with livestock grazing and on most dates (Figs. 1–3).

3.1. Altitude

Seedling survival of *P. australis* decreased toward lower altitudes on all sampling dates (Fig. 1a–c). In contrast, the response of seedling growth to altitude differed between dates (Fig. 1d–f). After three growing seasons, seedling height decreased towards both altitudinal extremes (Fig. 1f), with the highest values of seedling survival and growth being recorded inside the exclosure at between 2200 and 2400 m asl. Maximum accumulated seedling survival after three growing seasons reached 60% inside the exclosure at 2200 and 2400 m asl, with no survival being recorded below 2200 m asl outside the exclosure (Fig. 1c). The highest mean growth rate was 10 cm/year at 2200 m asl. Moreover, the situation at 2200 m asl was unique in that we recorded flowering in 8% of the seedlings inside the exclosure in the third spring (2011).

Seedling survival of *M. boaria* decreased towards both altitudinal extremes after the first growing season, with the highest seedling survival recorded at 1200 and 1600 m asl (Fig. 2a). After the second growing season, seedling survival decreased towards lower altitudes (Fig. 2b) and after the third growing season, it was not related to altitude (Fig. 2c; Table 2). By contrast, seedling height decreased toward upper altitudes after each growing season (Fig. 2d–f). Maximum seedling survival after three growing seasons was 40% inside the exclosure at 2400 m asl, with no seedling survival outside the exclosure (except at 2400 m asl) or inside the exclosure at 900 and 1800 m asl (Fig. 2c). The highest mean growth rate was 23 cm/year in 1200 m asl.

Regarding seedling survival of *E. cordobensis*, altitude was not statistically significant at any of the three growing seasons (Table 2; Fig. 3a–c). However, seedling survival decreased toward both altitudinal extremes, although such pattern was interrupted by a high mortality at 1800 m asl (Fig. 3b and c). On the other hand, seedling height of *E. cordobensis* decreased toward both altitudinal extremes after each growing season (Fig. 3d–f). After three growing seasons, maximum seedling survival reached 87% at 1600 m asl inside the exclosure, with no survival outside the exclousure except at 900 and 2400 m asl (Fig. 3c). The highest growth rate was 20 cm/year inside the exclosure at 1200 m asl. In the spring of the third year (2011), we recorded flowering in 4% and 15% of the surviving seedlings inside the exclosure at 1200 and 1600 m asl, respectively.

3.2. Livestock

All seedlings outside the exclosure were browsed and the three species were able to sprout after browsing. After the three growing seasons, seedling survival was 66%, 95% and 80% lower outside than inside the exclosure for *P. australis*, *M. boaria* and *E. cordobensis*, respectively. In turn, mean seedling height was 58%, 29% and 83% lower outside than inside the exclosure for *P. australis*, *M. boaria*, and *E. cordobensis*, respectively. The differences in survival and height between inside and outside the exclosure were significant in all seasons (Figs. 1–3), except in *M. boaria* after the second growing season (Tables 2 and 3).

The average dung counts from 2008 to 2011 were moderate (*sensu* Teich et al., 2005) at the highest altitude (2700 m asl) and were high at the other six sites (900–2400 m asl) (Fig. 4). At all altitudes, the highest proportion of dung was of cattle, and at some altitudes and in a lower proportion, of horses, sheep and goats.

Table 2
Summary of the effect of altitude, exclosure and their interaction on seedling survival of *Polylepis australis*, *Maytenus boaria* and *Escallonia cordobensis*, for each growing season analyzed with General Lineal Models. Significant *P*-values (<0.05) are marked in bold. Factors without *P*-value were removed manually in backward procedure.

Seedling survival					
Species	Growing season	Altitude(Altitude^2)	Exclosure	Altitude × exclosure	Adj R^2
P. australis	First	0.432 (0.221)	**0.005**	**0.030**	0.710
	Second			**0.012**	0.471
	Third	**0.015**		**0.033**	0.482
M. boaria	First	**0.025 (0.018)**		**0.009**	0.569
	Second	**0.034**			0.266
	Third		**0.040**		0.249
E. cordobensis	First	0.170	**0.004**		0506
	Second	0.839 (0.690)	**0.048**		0.267
	Third		**<0.001**		0.670

Table 3
Summary of the effect of altitude, exclosure and their interaction on seedling height of *Polylepis australis*, *Maytenus boaria* and *Escallonia cordobensis*, for each growing season analyzed with General Lineal Models using backward stepwise selection of best models. Significant *P*-values (<0.05) are marked in bold. Factors without *P*-value correspond to those removed manually in backward procedure. The 'altitude × exclosure' interaction was not included in the case of seedling height of *P. australis* and *M. boaria* after the second and third growing seasons, and *E. cordobensis* after the third growing season. Exclosure factor was also not included in the analysis of seedling height of *M. boaria* after the third growth season (see details in Section 2.4).

