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Effect of browsing by ungulates on sapling growth of Scots pine in a Mediterranean environment: consequences for forest regeneration

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Abstract

The impact of mammalian herbivory on Scots pine (*Pinus sylvestris* L.) sapling performance was quantified in three native forests located in two Mediterranean mountains, the Sierra Nevada and Sierra de Baza (SE Spain). More than 98% of the damage to terminal shoots was caused by goats and Spanish ibex in Sierra Nevada and sheep in Sierra de Baza. Some 72% of the tagged saplings ($n = 619$) were browsed during at least 1 year of monitoring (1995–1997). There were between-forest differences in herbivory pressure. Moreover, the herbivory pressure was significantly higher during a dry year (1995) than during wet ones (1996 and 1997). Overall, when browsing a sapling, ungulates consumed almost 30% of its apical shoots, and 85% of saplings were browsed more than once after establishment. As a consequence, ungulates severely affected the Scots pine sapling growth rate, and therefore browsed saplings grew slower than saplings unbrowsed by ungulates. Thus, according to exponential growth equations, the time necessary to attain a height threshold to escape from mammalian herbivores (150 cm height in our study forests) and start reproduction was retarded by the herbivory up to 12 years. Ungulates are a major factor hindering the natural regeneration and conservation of the last relict forests of Scots pines in SE Spain. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Forest regeneration; Mediterranean environments; Mammal herbivory; *Pinus sylvestris*; Sapling growth

1. Introduction

Mediterranean forests have historically been decimated by cutting, fires and overgrazing, being reduced presently to a mosaic of fragmented small forests. Several factors limit the regeneration ability of these relict forests. Irregularities in rainfall and the strong summer drought typical of the Mediterranean climate dramatically reduce seedling survival and sapling growth (Arista, 1993, 1994; García et al., 1999). Also, herbivores consume many ecologically and silviculturally important woody plant species (Crawley, 1983,

1997; Duncan et al., 1998). In this sense, mammalian browsing on saplings can change their shape and architectural pattern, retarding tree growth rate (Danell et al., 1997 and references therein), and even killing them when herbivory pressure is too strong (Faber, 1996; Izhaki and Ne'eman, 1996 and references therein). As a consequence, browsing mammals can prevent saplings from growing into adults, affecting plant population regeneration disproportionately to the amount of biomass removed (Crawley, 1983; Zamora et al., 1999) and changing the forest composition and development (Huntly, 1991; McInnes et al., 1992; McPherson, 1993; Buckley et al., 1998).

The effect of herbivorous mammals on forest regeneration is expected to be especially dramatic

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in Mediterranean environments, where the typical slow growth rate of most sapling species exacerbates the impact of ungulates (e.g. Egli, 1998). In recent decades, the populations of wild ungulates (Spanish ibex *Capra pyrenaica*, red deer *Cervus elaphus*, fallow deer *Dama dama*, etc.) have increased beyond carrying capacities, this problem being especially critical in some protected areas (Zamora et al., 1996). In addition, subsidies from the European Union have provoked an uncontrolled increase of livestock in many Mediterranean mountains (see e.g. Dubost, 1998). When these animals are mostly browsers, as for example goats, overgrazing severely affects forest regeneration, due to the selective consumption of saplings and resprouts.

Scots pine *Pinus sylvestris* L. is widely distributed throughout the boreal and temperate Palearctic, although it is relict in many Mediterranean mountains (Boratynski, 1991). In Andalusia, SE Spain, this pine species (*Pinus sylvestris* var. *nevadensis* Christ.) inhabits only two mountain ranges, the Sierra Nevada and Sierra de Baza, the southernmost populations in the distribution area of this pine species (Boratynski, 1991). These areas are inhabited by extensive livestock and wild ungulates. Although the effect of browsing mammals on Scots pine performance and population dynamics has been frequently documented in northern latitudes (e.g. Miller and Cummins, 1982; Danell et al., 1991a, b, 1994; Edenius et al., 1993), there is a lack of information about the magnitude and effect of herbivory on Scots pine in Mediterranean areas. In the present paper, we analyse the impact of mammalian herbivory on Scots pine sapling performance in SE Spain, and the subsequent impact on the natural forest regeneration. Specifically, we quantified (1) the abundance and density of saplings; (2) the type and magnitude of the main mortality factors of saplings; (3) the several sources of meristem loss; (4) the impact of herbivory on sapling growth, assessing the spatio-temporal variability in herbivory magnitude; and (5) the potential effect of mammal herbivory on forest regeneration and management.

