Capítulo 5

Respuesta aérea y subterránea de las plantas al pastoreo por herbívoros de diferente tamaño bajo diferentes condiciones de productividad en un pastizal mediterráneo

Este capítulo reproduce íntegramente el texto del siguiente manuscrito:

Rueda, M.& Rebollo, S. *In preparation*. Above and belowground plant responses to grazing by different-sized herbivores under different productivity conditions in a Mediterranean grassland.

Resumen

Los herbívoros influyen en los ecosistemas de pastizal porque modifican los componentes aéreos y subterráneos de las comunidades vegetales. Diferentes estudios sugieren que las respuestas al herbivorismo pueden varíar con la intensidad de pastoreo, tamaño del herbívoro, productividad primaria e historia evolutiva de pastoreo. Mientras muchas de las teorías existentes están centradas en los pastizales dominados por especies perennes, hay una información escasa sobre la repuesta de los pastizales anuales. En el presente trabajo estudiamos la respuesta de la comunidad de plantas al pastoreo por herbívoros de diferente tamaño en un pastizal semiárido dominado por plantas anuales y caracterizado por tener una larga historia evolutiva de pastoreo por herbívoros domésticos y silvestres. Comparamos los efectos de ovejas y conejos en dos posiciones topográficas (zonas altas y bajas del ecosistema) con diferente productividad, mediante un experimento con parcelas de exclusión de herbívoros que excluían a ovejas o a ovejas más conejos. Analizamos los efectos de los herbívoros sobre la biomasa aérea, necromasa, cobertura y altura de la vegetación, suelo desnudo, masa de raíces, distribución vertical de las raíces y ratio ráiz:tallo. Nuestra hipótesis es que los herbívoros de diferente tamaño afectaran de manera diferente a estos parámetros dependiendo de la productividad, ya que en las zonas menos productivas el rebrote de las plantas tras la defoliación está más limitado por las condiciones de estrés hídrico y de nutrientes además de por el pastoreo. El efecto de los herbívoros sobre los parámetros estimados varió mucho con la productividad del sitio pero no con el tipo de herbívoro. En las zonas menos productivas, la exclusión de herbívoros causó un aumento en la cobertura y altura de la vegetación y, como consecuencia, un aumento en la biomasa aérea. En las zonas más productivas, el herbivorismo causó un aumento en la cobertura aérea ya que una mayor disponibilidad de agua y nutrientes favorece la recuperación de tejidos tras el pastoreo. El pastoreo redujo la masa de raíces en las zonas menos productivas pero tuvo el efecto opuesto en las más productivas. El ratio ráiz:tallo aumentó con el pastoreo en ambos sitios, indicando que las plantas invierten más en tejidos subterráneos para favorecer la absorción de nutrientes y agua como un modo de recuperar los tejidos perdidos. Concluimos que las teorías globales sobre la respuestas de las plantas al pastoreo a menudo no pueden aplicarse a los ecosistemas mediterráneos debido a su heterogeneidad y a las condiciones ambientales fluctuantes.

Above and belowground plant responses to grazing by different-sized herbivores under different productivity conditions in a Mediterranean grassland

Rueda, M. & Rebollo, S.

Departamento de Ecología, Edificio de Ciencias, Universidad de Alcalá, E-28871 Alcalá de Henares. Madrid. Spain. Phone: +34 918856406; Fax: +34 918854929, E-mail: marta.rueda@uah.es

Abstract

Mammalian herbivores influence grassland ecosystems by modifying above and belowground components of plant communities. Different studies suggest that plant responses to herbivory can vary with grazing intensity, herbivore body size, primary productivity and evolutionary history of grazing. Whereas most of the existing theories are focus on perennial grasslands, there is a scarcity of information from annual pastures. We studied plant responses to grazing by different-sized herbivores in a semi-arid annual plant community characterised by a long history of grazing by domestic and wild herbivores. We compared the effects of sheep and rabbits in two neighbouring topographic sites (uplands and lowlands) with different productivity by means of a replicated size-selective fence experiment which excluded sheep, and rabbits-plus-sheep. We analysed herbivore effects on aboveground biomass, litter build-up, aerial cover, height, bare soil, root mass, root vertical distribution and root:shoot ratio. We expected that different-sized herbivores differentially affected these parameters but with divergent patterns between productivity sites, since in uplands plant growth after defoliation will be limited by water and nutrient stress conditions as well as grazing. Grazing effects on plant parameters varied greatly with site productivity but not with grazing by herbivores of different sizes. At uplands, herbivore exclusion caused an increase in cover and height of vegetation, leading to an increment in aboveground biomass. At lowlands, grazing caused an increase in plant cover as higher soil water and nutrient abundance can favour plant tissue regrowth after grazing. Grazing reduced root mass in uplands but had the opposite effect in lowlands. Root:shoot ratio increased with grazing in both productivity sites, indicating that grazed plants invest more in subterranean tissues to favour the absorption of nutrients and water as a way to recover the tissues lost in the aerial part. We conclude that the global theories of plant responses to grazing are often not supported in Mediterranean ecosystems due to their complex, fluctuating conditions.

Keywords: Aboveground biomass, annual plant community, litter, root mass, root:shoot ratio, different-sized herbivores, primary productivity, *Oryctolagus cuniculus*.