Seedling height					
Species	Growing season	Altitude(Altitude^2)	Exclosure	Altitude × exclosure	Adj R^2
P. australis	First		**<0.001**		0.206
	Second	**0.056**	**0.013**		0.148
	Third	**0.012 (0.015)**	**<0.001**		0.381
M. boaria	First	**0.016 (<0.001)**		**<0.001**	0.495
	Second	**<0.001**	0.249		0.556
	Third	**0.028** (0.056)			0.454
E. cordobensis	First	**<0.001 (<0.001)**		**0.026**	0.431
	Second	**0.034 (0.001)**	**0.002**	**0.027**	0.603
	Third	**0.021 (0.001)**	**0.013**		0.604

3.3. Interaction between altitude and livestock

The differences in *P. australis* seedling survival between inside and outside the exclosure increased toward lower altitudes after the first growing season (Fig. 1a). Differences in seedling height also increased towards lower altitudes for *M. boaria* and *E. cordobensis* after the first growing season (Figs. 2d and 3d, respectively). By contrast, differences in *M. boaria* seedling survival increased towards upper altitudes after the first growing season (Fig. 2a).

4. Discussion

This study provides clear evidence about the negative effect of livestock grazing on seedling establishment of the three principal woody species of Sierras Grandes in central Argentina. Contrary to the uniform response of seedlings to livestock, the response to altitude differed among species and between seedling survival and height.

4.1. Altitude

Inside the exclosures, seedling survival of the three species decreased toward lower altitudes and toward both altitudinal limits in the case of *M. boaria* and *E. cordobensis*. In the case of *P. australis*, our result is consistent with a previous study that found lower rates of seedling emergence toward lower altitudes (País Bosch et al., in press). To the best of our knowledge, this is the first report on the response of *M. boaria* and *E. cordobensis* to altitude.

On the other hand, the seedling growth of the three species followed a unimodal pattern in response to altitude, at least in one of the three growing seasons studied. In the case of *P. australis*, our results are in agreement with Marcora et al. (2008) who have reported radial growth of *P. australis* adults following a unimodal pattern in response to altitude, with maximum growth rates recorded between 2100 and 2400 m asl and decreasing toward both altitudinal extremes.

The decline in survival and height growth with increasing altitude is at least in part due to extreme events such as late spring frosts and low temperatures (Cárdenas and Lusk, 2002; Körner, 2007; Körner and Paulsen, 2004). Towards the lower altitudes, loss of carbohydrates and water stress would be the reasons for lower seedling growth and survival (Bruelheide and Lieberum, 2001; Jump et al., 2009; Mäkinen et al., 2002). Accordingly, in the upper belt of the Córdoba Mountains, the climate is cold and damp, whereas it is warmer (Marcora et al., 2008) and drier (País Bosch et al., in press), with decreasing altitude and the vegetation is increasingly xeromorphic (Cingolani et al., 2003). Similar unimodal patterns in response to elevation were found in other mountain systems for tree growth of *Nothofagus solandri* and *Picea abies* (Mäkinen et al., 2002; Norton, 1984) and for seedling establishment of *Nothofagus pumilio* (Cuevas, 2002).

The increasing temperatures and drought stress towards lower altitudes would also explain the decrease in survival of the three species toward lower altitudes. On the other hand, while a reduction in survival toward the highest extreme would be expected, seedling survival of *P. australis* increased with altitude. This response could be related to the capacity of this species to grow at altitudes beyond the upper altitudes of the Sierras Grandes (2800 m asl). In fact, *P. australis* reaches 3500 m asl at its northern distribution in northwestern Argentina (Renison et al., unpublished data).

The highest values of different fitness parameters of *P. australis* in mountains of central Argentina were recorded between 1800