2. Study sites

This study was conducted in three native forests of southern Spain. The first forest is located in the Sierra

Nevada (Granada, Spain), near Trevenque peak (Trevenque, hereafter). This is a small isolated forest (1700–1950 m a.s.l.) composed of Scots pines, with some *Taxus baccata*, *Acer granatense* and *Lonicera arborea* and with an understory composed of *Juniperus communis*, *J. sabina*, *Berberis hispanica*, *Prunus ramburii*, *Salvia oxyodon*, and other shrubby species.

The second forest, Boleta hereafter, is located in Sierra de Baza (Granada, Spain), 80 km north of Trevenque, and it is a mixed forest (1700–2100 m a.s.l.) composed of Scots and Black pines (*Pinus nigra salzmanii*) growing intermingled with an understory composed mainly of *J. communis*, *J. sabina*, *B. hispanica*, *P. ramburii*, *Astragalus granatensis*, and *Hor-mathophylla spinosa*.

The third forest, Fonfría hereafter, is also located in the Sierra de Baza (1500–2100 m a.s.l.), near the Boleta site. It is composed exclusively of Scots pine, with some scattered *J. communis* and *J. sabina*.

The climate in the study area is of the Mediterranean type, with rain (867 mm on average, period 1990–1998) heaviest in autumn and spring, hot dry summers and cold winters. The study years ranged between extremely dry years (1993–1995) and rainy years (1996 and 1997; see Fig. 1).

3. Methods

In each forest, the density of reproductive and pre-reproductive Scots pine individuals was quantified by $50 \times 20 \text{ m}^2$ transects ($n = 30$ per forest). In each transect, we measured the trunk diameter at breast height (dbh) of the adults, and the height of the saplings. During 1995 and 1996, every month, we indexed the abundance

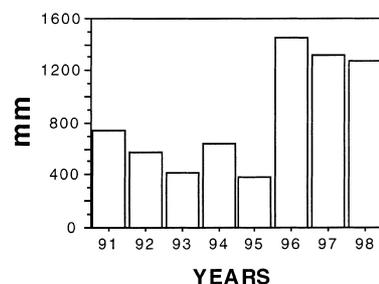


Fig. 1. Temporal variability of annual rainfall (mm) at the study sites, between 1991 and 1998.

of ungulates in each forest, by collecting excrements in six 50 m × 2 m transects (Sutherland, 1996).

In each forest, we established two plots (approximately 1 ha surface), one in the woodland and the other at the treeline, in which we permanently tagged all pine saplings ($n = 619$ saplings) in 1995, to enable individual identification over the study years. For each of these saplings, we recorded: (1) height (cm); (2) age, estimated as number of whorls; this estimate has proven very accurate for Scots pines <30 years (Edenius et al., 1995); (3) stem diameter at soil surface (in mm, by a digital caliper); (4) number of vegetative buds, and (5) internode growth (cm/year), quantified as the growth of the central internode every year of study.

The tagged saplings were monitored twice (at the end of the winter and at the end of the summer) each year from 1995 to 1997 to quantify different sources of mortality and/or damage. We identified the following sources of damage to the apical shoots of tagged saplings: herbivory by browsing ungulates, herbivory by the caterpillar *Retinia resiniella* (Tortricidae) and frost damage to terminal shoots. In addition, we observed other herbivores feeding on saplings needles (e.g. grasshoppers and caterpillars), but this herbivory was minor and did not affect the shoots. No bark damage by hares (*Lepus granatensis*) or voles (*Microtus duodecimcostatus*) was found.

The intensity of ungulate herbivory was quantified by using the following estimates. (1) Risk of herbivory, percentage of herbivorized plants. (2) Damage intensity, proportion of apical shoots consumed by ungulates. This was quantified by marking the apical zone of each pine from 1993 onwards, and by counting the number of total shoots as well as the number of shoots herbivorized by ungulates. This estimate represents a cumulative estimate of herbivory intensity, since it is the number of shoots removed by ungulates over the entire period. (3) Chronic herbivory, estimated as the percentage of terminal leader shoots lost to herbivory since sapling establishment. Given that ungulate herbivory caused more than 98% of the losses of apical dominance in Scots pine in the study areas (see below), we considered the proportion of losses of apical dominance (that is, the number of apical dominance losses divided by the pine age) as an estimate of herbivory pressure that each sapling suffered from the time of establishment. This provides a conservative estimate of the real magnitude of chronic

herbivory, because ungulates can browse on a pine without affecting the terminal leader shoot (see below).