1. Introduction

Mammalian herbivores influence the function and dynamics of grassland ecosystems by modifying above and belowground features of plant communities. They affect the cover and height of plants, aboveground biomass, and litter accumulation (Nicholson *et al*. 1970, McNaughton 1984, Huntly 1991, Olff *et al*. 1997), regulating the amount of energy and nutrients passing onto higher trophic levels and the availability of plant material for detrivores and decomposers (Olff *et al*. 1999). Grazing can also determine belowground plant patterns, such as root mass, root vertical distribution, and root:shoot ratio (Milchunas and Lauenroth 1989, Rodríguez *et al*. 1995, McNaughton *et al*. 1998), affecting the efficiency of water and nutrient absorption (Lecompte *et al*. 2001). These changes in belowground structure may have important implications for plant-plant interactions, since the majority of plant biomass in grasslands is belowground (Sims and Singh 1978, Leetham and Milchunas 1985, Titlyanova *et al*. 1999, Maarel and Titlyanova 1989). However, the available information about belowground biomass and its distribution in grasslands is still quite limited (McNaughton *et al*. 1998), essentially because of the methodological difficulties associated with observing and measuring root biomass (Vogt *et al*. 1996, Titlyanova *et al*. 1999). Knowledge about above and belowground plant responses to grazing is fundamental to improve our understanding of the ecological role of herbivores in grassland ecosystems, and have profound conservation and land management implications.

Above and belowground plant responses to grazing can vary with the intensity of grazing, herbivore body size, primary productivity, and evolutionary history of grazing (Milchunas and Lauenroth 1993, McNaughton *et al*. 1998, Ritchie and Olff 1999). Herbivores of different body size potentially consume different plant species (Bell 1970, Jarman 1974, Prins and Olff 1998). Large herbivores preferentially graze on multiple, usually low-quality plants, as they are less selective; whereas small herbivores can feed on high-quality individual plants or even select plant parts (Laca and Demment 1996). Large and small herbivores can therefore have different impacts on plant community characteristics. An increase in primary productivity usually results in a more abundant and diverse community of herbivores (Ritchie and Olff 1999) and the most productive sites are generally influenced by grazing to a greater extent (Milchunas and Lauenroth 1993). The long-term history of herbivory in an ecosystem must also be considered because a long history of coevolution between grasslands and herbivores may lead to a feedback mechanism which reduces the negative effects that defoliation has above and belowground (Milchunas *et al*. 1988, Milchunas and Lauenroth 1993).

Whereas most of these studies are based mainly on grazing responses observed in perennial grasslands and shrublands, there is a scarcity of information about above and belowground plant responses in annual grasslands, particularly from those of semi-arid regions. Few studies have investigated the biomass structure of these plant communities, particularly in relation to grazing effects and productivity gradients. As Osem *et al*. (2004) suggested, the response of annual grasslands is expected to be different, as annuals lack temporary continuity in competitive interactions. Additionally, as aboveground biomass and litter are periodically removed by grazers, in the case of semi-arid grasslands, the main organic matter and nutrient inputs could be mainly derived from belowground productivity. Yet little is known about factors that control biomass patterns in these ecosystems, where belowground processes probably have an important role regulating ecosystem structure and function.

We studied above and belowground plant responses to grazing by different-sized herbivores in an annual plant community in two neighbouring topographic sites with different primary productivity. The study was conducted in a Mediterranean man-made savannah (dehesa) in Spain during three years. These grasslands are characterised by a long history of grazing by large domestic herbivores (Noy-Meir 1998) and by the native European wild rabbit (*Oryctolagus cuniculus* (L.)), the most abundant and widely distributed vertebrate in the semi-arid Spanish ecosystems (Muñoz-Goyanes 1960). In this type of semi-arid grassland water is the limiting factor for primary productivity and perennial plant strategies due to the extreme summer drought. The typical dehesa undulating topography leads to a differential distribution of edaphic fertility and water among uplands and lowlands, lowlands being areas of water and nutrient accumulation. We compared the effects of large (sheep) and small (rabbits) herbivores in uplands and lowlands, by means of a replicated size-selective fence experiment which excluded sheep, and rabbits-plus-sheep. The objectives of this study were to: (1) asses consumption by small and large herbivores in the two productivity environments; (2) examine the effects of productivity and herbivory on above and belowground plant responses. We studied specific effects of sheep and rabbits on: (a) aboveground biomass, litter, bare soil, plant cover and height, and (b) root mass, root vertical distribution and root:shoot ratio. We expected a high consumption by both herbivores at productive lowlands, and less impact in upland areas, which are mainly used by rabbits. Within each productivity site, grazing by different-sized herbivores will differentially affect above and belowground features. However, we predict different patterns between productivity sites, since in less productive (upland) conditions plant growth after defoliation will be limited by water and nutrient stress conditions as well as grazing.

2. Material and methods

Study area

The research was conducted in a 330 ha dehesa located in the south-west of Madrid, Central Spain (40º 23´ N, 4º 12´ W) during 2002, 2003 and 2004. Mean elevation is 690 m. Climate is semi-arid continental Mediterranean with a mean annual temperature and precipitation of 12.6º C and 432.6 mm. Precipitation is characterised by a high year-to-year fluctuation in timing and amount, and by a pronounced summer drought. The amount of annual precipitation during the experiment was 676, 550 and 584 mm, respectively for each year.

The substrate is sandy to sandy-loamed textured, upon a fractured bedrock of granite, which outcrops all over the estate. Geomorphology is conditioned by a gentle undulating topography. Vegetation physiognomy is a typical dehesa system, sparsely punctuated by holm oak trees *Quercus ilex* on a pasture matrix. The herbaceous layer is mainly composed by annual species that germinate after the first heavy autumn rains (October-November), flower during spring, die at the beginning of summer and pass the unfavourable season (summer) as seeds in the soil (Fernandez-Alès *et al.* 1993). In slopes and uplands, the herbaceous community is mainly composed of short annual plants. In lowlands, the vegetation is mainly composed by taller species and some perennial grasses can be abundant.