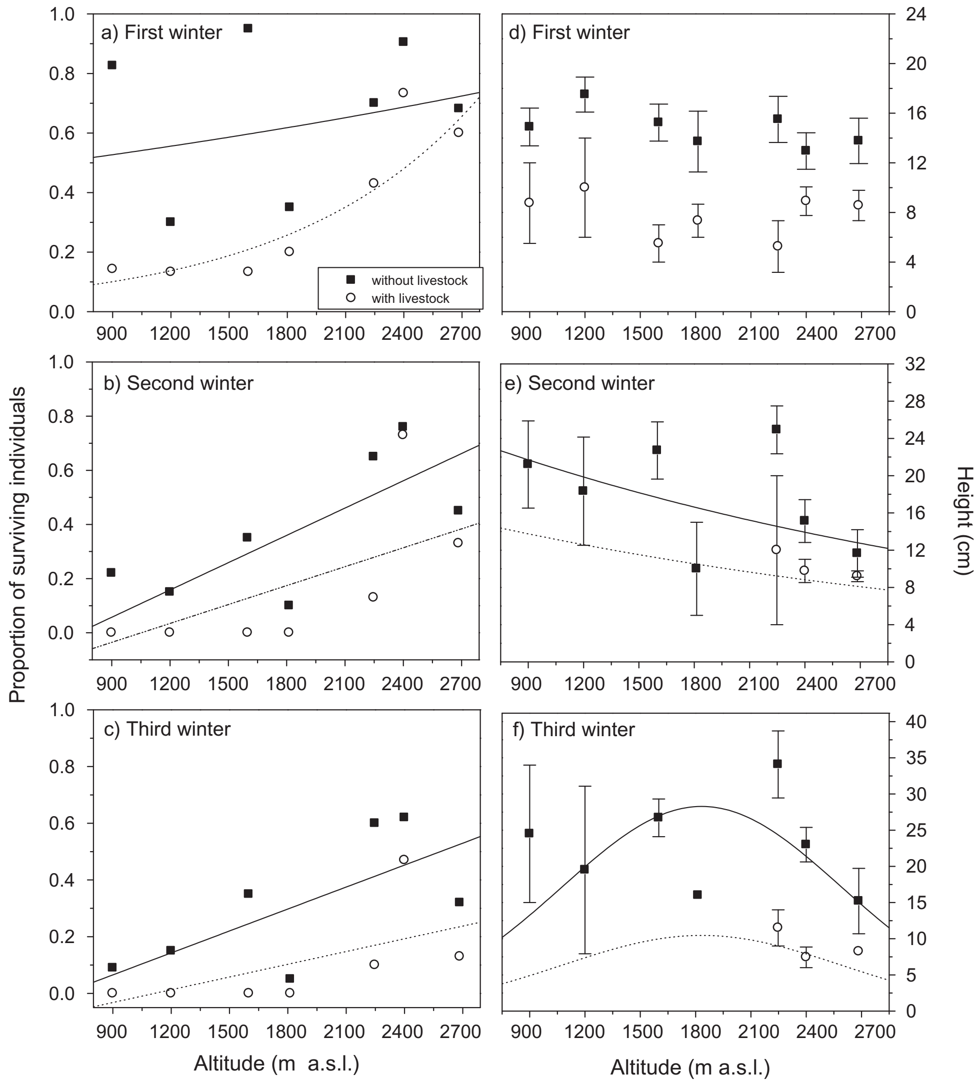

Fig. 1. Proportion of seedling survival (a–c) and seedling height (f–g) of *Polylepis australis* in response to altitude and exclosure effects in the three growing seasons. Solid lines show GLM for seedlings inside exclosure (without livestock) and dotted lines, for seedlings outside exclosure (with livestock).

and 2400 m asl (Marcora et al., 2008; this study). Hence, this altitudinal belt would be optimum for this species in Sierras Grandes. Accordingly, seedlings of *P. australis* at 2200 m asl produced flowers after the third spring. In the case of *M. boaria* and *E. cordobensis*, our data are not enough to determine optimum altitudes for both species. However, highest values of seedling survival and height at 1200 and 1600 m asl, as well as the event of fruit production of *E. cordobensis* inside these plots, suggest that these altitudes are better for seedling performance. Accordingly, we observed small forests of *M. boaria* on inaccessible slopes and valley bottoms at about 1200 m asl (personal observation).

Seedling growth and survival could be better at the altitude where seeds were collected (1400–1900 m asl) because the effect of local adaptation (Mátyás, 1994). However, only seedling survival of *E. cordobensis* was higher within this altitudinal range. Moreover, seedling response of *P. australis* was consistent with patterns previously reported (Marcora et al., 2008), suggesting that in our study the provenance effect is lower than the altitudinal effect.

4.2. Livestock

Our results show that livestock grazing markedly reduced seedling survival and height of the three principal woody species of the Sierras Grandes. Although seedlings of the three species were able to sprout after browsing, livestock effect was enough to hinder seedling establishment in most sites along the gradient (Figs. 1–3). Moreover, flowering of *P. australis* and *E. cordobensis* recorded inside the exclosure further supports the negative effects of livestock grazing on seedling fitness.