Herbivory intensity was compared between forests by χ^2 and one-way ANOVAs. Temporal variability in herbivory was analysed by a nested, repeated-measures analysis of variance (rmANOVA). This type of analysis requires a balanced design over time (von Ende, 1993). However, the inability to obtain data for all forest \times year combinations caused an imbalance in the design of the rmANOVA when considering all years of the study. Since the Fonfría site had very low herbivory intensity (see below), we performed the rmANOVA introducing data from the 3 years of study and the two main forests (Boleta and Trevenque).

3.1. Analysis of growth rate

Growth rate of saplings was fitted to an exponential equation, since this type of equation best describes the early growth of plants, when individuals are still allocating energy only to growth (Leopold and Kriedemann, 1975; Peters, 1983; Fitter and Hay, 1987; Niklas, 1994), and the saplings monitored were all pre-reproductive. This exponential growth curve assumes that the relative growth rate (RGR) is constant and is simply related to the existing sapling biomass (Fitter and Hay, 1987). We tested whether the RGR was constant during the temporal application period of the curve. For this, we calculated for each tagged sapling the mean value of the RGR over a period of time (Leopold and Kriedemann, 1975; Fitter and Hay, 1987):

$$\text{RGR} = \frac{\ln W_2 - \ln W_1}{t_2 - t_1}$$

where W_1 and W_2 are sapling heights at times 1 and 2, respectively. Afterwards, we plotted these RGR values against sapling height by a linear regression equation. If the RGR was constant for our sapling sample, we expected the slope of the resulting line not to differ significantly from zero.

For our study, we used the following growth-curve equation (see Peters, 1983; Niklas, 1994):

$$W = W_0 e^{kt}$$

where W is the sapling height in cm, W_0 is a constant which refers to the expected W when $t = 0$, e is the base of the natural logarithms 2.71828, k is a constant

Table 1

Number of Scots pines per ha in each plot of the three forests studied, differentiating between pre-reproductive (PRE) and reproductive (REP) individuals^a

Forest	Plot 1 (treeline)			Plot 2 (woodland)		
	PRE	PRE (%)	REP	PRE	PRE (%)	REP
Trevenque	72 ± 13	50.3	71 ± 25	137 ± 16	64.3	76 ± 2
Boleta	29 ± 3	39.7	44 ± 10	161 ± 5	61.0	103 ± 14
Fonfría	137 ± 15	62.3	93 ± 12	995 ± 22	71.0	407 ± 38

^a The relative abundance (%) of pre-reproductive individuals are shown for each plot.

that refers to the per capita growth rate, and t is the time in years. This equation takes the form of a straight line when plotted semi-logarithmically, with RGR being the slope of the resulting regression line (Leopold and Kriedemann, 1975). We fit a different growth equation for each forest (Trevenque and Boleta) and for each group of saplings, depending whether they were herbivorized or not. To test whether the growth rate differed between herbivorized and non-herbivorized saplings, we used ANCOVAs with interaction terms to contrast the slopes of the semi-logarithmic lines between those sapling groups (Dowdy and Wearden, 1991). For this, we introduced in the ANCOVA analyses both age and herbivory as independent variables, and \ln height as the dependent one, assuming that saplings belonging to different groups grew at different rates if the interaction term was significant (Dowdy and Wearden, 1991).

4. Results

The number of reproductive Scots pine individuals/ha varied between forests, since the abundance of adults was higher in Fonfría than in either Boleta or Trevenque ($H = 23.52$, $P = 0.0001$, Kruskal–Wallis test; Table 1). The frequency distributions of adult size, estimated as dbh, were different between the three forests ($P < 0.0001$ in all cases, Kolmogorov–Smirnov test). The Fonfría forest was composed of even-sized adults of around 25 cm diameter, while in Trevenque and Boleta there were individuals >1 m dbh.