The dehesa is managed for small game hunting as well as livestock grazing. The main wild herbivore is a dense population of European rabbits. The dehesa is grazed by a transhumant flock of 600 free-ranging sheep (about 2 sheep/ha), from December until the end of June. In summer, when most above ground herbaceous biomass is dry, sheep are moved to nearby mountain pastures.

Experimental design and sampling

In August 2001, five replicate blocks with three grazing treatments were placed at both low and high productivity sites. The three grazing treatments were rabbit-grazed, non-grazed and control (free herbivore grazing). They consisted of 36-m² fenced herbivore exclosure plots with a 1 m high chicken mesh (width 2.5 cm). The mesh in rabbit-grazed plots was lifted 20 cm above ground level to allow rabbit access but exclude sheep. In the non-grazed plots, the mesh was buried 30 cm into soil and forming a "L" shape to avoid rabbits burrowing underneath it. Free-grazing plots had no fences to allow access to both herbivores.

Visual aerial green cover, bare soil and mean vegetation height were recorded in seven 20 x 20 cm quadrats per plot in April and May (for uplands and lowlands respectively), approximately the time of peak biomass production. After data were recorded, aboveground plant biomass was clipped up to ground level and collected. Samples were sorted in the laboratory into live and dead (litter) fractions, dried to constant mass at 55ºC and weighed. In order to calculate plant consumption by rabbits and sheep, we compared the differences in biomass between fenced and unfenced plots, which allowed an approximate estimation of the biomass consumed by each herbivore (McNaughton *et al.* 1998). Consumption was only calculated with data from the first year of treatment (2002) as litter accumulation in successive years may alter the estimations.

Root biomass was estimated from 7 cm diameter and 12 cm deep soil cores. Previous research in similar plant communities has demonstrated that in intensively grazed communities the majority of root biomass is concentrated in the uppermost 7 cm of the soil (Rodríguez *et al.* 1995). Five soil cores were collected per plot. Cores were trimmed to remove aboveground plant material. Root samples were washed with

tap water and separated from soil by successive decanting through a 0.5 mm sieve. Roots were dried to constant mass at 55ºC and weighed. After that, roots where combusted in a furnace at 500ºC for 8 h in order to determine ash content and apply an ash-free correction factor for each sample. In the last year of treatment (2004), we also analysed vertical root mass distribution. For this, soil core samples were previously divided into three fractions (0-4, 4-8 and 8-12-cm depths) that were treated as explained above.

Data analyses

Grazing effects on aerial visual green cover, bare soil, vegetation height, aboveground biomass, litter, root mass and root:shoot ratio in individual years were analysed with ANOVA, where grazing treatment was used as fixed factor and block as random factor. Repeated-measures ANOVAs were used to estimate overall significance of treatment effects from year 2002 to year 2004 in fully factorial analysis with grazing treatment as between subject factor, and year and year × grazing treatment interaction as within subject factors. Grazing effects on vertical root mass distribution were analysed with two way ANOVAs, where grazing treatment and depth were factors. We did not include productivity as a factor in the analyses, but analysed more and less productive sites separately. This was decided due to the high differences in community parameters and species composition between both sites. Post-hoc tests (Tukey-test, $p < 0.05$) were used to assess differences between treatments within each year. We used t-tests to compare some individual pairs of results between the first and last study years (2002 and 2004). All response variables were tested for normality and homogeneity of variances and transformations were performed where needed. The statistical package SPSS 12.0 (SPSS Inc., 1989-2003) was used for all analyses.

3. Results

Herbivore consumption rates

From August 2001 to April-May 2002 both herbivores consumed a mean of 121.5 g/m² and 347.75 g/m² of the available aboveground biomass in uplands and lowlands, respectively. In uplands, rabbits consumed a mean of 96.25 g/m² of aboveground biomass and in lowlands they consumed 151.25 g/m². With regards to the percentage of total available biomass, sheep and rabbits together consumed 53% and 41.5% in uplands and lowlands, respectively. In uplands rabbits consumed 42% of the available aboveground biomass and they were the main consumer, whereas in lowlands rabbits consumed 18%, being sheep consumption slightly greater (23%).

Effects of grazing on aboveground biomass and litter

In uplands, aboveground biomass was higher in the non-grazed plots from 2002 to 2004 and this effect increased with year (**Tables 5.1** and **5.2**, **Fig 5.1a**). Excluding grazing by rabbits and sheep for 3 years resulted in an increase in aboveground biomass, from 225 g/m² in 2002 to 347 g/m² in 2004. Litter accumulation was significantly higher in the non-grazed plots in 2003 and 2004 (**Fig. 5.1b**). Litter accumulation changed significantly in non-grazed plots, increasing from 10.5 g/m² in 2002 to 36.25 g/m² in 2004 (df = 8, t = -4.33, p = 0.002). In lowlands, grazing affected aboveground biomass only in the first year of treatment, being higher in the rabbit-grazed plots (**Fig. 5.1a**). With time, aboveground biomass decreased in the non-grazed plots from 607 g/m² in 2002 to 476 g/m² in 2004. Litter accumulation was significantly higher in the non-grazed plots during 2003 and 2004 (**Fig. 5.1b**). In these plots, there was a significant accumulation of litter, from 2.25 g/m² in 2002 to 55.5 g/m² in 2004 (df = 8, t = -3.20, p = 0.012).