The marked livestock effect on seedlings could be due to livestock preference for these species or to the high stocking rates in most sites (Fig. 4). In the case of *P. australis*, previous studies showed that livestock browse most of the annual shoot production both under moderate and high stocking rates, maintaining trees within livestock reach for several years (Giorgis et al., 2010; Teich et al., 2005). Likewise, many browsed old trees of *E. cordobensis* persist within livestock reach (personal observation). However, this would not be the case of *M. boaria*, because no dwarf trees were found. Moreover, previous studies found that *M. boaria* is selected by livestock (Donoso and Wendler, 1985); hence, we could speculate that under livestock pressure immature trees of this species might not persist as dwarf trees and would die. Considering that *M. boaria* does not form a seed bank (Cabello and Camelio, 1996), livestock effects on population of this species would be severe.

On the other hand, under high stocking rates, livestock diet is expected to become broader, including less preferred groups such as shrubs (Mobæk et al., 2009). In most areas on high topographic

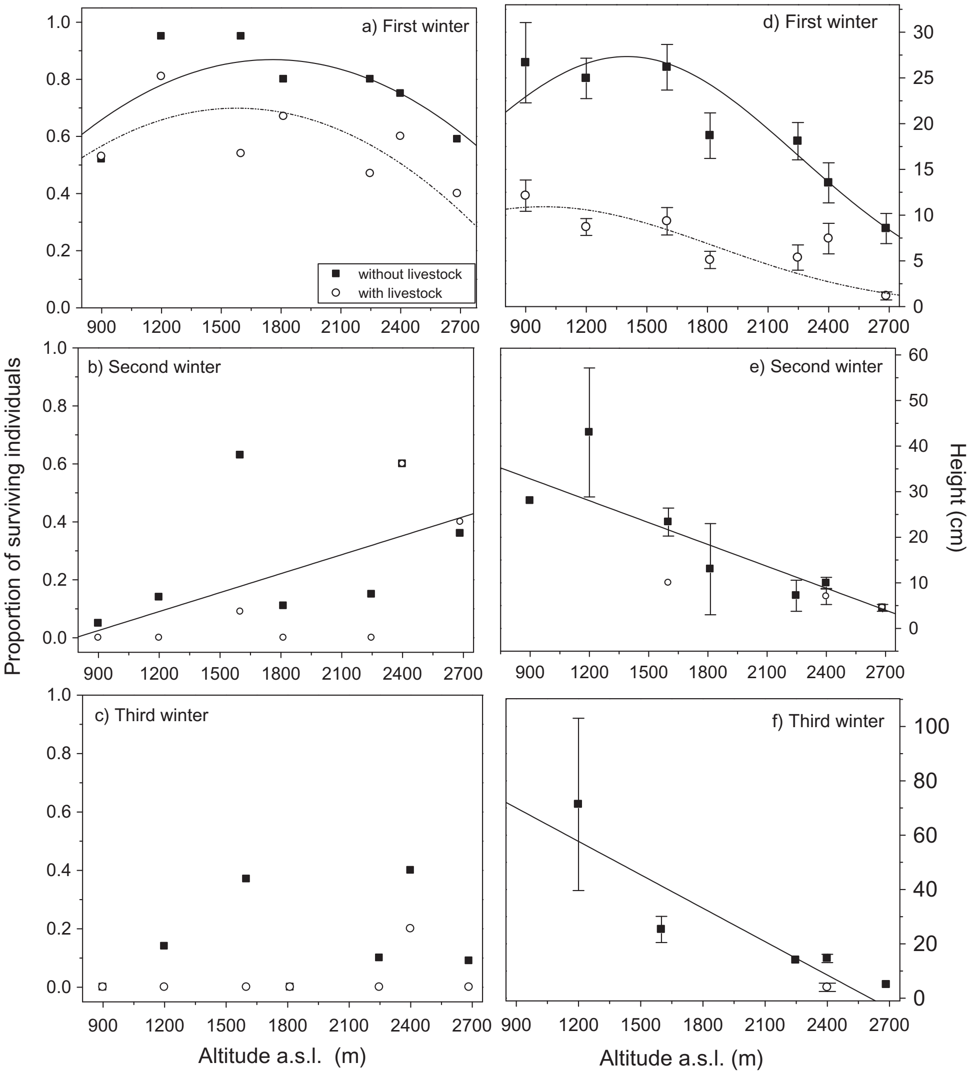

Fig. 2. Proportion of seedling survival (a–c) and seedling height (f–g) of *Maytenus boaria* in response to altitude and exclosure effects in the three growing seasons. Solid lines show GLM for seedlings inside exclosure (without livestock) and dotted lines, for seedlings outside exclosure (with livestock).

positions in the Sierras Grandes, stocking rates are high, as observed in our study sites, especially near houses and roads (Cingolani et al., 2008; Renison et al., 2010). Altogether, this evidence and our findings about seedling performance suggest that browsing at such high stocking rates might be reducing seedling survival and maintaining seedling height within livestock reach. In turn, this might increase the time a plant needs to reach a size that can be out of the reach of herbivores, overall delaying forest development. A similar livestock effect on woody vegetation has been reported for *Sorbus aucuparia*, *Abies alba*, *Acer pseudoplatanus*, *Fagus sylvatica*, and *P. abies* (Motta, 2003; Vandenberghe et al., 2007). In contrast, other woody species (including other *Polylepis* species) occurring in similar ecosystems are not browsed by livestock. Hence, in those systems, unlike in the Sierras Grandes, livestock might have far less influence on forest distribution (Cierjacks et al., 2007, 2008).