Sapling abundance was also higher in Fonfría than in the other two forests ($H = 32.89$, $P < 0.0001$, Kruskal–Wallis test, Table 1). Furthermore, the relative abundance of pre-reproductive individuals per popu-

lation also differed between forests, being higher at Fonfría than at Boleta ($G = 5.64$, $P = 0.02$) and Trevenque ($G = 3.44$, $P = 0.06$).

Scots pine saplings ranged between 2 and 41-year old, although there were between-forest differences in average age ($H = 6.87$, $P = 0.03$, Kruskal–Wallis test). Frequency distributions of sapling heights were also different between Fonfría and Trevenque ($\chi^2 = 12.87$, $P = 0.003$; Kolmogorov–Smirnov test) and Boleta ($\chi^2 = 13.15$, $P = 0.003$; Kolmogorov–Smirnov test), but not between Trevenque and Boleta ($\chi^2 = 5.64$, $P = 0.12$; Kolmogorov–Smirnov test). In Fonfría, there was a higher proportion of large saplings (Fig. 2).

4.1. Herbivore abundance

The activity period of ungulates ranged from early summer (June) to late autumn (September/November). The abundance of ungulates varied between

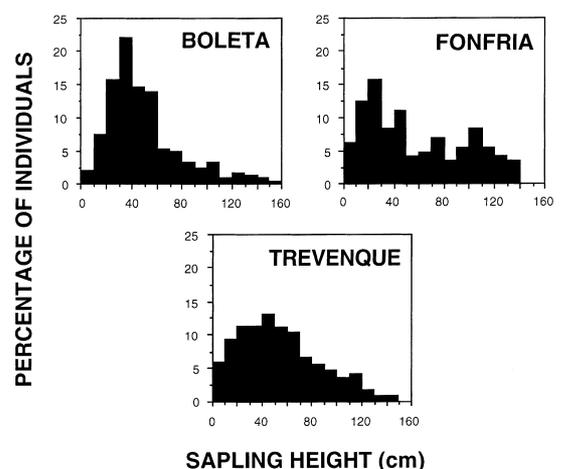


Fig. 2. Distribution of frequencies of sapling heights in the three forests.

forests ($H = 22.72$, $P < 0.001$, Kruskal–Wallis test) but not between years ($P > 0.11$ for all comparisons, Mann–Whitney tests). Thus, ungulate abundance was higher in Boleta (0.55 ± 0.08 g of dry excrements per m^2 , $n = 132$ censuses) than in Trevenque (0.30 ± 0.03 g, $n = 132$), and above all in Fonfría (0.11 ± 0.03 g, $n = 60$). The ungulates were domestic goats (*Capra hircus*) and Spanish ibex (*Capra pyrenaica*) in Trevenque (Sierra Nevada), and domestic sheep (*Ovis aries*) in Boleta and Fonfría (Sierra de Baza).

4.2. Sapling damage and herbivory pressure

Only three out 619 tagged saplings died, two of these due to summer drought.

More than 98% of the damage to terminal shoots was caused by goats and ibex in Sierra Nevada and sheep in Sierra de Baza, whereas frost and herbivory by *R. resiniella* represented less than 1% of total losses.

Scots pines were herbivorized at our study sites only during summer. In total, 72% of the tagged saplings were herbivorized by mammals during at least 1 year of the study. Overall, when browsing a sapling, ungulates consumed $28.36 \pm 1.36\%$ of the apical shoots in Scots pines. Furthermore, ungulates devoured the leader shoot in 33% of the saplings.

Chronic herbivory on saplings of Scots pines was very frequent in our study sites, since saplings lost their apical leader shoot in $37.1 \pm 1.3\%$ of the years of their life. In addition, more than 85% of saplings were browsed more than once after establishment, and 16.5% of the tagged pines were browsed all 3 years of the study (Fig. 3).

4.3. Spatio-temporal variability in herbivory pressure

There was spatial, between-forest variability in all herbivory estimates. Thus, risk of herbivory was much higher in Trevenque (73% of saplings were browsed) and Boleta (85% of pines) than in Fonfría (4.2% of the pines; $\chi^2 = 77.5$, d.f. = 2, $P = 0.0001$). Damage intensity during the study period also differed among forests ($F_{1,451} = 8.22$, $P = 0.004$, Fonfría was excluded from analysis due to the low number of damaged pines), being higher in Trevenque ($20.87 \pm 1.1\%$ of shoots