Effects of grazing on vegetation height, green cover and bare soil

In uplands, vegetation was higher in the non-grazed plots during the three sampling years, having similar values in the free-grazing and rabbit-grazed plots (**Tables 5.1** and **5.2**, **Fig. 5.1c**). Grazing only affected green cover in 2004, being higher in the non-grazed plots (**Fig. 5.1d**). Bare soil cover decreased under the non-grazing treatments during 2003 and 2004 (**Fig. 5.1e**). In lowlands, grazing had significant effects on vegetation height only in 2002 and was lower in free-grazing plots (**Fig. 5.1c**). Green cover was significantly lower in the non-grazing plots in 2003 and 2004 (**Fig. 5.1d**) and grazing did not affect bare soilcover (**Fig. 5.1e**).

Table 5.1: Results of two-way ANOVAs for aboveground (biomass, litter, height, green cover and bare soil) and belowground plant fraction (root mass and root:shoot ratio) in each of the three years of grazing treatments in uplands and lowlands. * = p < 0.05; ** = p < 0.01; *** p < 0.001

		Uplands			Lowlands		
		Year			Year		
		2002	2003	2004	2002	2003	2004
Vegetation parameters		F	F	F	F	F	F
Aboveground biomass	df = 2	**5.97***	**10.81**	**20.03**	**6.41***	2.28	3.57
Litter	df = 2	2.61	**7.82***	**18.52**	1.47	**15.92**	**5.79***
Vegetation height	df = 2	**13.22**	**101.20***	**16.14**	**6.33***	0.85	1.89
Green cover	df = 2	1.48	2.58	**10.17**	0.30	**8.13***	**14.35**
Bare soil	df = 2	1.38	**4.86***	**8.52***	0.75	1.76	1.10
Root mass	df = 2	1.04	0.72	**5.26***	1.17	2.37	**5.19***
Root : shoot ratio	df = 2	**7.62***	**17.98**	**11.30**	**14.56**	**4.55***	2.51

Table 5.2: Results of repeated measures ANOVAs for aboveground (biomass, litter, height, green cover and bare soil) and belowground plant fraction (root mass and root:shoot ratio) throughout the three years of grazing treatments in uplands and lowlands.
* = $p < 0.05$; ** = $p < 0.01$; *** $p < 0.001$

	Uplands			Lowlands		
	Grazing	**Year**	**Grazing × Year**	**Grazing**	**Year**	**Grazing × Year**
	df = 2	df = 2	df = 2	df = 2	df = 2	df = 2
Vegetation parameters	F	F	F	F	F	F
Aboveground biomass	**10.78****	**15.15****	**3.97***	1.01	1.13	1.50
Litter	2.13	0.21	**5.95****	**19.39*****	**14.14*****	**4.81****
Vegetation height	**45.76*****	**36.49*****	**7.50****	2.38	**25.10*****	0.55
Green cover	1.87	**9.61****	0.75	**15.26****	**11.00*****	**4.48****
Bare soil	3.76	**14.76*****	0.49	0.06	0.50	1.21
Root mass	0.06	**5.24***	1.87	0.70	0.58	1.04
Root : shoot ratio	**7.45****	**4.95***	0.15	**5.85***	2.02	0.70

Effects of grazing on root mass, vertical root distribution and root/shoot ratio

Grazing affected root mass only in the last year of treatment (2004) at both (upland and lowland) sites (**Table 5.1**, **Fig 5.2**). In uplands, root mass was lower in the free-grazing plots while in lowlands it was lower in the non-grazed plots. Grazing did not affect root vertical mass distribution up to 12 cm depth both in uplands (grazing: F = 1.71, p = 0.194; depth: F = 132.29, p = 0.000; grazing × depth: F = 0.055, p = 0.994) and lowlands (grazing: F = 2.61, p = 0.087; depth: F = 62.59, p = 0.000; grazing × depth: F = 0.342, p = 0.848). Root mass decreased with depth, with the first 4 cm accounting for 71.6% and 59.6% of the total root mass for uplands and lowlands, respectively (**Fig. 5.3**). In uplands, root/shoot ratio was always higher in both grazed treatments (rabbit-grazed and free-grazing) from 2002 to 2004 (**Fig 5.4**). In lowlands, the root/shoot ratio was higher in the free-grazing plots in 2002 and 2003.

4. Discussion

Plant consumption by herbivores

Sheep and rabbits were responsible for the consumption of about half the total available aboveground biomass in uplands and lowlands during the period of plant growth (Autumn 2001-Spring 2002). Total consumption was probably higher because herbivores (mainly rabbits, as sheep spent part of the summer and autumn away from the system) continue eating herbaceous vegetation (as dry plants) throughout the summer and autumn until the autumn rains promote a new germination cycle. Taking into account the amount of litter recorded in the following spring in the free-grazing treatment (8.23 g/m² at uplands and 0.63 gr/m² at lowlands, see **Fig. 5.1b** in 2003), the total annual consumption of aboveground net primary production could be larger than 80% in uplands and lowlands, however, further information about litter decomposition rates is needed in order to calculate this value more accurately. Worldwide, large native mammalian herbivores and livestock consume an average of 30-40% of the aboveground net primary production (Detling 1988). For semi-arid Mediterranean pastures several authors have pointed out that the mean annual consumption is around 49% (Rossiter 1966), although it is frequently above 50% (Andrzejemaska 1979, Abaturov 1979). Vertebrate herbivores therefore exert an intense control on the annual herbaceous biomass production in the studied dehesa ecosystem.