Our data regarding the combined influence of altitude and livestock suggest a higher effect of livestock on seedling survival and growth at lower and intermediate altitudes. Livestock influence is expected to increase toward the upper limit of distribution, especially on mountains and cold ecosystems because the susceptibility of vegetation to livestock pressure would be increased under harsh weather conditions that delay growth (Körner, 2003; Hofgaard et al., 2009; Speed et al., 2011). On the other hand, the combined effect of climate and livestock on seedlings could well increase towards the lower edge of distribution (e.g., browsing suppresses both shoot and root growth, reducing likelihood of surviving to drought of lower altitudes). This would be the case of *P. australis*, which reaches its lower limit at the lowest altitudes included in our study. Unfortunately, since stocking rates at lower and intermediate altitudes were higher than at upper altitudes (Fig. 4), we cannot infer if this response is due to a higher effect of livestock at these altitudes or just to higher stocking rates.

Alternatively to the idea that at high altitudes forests in the Sierras Grandes are climatically restricted to deep ravines (Cabido et al., 1985; Cingolani et al., 2003; Enrico et al., 2004), recent studies suggest that vegetation of these mountains would be strongly “consumer controlled” at present and that the forest could be more extensive under lower pressure of livestock and fire (Cingolani et al., 2008; Renison et al., 2006). In line, our results do not support a climatic altitudinal limit of species distribution between 1300 and 1700 m asl. or the overlapping of altitudinal limits and livestock effects. The results rather stress livestock as the major driver of the lack of forest in this altitudinal belt (Cingolani et al., 2008; Renison et al., 2006).