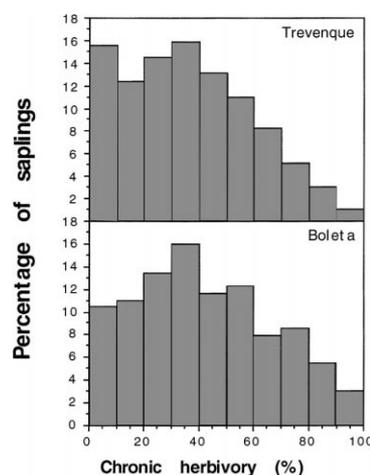


Fig. 3. Distribution frequencies of saplings suffering chronic herbivory (estimated as percentage of apical dominance losses) in Boleta and Trevenque forests.

damage) than in Boleta ($15.04 \pm 1.07\%$) and Fonfría (less than 5%, see Fig. 4). The magnitude of chronic herbivory also varied among forests ($F_{1,552} = 6.76$, $P = 0.0001$), being higher in Boleta ($40.89 \pm 1.96\%$ of terminal leader shoot loss to herbivory per sapling) than in Trevenque ($34.83 \pm 1.37\%$, see Fig. 3). In fact, as revealed in Fig. 3, Boleta had a higher proportion of saplings that suffered herbivory during more than 50% of the years.

There was also temporal variability in herbivory pressure. In fact, 51% of the Trevenque saplings and 86% of the Boleta saplings were browsed during 1995, whereas only 31 and 22% were browsed during 1996,

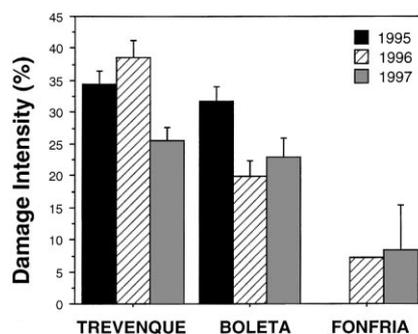


Fig. 4. Spatio-temporal variability in the damage intensity (estimated as percentage of apical shoots removed by ungulates) suffered by the saplings during the study period. Only saplings actually herbivorized by ungulates are considered.

and 43 and 27% during 1997, respectively ($P < 0.0001$, χ^2). Similarly, damage intensity was temporally variable, being overall higher in 1995 versus 1996 and, above all, 1997. However, the forest \times year interaction term was significant (Table 2), since damage intensity decreased from 1995 to 1997 in Boleta, but in Trevenque was highest in 1996 (Fig. 4).

4.4. Relationship between sapling size and herbivory pressure

Risk of herbivory was related to pine height ($\chi^2 = 54.81$, $P = 0.0001$, logistic regression), since no sapling higher than 1.5 m height was browsed in its apical part. However, for the saplings below that threshold, taller pines were more frequently browsed than smaller ones in both Trevenque ($\chi^2 = 12.72$, $P = 0.0004$, logistic regression) and Boleta ($\chi^2 = 10.45$, $P = 0.0012$). Similarly, herbivores more intensely damaged the taller (Trevenque $\beta = 0.15 \pm 0.01$, $t = 2.66$, $P = 0.008$; Boleta $\beta = 0.24 \pm 0.002$, $t = 3.12$, $P = 0.002$) and older pines in both forests (Trevenque $\beta = 0.26 \pm 0.01$, $t = 4.51$, $P = 0.0001$; Boleta $\beta = 0.26 \pm 0.01$, $t = 3.45$, $P = 0.0007$). Finally, chronic herbivory also proved to be related to sapling height (Trevenque $\beta = 0.33 \pm 0.003$, $t = 5.87$, $P = 0.0001$; Boleta $\beta = 0.26 \pm 0.006$, $t = 3.41$, $P = 0.0008$) and age ($P < 0.006$ in all cases).

4.5. Effect of herbivory on sapling growth

There was no between-forest differences in internode growth ($H = 5.21$, $P = 0.07$, Kruskal–Wallis test) in saplings not browsed, despite that Fonfría saplings had larger internodes than both Boleta and Trevenque saplings (Table 3).

Table 2
Summary of the nested repeated-measures analysis of variance for damage intensity^a

	d.f.	MS	F	P
Forest	1	716.7	1.05	0.307
Pine (forest)	322	330549.7		
Year	2	20779.7	27.43	0.0001
Year \times forest	2	11595.3	15.31	0.0001
Error	644	243887.2		

^a Only two forests in which we monitored saplings for 3 years were included in the model.