In the less productive areas, the main consumers were rabbits, which ate 42% of the total aboveground biomass, i.e. the 80% of the biomass consumed by vertebrate herbivores.
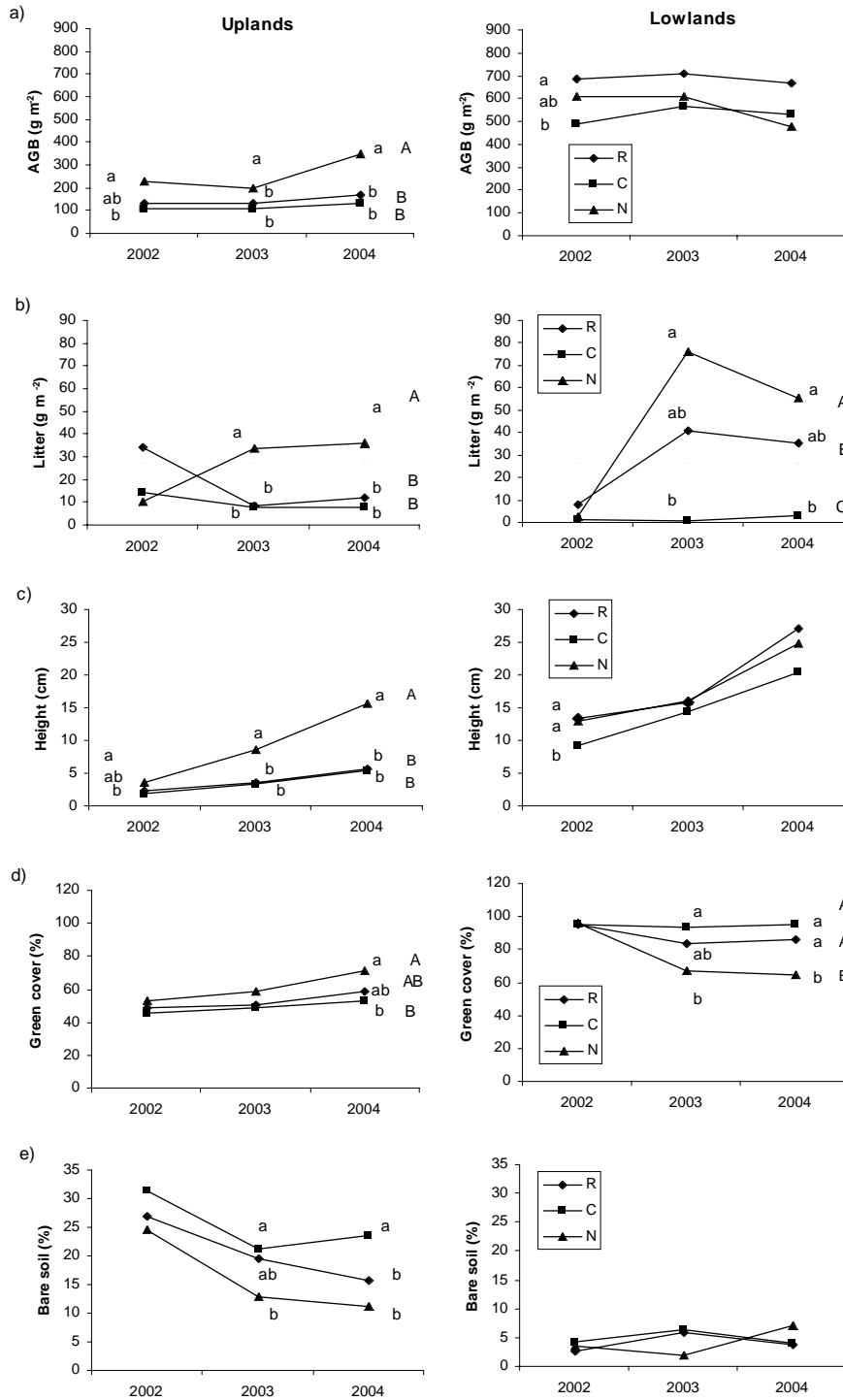
Figure 5.1: Aboveground grazing effects in uplands and lowlands throughout 2002, 2003 and 2004: a) aboveground biomass, b) litter, c) vegetation height, d) green aerial cover, e) bare soil. R = rabbit only grazing, C = free grazing (rabbit-plus-sheep) and N = non-grazing. Capital letters indicate effects detected throughout years using the repeated measures ANOVAs and lower case letters indicate effects detected using the two-way ANOVAs in particular years. Treatments or points with different letters indicate statistical differences (Tukey-test, $p < 0.05$). No letters indicate not statistical differences found in any treatment. A > B > C and a > b > c. See Tables 5.1 and 5.2 for F and p-values.
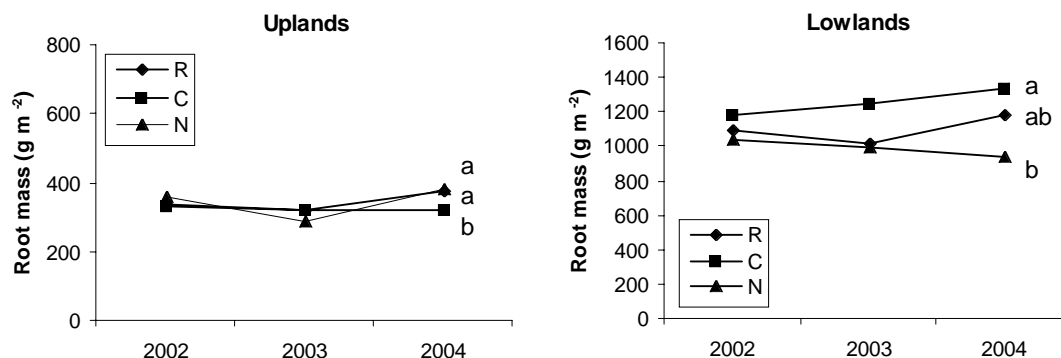
Figure 5.2: Grazing effects on root mass in uplands and lowlands. R = rabbit only grazing, C = free grazing (rabbit-plus-sheep) and N = non-grazing. Only effects in 2004 were found. Treatments or points with different letters indicate statistical differences (Tukey-test, p<0.05), a>b>c. See Tables 5.1 and 5.2 for F and p-values.