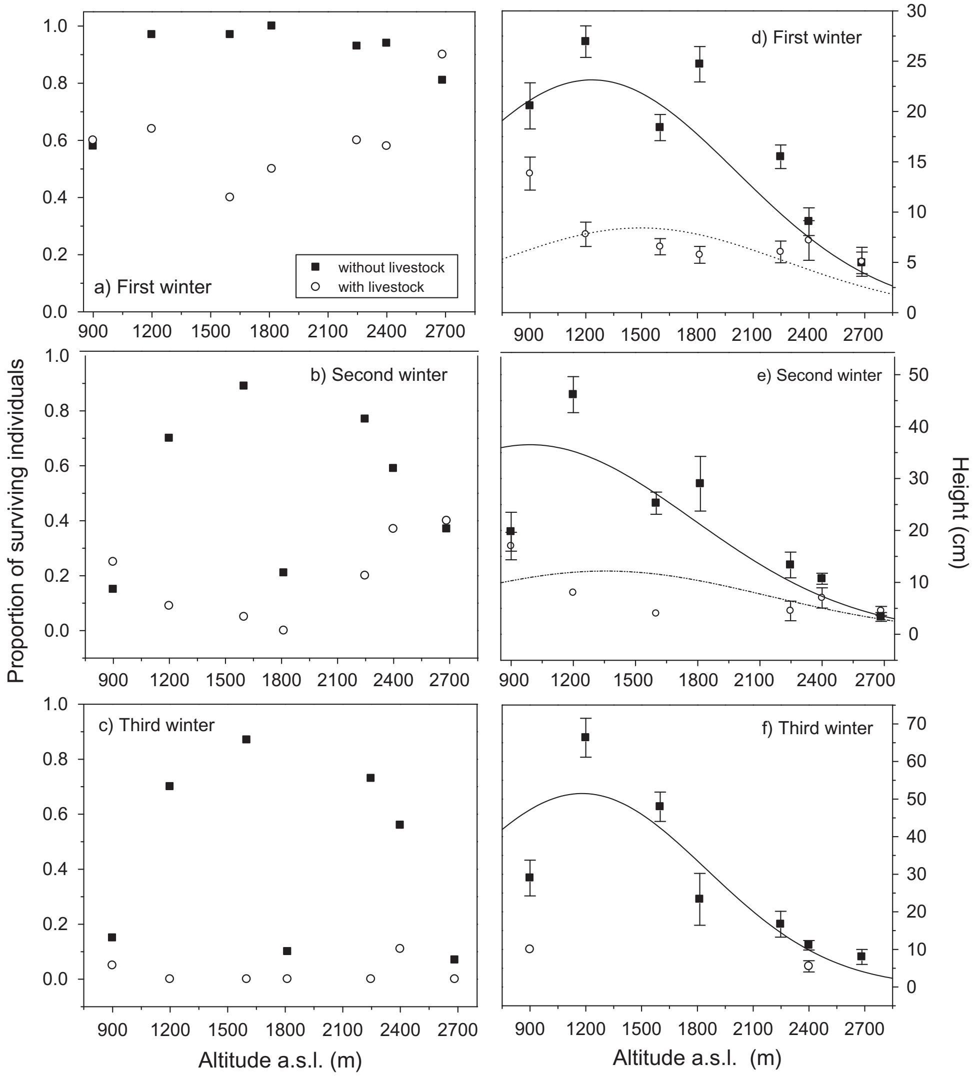

Fig. 3. Proportion of seedling survival (a–c) and seedling height (f–g) of *Escallonia cordobensis* in response to altitude and exclosure effects in the three growing seasons. Solid lines show GLM for seedlings inside exclosure (without livestock) and dotted lines, for seedlings outside exclosure (with livestock).

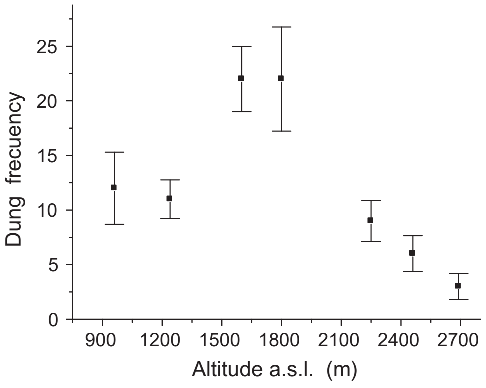

Fig. 4. Mean number of squares with presence of dung outside exclosure. Average values of the total study period (±S.E.).

Finally, although temperatures can explain vegetation patterns at a global scale (Körner and Paulsen, 2004; Körner, 2007), other factors, such as livestock grazing, can determine patterns at local and regional scales (Aune et al., 2011; Bond, 2005; Hofgaard et al., 2009; Speed et al., 2010). While the Sierras Grandes are below the global position of treelines (Körner and Paulsen, 2004), our results support the idea that the current lack of forests in most of the area, and perhaps in similar mountain regions with palatable tree species (Byers, 2000; Cuevas, 2002; Hensen, 2002; Hofgaard et al., 2010; Kessler, 1995), is possibly due to the occurrence of disturbances, such as livestock grazing.

Acknowledgments

Research was supported by Universidad Nacional de Córdoba, CONICET (research grant to DR, PAT and MRC and scholarships to PIM and AIPB), FONCyT (BID PICT 953) and the Inter-American Institute for Global Change Research (CRN II 2005; supported by the US National Science Foundation Grant GEO-0452325). We are grateful to A. Cingolani and two anonymous reviewers for useful comments on an earlier version of the manuscript. We also thank R. Renison for seedling production, many volunteers for seed collection, seedling planting and seedling measurements, especially Natalia Noda and Iván Barberá; and land owners for allowing us to establish the exclosures in their properties.

References

Anderson, R.C., 1981. An evolutionary model summarizing the roles of fire, climate, and grazing animal in the origin and maintenance of grasslandes: an end paper. In: Estes, J.R., Tyrl, R.J., Brunken, J.N. (Eds.), Grasses and Grasslands; Systematic and Ecology. University of Oklahoma Press, Norman, Oklahoma, pp. 297–308.

Aune, S., Hofgaard, A., Söderström, L., 2011. Contrasting climate- and land-use-driven tree encroachment patterns of subarctic tundra in northern Norway and the Kola Peninsula. Can. J. For. Res. 41, 437–449.

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

Bond, W.J., Woodward, F.J., Midgley, G.F., 2005. The global distribution of ecosystems in a world without fire. New Phytol. 165, 525–538.

Bruelheide, H., Lieberum, K., 2001. Experimental test for determining the causes of the altitudinal distribution of *Meun athamanticum* Jacq. in the Harz Mountains. Flora 196, 227–241.

Byers, A.C., 2000. Contemporary landscape change in the Huascarán National Park and Buffer Zone, Cordillera Blanca, Peru. Mountain Res. Dev. 20 (1), 52–63.

Cabello, A., Camelio, M.E., 1996. Germinación de semillas de maitén (*Maytenus boaria*) y producción de plantas en vivero. Rev. Ciencias Forestales 11 (1–2), 3–17.