Table 3

Internode growth (cm/year) in pines with (yes) or without herbivory (no)

Herbivory	Trevenque	Boleta	Fonfría
Yes	5.58 \pm 0.35	4.43 \pm 0.50	
No	6.58 \pm 0.75	6.5 \pm 0.70	7.71 \pm 0.64

Internode growth was significantly higher in pines not browsed during the study period than in those browsed at least during 1 year (Table 3), both in Boleta ($\chi^2 = 7.13$, $P = 0.05$) and Trevenque ($\chi^2 = 7.49$, $P = 0.047$; no data for Fonfría). Moreover, Internode growth was also negatively related to damage intensity in Trevenque ($\beta = -0.11 \pm 0.07$, $F_{1,266} = 4.72$, $P = 0.03$) and Boleta ($\beta = -0.15 \pm 0.09$, $F_{1,154} = 4.34$, $P = 0.04$), with pines suffering higher rates of damage producing shorter internodes. Finally, herbivory caused internode growth to differ between sites ($U = 2.07$, $P = 0.038$, Mann–Whitney test), being greater in Trevenque than in Boleta (Table 3).

Herbivory also manifested effects in the following years. Thus, internode growth of the leader shoot was significantly lower in saplings browsed the previous year (see Fig. 5).

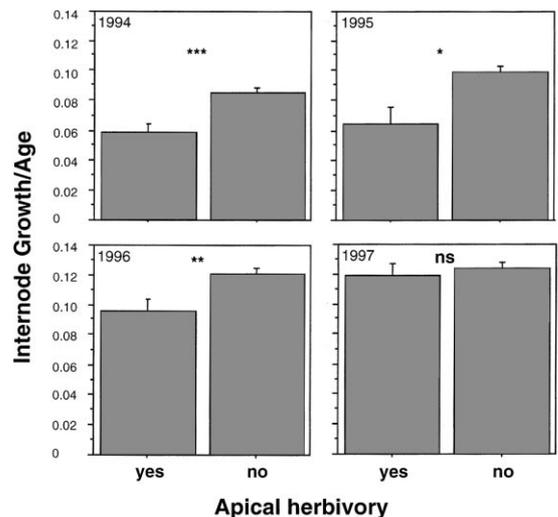


Fig. 5. Internode growth of the terminal leader shoots in saplings suffering herbivory the previous year (yes) vs. those escaping herbivory (no) * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ according to one-way ANOVAS.

The empirical RGRs calculated for tagged saplings did not depend on initial sapling height, since regression slopes of RGR versus height were not significantly different from zero for either Trevenque ($F_{1,239} = 0.23$, $P = 0.635$) or Boleta ($F_{1,76} = 0.27$, $P = 0.608$). This suggests that we can fit pine growth during this pre-reproductive stage to an exponential curve.

The fitting to this exponential growth curve shows that growth in unbrowsed saplings was faster than in browsed ones (Fig. 6). The RGR calculated by the regression equations were higher without herbivory (0.126 and 0.122) than with herbivory (0.084 and 0.059), and the slopes of these regression lines were statistically different for each forest, according to the ANCOVA analyses (Table 4).

5. Discussion

Our results have shown that Scots pine saplings rarely die from drought in our study areas, since summer drought killed only two out of 619 tagged saplings. Furthermore, most damage was caused by

Table 4

Summaries of the ANCOVA analyses to compare in each forest the regression slopes between herbivorized and non-herbivorized saplings resulting from Fig. 5

Forest	d.f.	SS	F	P
<i>Trevenque</i> ^a				
Herb	2	0.750	8.313	0.0003
Age	1	0.168	3.723	0.054
Herb×age	2	0.521	5.775	0.003
Error	299	13.496		
<i>Boleta</i> ^b				
Herb	2	9.629	59.424	0.0001
Age	1	1.357	8.377	0.004
Herb×age	2	1.197	7.386	0.007
Error	157	25.440		

^a Trevenque whole model: $F_{5,299} = 82.96$, $P = 0.0001$, $R^2 = 0.57$.