Rogers (1979) in France and Soriguer (1983) in Spain found that rabbit consumption of above-ground biomass was 19.9% and 15.5% respectively, which emphasizes the strong influence of rabbit vegetation consumption in our system. As a result of these heavy grazing intensities, rabbits have a substantial impact on the above-ground flow of energy and materials, as they are able to consume a high proportion of the primary production in vast areas. This, together with their relatively small size and the high local densities they can reach (densities of 40 rabbits per ha has been recorded in the highest quality habitat (Angulo 2004)), make rabbits a keystone species which supports up to 39 predator species in Mediterranean semi-arid grasslands (Delibes and Hiraldo 1981).

Topography was one of the most important factors causing large-scale heterogeneity in herbaceous biomass in our system. These differences determined variations in the intensity of consumption by large and small herbivores. Lowlands are generally more productive and, therefore, more likely to be preferred by grazing animals (Milchunas and Lauenroth, 1993). However, in our study area, lowlands were less used than expected, especially by rabbits. This result is in agreement with predictions of van de Koppel *et al.* (1996), who suggested that in contrast with classical exploitation theory (e.g., Hairston *et al.* 1960, Rosenzweig 1973,

DeAngelis 1992), herbivores may not prefer the more productive areas for foraging, as in these areas grazing probably becomes less efficient in the midst of tall vegetation and a high standing crop. Sheep are generalist ruminant herbivores, large enough to be unaffected by the tall, dense structure of productive communities, and are therefore more efficient grazers of the relatively less digestible but abundant swards of lowland areas.

Herbivore effects on plant community parameters

Grazing had strong effects on above and below-ground plant parameters and these effects varied greatly with site productivity. However, in general, results showed no large differences between plots grazed only by rabbits and those grazed by sheep-plus-rabbits, being the trends of the effects on the measured variables rather similar under both types of grazing treatments. There may be some reasons why we failed to detect the differential effect of grazing by rabbits alone, or both sheep and rabbits. First, uplands were mainly grazed by rabbits, so sheep effects may have been minimal, and thus the lack of differences between grazing treatments in upland areas. Secondly, the temporary absence of sheep grazing in lowlands between July and November may be an important influence, as the grazing pressure was not maintained. Additional to the temporal absence of sheep,

90

we observed that rabbits used lowlands mainly in summer and autumn, whereas rabbit grazing in these areas was incidental the rest of the year. We believe that tall herbaceous vegetation in spring and a partly flooded lowland scenario in winter constrain rabbit access to these areas.

Productivity and grazing effects on aboveground parameters

At low productivity uplands the absence of grazing caused an increase in green cover and mean height of vegetation, which lead to an increment of aboveground biomass values. In contrast, at high productivity lowlands, the absence of grazing caused a decrease in green cover although without significant effects on aboveground biomass. This reduction in green cover was probably induced by the accumulation of litter. Inhibition by litter has been commonly observed in highly productive but undisturbed environments, where litter accumulation can be quite high (Goldberg and Werner 1983, Carson and Peterson 1990). In these environments, litter build-up may suppress germination and seedling establishment as it limits light penetration for new shoot growth, eventually reducing aboveground productivity (Knapp and Seastedt 1986). In fact, several studies point directly to litter accumulation as responsible for decreased species density under enriched conditions (Brewer *et al*. 1997, Foster and Gross 1997, 1998). It appears then, that in the absence of grazers, total productivity in lowlands

would be more limited by light than by nutrient availability. The role of herbivores in reducing litter build-up in productive systems can sometimes increase productivity and this has been reported for productive grasslands with a long evolutionary history of grazing (see Milchunas and Lauenroth 1993). Our results suggest that with time litter accumulation in lowland non-grazed plots will result in the reduction of aboveground biomass. The opposite effect seems to be happening in uplands, where litter increases are accompanied by augments in aboveground biomass, height, and green cover. It has been suggested that in semi-arid and arid environments plant litter may trap seeds, and even small amounts of litter can ameliorate stressful environmental conditions such as low moisture levels, leading to an increase in primary productivity (e.g., Fowler 1986, Willms *et al*.1986, Hamrick and Lee 1987). In these poor environments, litter also reduces soil erosion by reducing runoff and improves soil structure and fertilisation through addition of organic matter (Naeth 1988).