Cabido, M.R., 1985. Las comunidades vegetales de la Pampa de Achala, Sierras de Córdoba, Argentina. Docums. Phytosociol. 9, 431–443.

Cabrera, A.L. 1976. Regiones fitogeográficas Argentinas. Ed. Acme, Buenos Aires.

Cairns, D.M., Moen, J.M., 2004. Herbivory influences tree lines. J. Ecol. 92, 1019–1024.

Cárdenas, C.G., Lusk, C.H., 2002. Juvenile height growth rates and sorting of three Nothofagus species on an altitudinal gradient. Gayana Bot. 59 (1), 21–25.

Cierjacks, A., Iglesias, J.E., Wesche, K., Hensen, I., 2007. Impact of sowing, canopy cover and litter on seedling dynamics of two *Polylepis* species at upper lines in central Ecuador. J. Trop. Ecol. 23, 309–318.

Cierjacks, A., Rühr, N.K., Wesche, K., Hensen, I., 2008. Effects of altitude and livestock on the regeneration of two treeline forming *Polylepis* species in Ecuador. Plant Ecol. 194, 207–221.

Cingolani, A.M., Cabido, M., Renison, D., Solís Neffa, V., 2003. Combined effects of environment and grazing on vegetation structure in Argentine granite grasslands. J. Veg. Sci. 14, 223–232.

Cingolani, A.M., Renison, D., Zak, M.R., Cabido, M., 2004. Mapping vegetation in a heterogeneous mountain rangeland using Landsat data: an alternative method to define and classify land-cover units. Remote Sens. Environ. 92, 84–97.

Cingolani, A., Renison, D., Tecco, P., Gurvich, D., Cabido, M., 2008. Predicting cover types in a mountain range with long evolutionary grazing history: a GIS approach. J. Biogeogr. 35, 538–551.

Crawford, R.M.M., 1989. Studies in plant survival. Studies in Ecology, vol. 11. Blackwell Scientific Publications, Oxford, UK.

Cuevas, J.G., 2000. Tree recruitment at the *Nothofagus pumilio* alpine timberline in Tierra del Fuego. Chile. J. Ecol. 88, 840–855.

Cuevas, J.G., 2002. Episodic regeneration at the *Nothofagus pumilio* alpine timberline in Tierra del Fuego. Chile. J. Ecol. 90, 52–60.

Díaz, S., Acosta, A., Cabido, M., 1994. Community structure in montane grasslands of central Argentina in relation to land use. J. Veg. Sci. 5 (4), 483–488.

Donoso, C., Wendler, J., 1985. Antecedentes morfológicos y genecológicos de *Maytenus boaria*. Bosque 6 (2), 93–99.

Ellemberg, H., 1979. Man's influence on the tropical mountain ecosystems in South America. J. Ecol. 67, 401–416.

Enrico, L., Funes, G., Cabido, M., 2004. Regeneration of *Polylepis australis* Bitt. In the mountains of central Argentina. Forest Ecol. Manage. 190, 301–309.

Giorgis, M.A., 2011. Caracterización florística y structural del Bosque Chaqueño Serrano (Córdoba) en relación a gradientes ambientales y de uso. Universidad Nacional de Córdoba. Tesis de doctorado, pp. 183.

Giorgis, M.A., Cingolani, A.M., Teich, I., Renison, D., Hensen, I., 2010. Do *Polylepis australis* trees tolerate herbivory? Seasonal patterns of shoot growth and its consumption by livestock. Plant Ecol. 207, 307–310.

Hensen, I., 2002. Impacts of anthropogenic activity on the vegetation of Polylepis woodlands in the región of Cochabamba. Bolivia. Ecotropica. 8, 183–203.

Hofgaard, A., Dalen, L., Hytteborn, H., 2009. Tree recruitment above the treeline and potential for climate-driven treeline change. J. Veg. Sci. 20, 1133–1144.

Hofgaard, A., Løkken, J., Dalen, L., Hytteborn, H., 2010. Comparing warming and grazing effects on birch growth in an alpine environment – a 10-year experiment. Plant Ecol. Diversity 3 (1), 19–27.

Jump, A.S., Mátyás, C.M., Peñuelas, J., 2009. The altitude-for-latitude disparity in the range retractions of woody species. Trends Ecol. Evol. 24 (12), 694–701.

Kessler, M., 1995. Present and potential distribution of Polylepis (Rosaceae) forest in Bolivia. In: Churchill, S.P., Balslev, H., Forero, E., Luteyn, J.L. (Eds.), Biodiversity and Conservation of Neotropical Montane Forests. New York, pp. 281–294.

Körner, C., 1999. Alpine Plant Life. Functional Plant Ecology of High Mountain Ecosystems Ed. Springer-Verlag, Berlin Heidelberg, pp. 343.