^b Boleta whole model: $F_{5,157} = 43.20$, $P = 0.0001$, $R^2 = 0.44$.

herbivorous mammals, while herbivory by *R. resi-niella* and frost were negligible. In addition, although we did not register any sapling death due to mammalian herbivory, we have previously noted death due to ungulate trampling of seedlings or saplings younger than 3–4-year old (Hódar et al., 1998, see also Faber (1996) and Izhaki and Ne'eman (1996) for other pine species).

The magnitude of herbivory by ungulates was high, with more than 75% of the saplings being damaged in their apical shoots at least once during the years of study, and with almost all saplings having suffered chronic herbivory of leader shoots (Fig. 2). However, the impact of ungulate herbivory was not spatio-temporally constant, because of differences in ungulate type and abundance. Thus, Fonfría had the lowest herbivory pressure because ungulates were less abundant and were exclusively sheep, which feed mainly on grasses and forbs (e.g. García-González and Cuartas, 1989, 1992a, b; Fandós, 1991; Cuartas and García-González, 1992). Moreover, in Trevenque there was more herbivore pressure than in Boleta, because despite being less abundant, the ungulates were goats and ibex (*Capra* genus), which are mainly browsers and feed more frequently on woody plant species (e.g. García-González and Cuartas, 1989, 1992a, b; Fandós, 1991; Cuartas and García-González, 1992).

There was also high temporal variability in both risk of herbivory and damage intensity, despite that the ungulates were equally abundant all years. Thus,

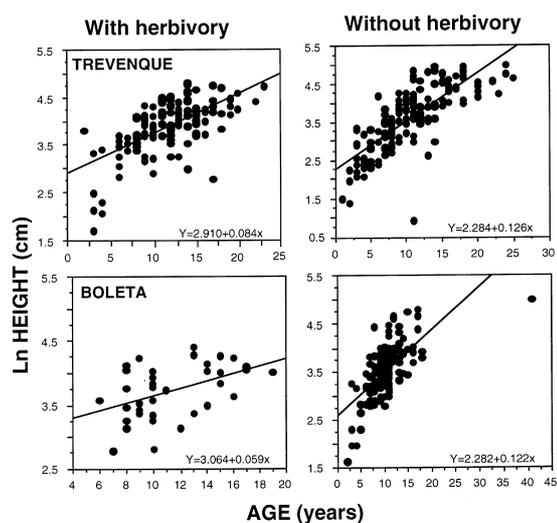


Fig. 6. Difference in individual growth rate of saplings browsed and unbrowsed in Trevenque and Boleta forests. The equations empirically obtained by data are for browsed saplings in Trevenque height = $18.3 e^{0.084Age}$ ($R^2 = 0.39$, $P < 0.0001$) and in Boleta height = $21.4 e^{0.059Age}$ ($R^2 = 0.21$, $P < 0.0001$), and for unbrowsed saplings in Trevenque height = $9.8 e^{0.126Age}$ ($R^2 = 0.61$, $P < 0.0001$) and in Boleta height = $9.8 e^{0.122Age}$ ($R^2 = 0.47$, $P < 0.0001$).

herbivory pressure was much higher during 1995, an extremely dry year, than during 1996 and 1997, two much wetter years. During the dry year, ungulates browsed heavily on pines due to the low pasture production. However, with the end of the drought, these animals preferentially grazed on pasture and forbs, decreasing the damage to pines although the quantity of livestock did not change. This suggests that during dry years, with the same stock number the herbivory pressure on saplings drastically increases.

5.1. Herbivory pressure and sapling growth rate: consequences for forest regeneration

Ungulates had severe impact on Scots pine sapling performance, since growth rate of pre-reproductive Scots pine saplings was significantly slower when browsed than when not browsed (see also Väisänen et al., 1992). A direct consequence of this is that the time necessary to reach a height threshold to escape from mammalian herbivores (150 cm height) and start reproduction is retarded by the herbivory. Thus, the growth equations predict that a sapling needs 21 years in Trevenque and 22 years in Boleta to reach 150 cm high. However, when browsed, this height takes 25 years in Trevenque and 34 years in Boleta, respectively.

This important effect of mammalian herbivory on sapling growth is related to several characteristics of our herbivory-plant system. First, herbivores did not affect all saplings with the same intensity. Saplings below 5–10 cm were not browsed by ungulates presumably because most of these young pines were hidden under shrubs, and saplings taller than 150 cm also escaped browsing in their apical shoots because they were inaccessible to goats and sheep. This indicates that there is a height interval within which saplings can be damaged. Within this interval, taller, and therefore older, saplings were more heavily browsed than shorter pines (see also Crawley, 1997). Therefore, saplings with higher potential growth because their larger size were also the most intensely affected by herbivory.