At lowlands, a lower relative grazing intensity and higher soil water and nutrient abundance could favour enhanced tissue regrowth of plants after grazing. After three years of treatment we found that at lowlands the grazed and non-grazed plots presented similar proportions of bare soil. In contrast, in uplands, grazing created more gaps, exposing more of the soil surface.
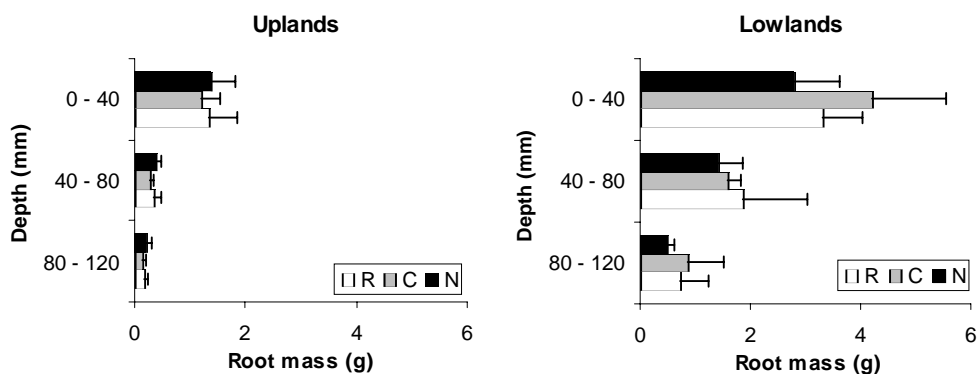

Figure 5.3: Grazing effects on root vertical distribution in uplands and lowlands. R = rabbit only grazing, C = free grazing (rabbit-plus-sheep) and N = non-grazing. There were no significant effects of grazing on root vertical distribution.
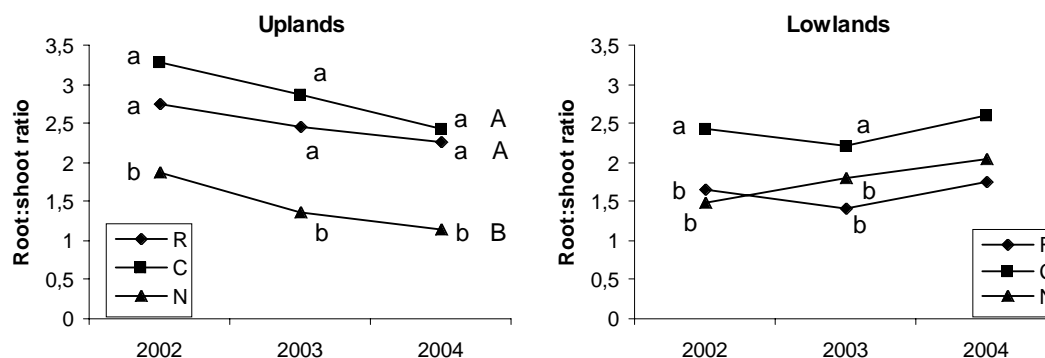
Figure 5.4: Grazing effects on root : shoot ratio in uplands and lowlands. R = rabbit only grazing, C = free grazing (rabbit-plus-sheep) and N = non-grazing. Capital letters indicate effects detected throughout years using the repeated measures ANOVAs and lower case letters indicate effects detected using the two-way ANOVAs in particular years. Treatments or points with different letters indicate statistical differences (Tukey-test, p<0.05). No letters indicate not statistical differences found between any treatment. A > B > C and a > b > c. See Tables 5.1 and 5.2 for F and p-values.

By reducing plant biomass, litter and green cover, and increasing bare soil, heavy rabbit grazing may cause erosion and microclimatic changes in the less productive sites, in such a way that higher insolation, higher surface temperatures, and evaporation losses can be expected (Johnston *et al.* 1971, Dormaar *et al.* 1989). This result shows that, in terms of green cover, uplands are more grazing-sensitive areas and emphasizes the fact that in the less productive areas the scarcity of water and nutrients in the soil can limit plant regrowth capacity after grazing events.

Our results suggest that grazing contributes to increase green cover in more productive environments but decrease it in the less productive ones. This effect accentuates even more the spatial heterogeneity of primary productivity at the landscape scale, which can accentuate, the spatial segregation of large and small herbivores in the Mediterranean grassland ecosystems.

Productivity and grazing effects on belowground parameters

The amount of belowground mass found in lowlands was much greater than in uplands. This may be related to the larger amounts of

aboveground biomass, green cover and some perennial species in lowlands. We found changes in root mass between grazing treatments after three years. Grazing reduced root mass in uplands but increased it in lowlands. These results are consistent with the decrease in aboveground biomass found in uplands (and the greater cover of bare soil), and the increase in green cover in lowlands as a consequence of grazing. The delay in the response of the root mass could be motivated by the estimation of root mass instead of root biomass.

We recorded a strong vertical concentration of belowground mass in the upper 4 cm of the soil profile. Root mass decreased drastically with depth in a similar way to other studies (Milchunas and Lauenroth 1989, Rodríguez *et al.* 1995, McNaugthon *et al.* 1998). Rodríguez *et al.* (1995) found that grazing can be important in determining the vertical distribution of the subterranean biomass of pasture communities. Our results suggest that the vertical distribution appears to be modulated by nutrient and water availability, controlled by topographical positions, in a similar way as proposed by Milchunas and Lauenroth (1989). This uppermost concentration was more relevant in uplands with 71.6% of the root mass in the first 4 cm in contrast to 59.6% in lowlands. The

capacity of belowground competition of a plant is predominantly determined by root density and root distribution (Nie *et al.* 1997). In uplands the roots were more amalgamated in the upper soil horizons, indicating that competition for water and soil nutrients could be intense. Shallow-rooted species are more efficient in absorbing moisture from low precipitation events. Similar results have been obtained in deserts (Gibbens and Lenz 2001) and in the semi-arid Russian steppes (Titlyanova *et al.* 1999). In these semi-arid systems, species of intermediate rooting depth would be more susceptible to drought events.