Körner, C., 2003. Carbon limitation in trees. J. Ecol. 91, 4–17.

Körner, C., 2007. Climatic treelines: conventions, global patterns, causes. Erdkunde 61, 316–324.

Körner, C., Paulsen, J., 2004. A world-wide study of high altitude treeline temperatures. J. Biogeogr. 31, 713–732.

Luti, R., Solis, M., Galera, F.M., Müller, N., Berzal, M., Nores, M., Herrera, M., Barrera, J.C., 1979. Vegetación. In: Vazquez, J., Miatello, R.y., Roque, M. (Eds.), Geografía Física de la Provincia de Córdoba, Buenos Aires, pp. 297–368.

Mäkinen, H., Nöjd, P., Kahle, H.P., Neumann, U., Tveite, B., Mielikäinen, K., Röhle, H., Spiecker, H., 2002. Radial growth variation of Norway spruce (*Picea abies* (L.) Karst.) across latitudinal and altitudinal gradients in central and northern Europe. Forest Ecol. Manage. 171, 243–259.

Marcora, P., Hensen, I., Renison, D., Seltmann, P., Wesche, K., 2008. The performance of *Polylepis australis* trees along their entire altitudinal range: implications of climate change for their conservation. Diversity Distrib. 14, 630–636.

Mátyás, Csaba., 1994. Modeling climate change effects with provenance test data. Tree Physiol. 14, 797–804.

Mobæk, R., Mysterud, A., Loe, L.E., Holand, O., Austrheim, G., 2009. Density dependent and temporal variability in habitat selection by a large herbivore; an experimental approach. Oikos 118, 209–218.

Motta, R., 2003. Ungulate impact on rowan (*Sorbus aucuparia* L.) and Norway spruce (*Picea abies* (L.) Karst.) height structure in mountain forest in the eastern Italian Alps. Forest Ecol. Manage. 181, 139–150.

Norton, D.A., 1984. Phenological growth characteristics of *Nothofagus solandri* trees at three altitudes in the Craigieburn Range, New Zealand. N.Z. J. Bot. 22, 413–421.

País Bosch, A.I., Tecco, P.A., Funes, G., Cabido, M., in press. Efecto de la temperatura en la regeneración de especies leñosas del Chaco Serrano e implicancias en la distribución actual y potencial de bosques. Bol. Soc. Argent. Bot.

Renison, D., Cingolani, A.M., Suárez, R., 2002. Efectos del fuego sobre un bosquecillo de *Polylepis australis* (Rosaceae) en las montañas de Córdoba. Argentina Rev. Chil. Hist. Nat. 75, 719–727.

Renison, D., Hensen, I., Suárez, R., Cingolani, A.M., 2006. Cover and growth habit of *Polylepis* woodlands and shrublands in the mountains of central Argentina: human or environmental influence? J. Biogeogr. 33, 876–887.

Renison, D., Hensen, I., Suarez, R., Cingolani, A.M., Marcora, P., Giorgis, M.A., 2010. Soil conservation in *Polylepis* mountain forests of Central Argentina: Is livestock reducing our natural capital? Aust. Ecol. 35, 435–443.

Speed, J.D., Austrheim, G., Hester, A., Mysterud, A., 2010. Experimental evidence for herbivore limitation of the treeline. Ecology 91 (11), 2414–3420.

Speed, J.D.M., Austrheim, G., Hester, A.J., Mysterud, A., 2011. Growth limitation of mountain birch caused by sheep browsing at the altitudinal treeline. Forest Ecol. Manage. 261, 1344–1352.

Teich, I., Cingolani, A.M., Renison, D., Hensen, I., Giorgis, M., 2005. Do domestic herbivores retard *Polylepis australis* Bitt. woodland recovery in the mountains of Córdoba, Argentina? Forest Ecol. Manage. 219, 229–241.

Tranquilini, W., 1979. Physiological Ecology of the Alpine Timberline. Tree Existence at High Altitudes with Special Reference to the European Alps. Springer, Berlin, Germany, pp. 137.

Vandenberghe, C., Freléchoux, F., Moravie, M.A., Gadallah, F., Buttler, A., 2007. Short-term effects of cattle browsing on tree sapling growth in mountain wooded pastures. Plant Ecol. 188, 253–264.

Vera, F.W.M., 2000. Grazing Ecology and Forest History. CABI Publishing, Wallingford, Oxon, pp. 506.

von Müller, A.R., Cingolani, A.M., Vaieretti, M.V., Renison, D., in press. Estimación de carga bovina localizada a partir de frecuencia de deposiciones en un pastizal de montaña. Ecología Austral.