Second, ungulates browsing Scots pine saplings usually consumed the leader shoot. Thus, the saplings most intensely damaged by ungulates had lower internode growth and a slower growth rate than did saplings escaping from herbivory. This disrupts apical dom-

inance and thereby seriously retards the overall growth of the saplings, resulting in the appearance of cushion-shaped individuals (Miller and Cummins, 1982; Crawley, 1983; Cuartas and García-González, 1992).

Third, the growth rate of Scots pine in Andalusia is very slow, much slower than in other northern localities (e.g. Danell et al., 1991a; Väisänen et al., 1992; Edenius et al., 1995). It has frequently been shown that mammalian herbivory is especially damaging to slow-growing trees, since these are less able to compensate for biomass losses (e.g. Danell et al., 1991a, 1997; Edenius, 1993; Honkanen et al., 1994; Edenius et al., 1995).

Fourth, Scots pines were damaged in our study sites only during summer, the period of active growth for this pine. Summer herbivory has major consequences for saplings, since the effect of the herbivory on sapling growth appeared not only in the current summer but also in the following summer after herbivory event. That is, the effect of mammalian herbivory on sapling growth is expressed the current year as a decrease in biomass, and the next year as a decrease in internode growth rate (see also Danell et al., 1994; Honkanen et al., 1994). This contrasts with most other studies on Scots pine herbivory in the north of Europe, which show that this pine species is damaged by moose only during winter, when pines are dormant (e.g. Danell et al., 1991a, b, 1994; Edenius et al., 1993).

Furthermore, the negative effect of the ungulate herbivory is magnified by chronic herbivory. We have shown that most saplings lost many of their terminal leader shoots to mammalian herbivory year after year, since every sapling was browsed, on an average, in 30% of the years during the pre-reproductive period. Furthermore, many saplings lost their leader terminal shoot 75% of the years. This chronic herbivory is related to the slow growth rate of the Scots pine saplings in Mediterranean environments, since these trees remain within the vulnerability height interval (below 150 cm height) for many years. This chronic herbivory aggravates the deleterious effect of mammalian herbivory by retarding the development of saplings to maturity (e.g. Edenius et al., 1993; Danell et al., 1994; Duncan et al., 1998).

Ungulates are, thus, a main factor explaining the structural differences we have found between the three forests studied. For example, Fonfría forest, the least affected by browsing ungulates, had a much higher

proportion of pre-reproductive individuals versus reproductive ones, an important estimate of sapling availability and regeneration ability. Moreover, this forest contains many large saplings, 150–200 m high, ready to enter the reproductive stage, whereas in Trevenque and Boleta, the forests most affected by browsing, the number of large saplings is very low (Fig. 2). These results agree with studies carried out in Scandinavian Scot pines forests, where moose is a keystone herbivore (Edenius et al., 1993; Danell et al., 1994).

In conclusion, our study suggests that herbivory on saplings, together with other mortality factors, such as a high level of seed predation (Castro et al., 1999) and seedling mortality due to summer drought (Hódar et al., 1998), might prevent the natural regeneration of Scots pine forests in SE Spain. This situation can lead to a living fossil forest, where adult mortality exceeds the recruitment of young reproductive individuals.

5.2. Ecological consequences for management

In view of the effect of herbivory on Mediterranean forest regeneration of Scots pines, some management guidelines can be suggested: (1) it is crucial to prevent chronic herbivory, by the avoidance of raising ungulates every year in the same sectors of the forests. This can be achieved by changing, after several years, the areas in which livestock are raised. The temporal interval should permit the saplings to grow enough to escape chronic herbivory (more than 5 years). (2) Since herbivore damage varies widely depending on the rainfall regime, a fixed number of stock adjusted to the carrying capacity of the site is not useful, because it assumes that the conditions for plant growth remain the same every year (Narjisse, 1998). Therefore, a flexible management of rangeland is needed, in which the livestock number must be adjusted year by year to the current climatic conditions, especially during the dry years. Also, livestock number must be adjusted to the abundance of wild ungulates, which are sharply increasing in most Mediterranean mountains (Pérez et al., 1994; Zamora et al., 1996).

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