Root:shoot ratio increased with grazing both in uplands and lowlands. This effect may be partly consequence of the decrease in aboveground biomass by herbivore consumption. Maarel and Titlyanova (1989) found that root:shoot ratios increase with increasing grazing pressure and with increasing aridity. These authors interpreted these trends as an adaptation to stress, both grazing and aridity. Plants concentrate their growth in parts of their anatomy whose function is most constrained by the environment, in such a way that if plant growth is limited by a substance to be absorbed by the roots (water and/or nutrients), root growth will be favoured, but when the limiting factors has to be processed by the shoot (e.g. light), growth of above-ground parts is relatively favoured (Brouwer 1983). If plants allocate more biomass to the roots (under limiting nutrient conditions, for instance), they will increase their competitive ability for belowground processes. In semi-arid environments, grazed plants invest more in subterranean tissues to favour the absorption of nutrients and water and recover the tissues lost in the aerial part. In highly productive environments, where plants are more light competitors, low root:shoot ratios are expected to indicate a greater investment in aerial parts. But grazing, by reducing the height of the vegetation, will favour the survival of short species which invest in subterranean biomass. Several authors

(Milchunas *et al.* 1988, McNaughton *et al.* 1998) suggested that a long history of co-occurrence of plants and grazers, such as in these Mediterranean grasslands, may lead to feedback mechanisms that reduce the immediately negative effects of grazing and contribute to the capacity of grasslands to sustain or increase the proportion of the root mass under defoliation stress.

5. Conclusions

Based on the findings of this study, we conclude that our annual plant community responded to grazing with opposite changes in high and low productivity sites for most of the variables measured. Only litter accumulation and root:shoot ratio changed in the same direction in uplands and lowlands. Litter build-up increased in herbivore exclusions but the future ecological consequences on vegetation dynamics will be quite different in uplands and lowlands. Dehesas are ecosystems with high spatial heterogeneity (Díaz *et al.* 1997) and a high plant species richness (Pineda *et al.* 1981, Marañon 1986). This heterogeneity and richness are probably the result of the wide spatial and temporal variety in soil and weather conditions, grazing by domestic and wild animals and other low-impact human-induced land management practices (Peco *et al.* 2006). Such ecosystem complexity influences annual plant responses to grazing which do not always conform with existing global theoretical frameworks. Therefore, the accurate prediction of above and below-ground plant responses in Mediterranean communities is a difficult task.

Acknowledgments

References

Angulo, E. 2004. "El Conejo". In: Herrera, C.M. (Coordinator), El Monte Mediterráneo en Andalucía. Consejería de Medio Ambiente, Junta de Andalucía, Sevilla, Spain, pp. 122-125.

Abaturov, B.D. 1979. Peculiarities of trophic interrelationships involving plant-animal interactions in pasture ecosystems. Agro-Ecosystems 5: 317-327.

Andrzejemaska, L. 1979. Herbivorous fauna and its role in the economy of grassland ecosystems II. The role of herbivores in trophic relationships. Polonia Ecological Studies 5: 45-76.

Bell, R.H.V. 1970. The use of herb layer by grazing ungulates in the Serengeti. In: Watson, A. (ed.), Animal Populations in Relation to Their Food Resources. Blackwell Scientific Publications, Oxford, pp. 11-123.

Brewer, J.S., Levine, J.M. and Bertness, M.D. 1997. Effects of biomass removal and elevation on species richness in a New England salt marsh. Oikos 80: 333-341.

Brouwer, R. 1983. Functional equilibrium: sense or nonsense? Netherlands Journal of Agricultural Science 31: 335-348.

Carson, W.P. and Peterson, C.J. 1990. The role of litter in an old-field community: impact of litter quantity in different seasons on plant species richness and abundance. Oecologia 85: 8-13.

DeAngelis, D.L. 1992. Dynamics of nutrient cycling and food webs. Chapman and Hall, London, England.

Delibes, M. and Hiraldo, F. 1981. The rabbit as a prey in the Iberian Mediterranean ecosystems. In: Myers, K and MacInnes, C.D. (eds.), Proceedings of the Old World Lagomorph Conference. University of Guelph and Wildlife Research, Ontario Ministry of Natural Resources, Toronto, pp. 614-662.

Detling, J.K. 1988. Grassland and savannas: regulation of energy flow and nutrient cycling by herbivores. In: Pomeroy, L.R. and Alberts, J.J. (eds.). Concepts of Ecosystem Ecology. Springer-Verlag, New York, pp. 131-148.

Díaz, M., Campos, P. and Pulido, F.J. 1997. The Spanish dehesas: a diversity of land-use and wildlife. In: Pain, D. and Pienkowsky, M. (eds.). Farming and birds in Europe: The Common Agricultural Policy and its implications for bird conservation. Academic Press, London, UK, pp. 178-209.

Dormaar, J.F., Smoliak, S. and Willms, W.D. 1989. Vegetation and soil responses to short-duration grazing on Fescue grasslands. Journal of Range Management 42: 252-256.

Fernández-Alès, R., Laffarga, J.M. and Ortega, F. 1993. Strategies in Mediterranean grassland annuals in relation to stress and disturbance. Journal of Vegetation Science 4: 313-322.

Foster, B.L. and Gross, K.L. 1997. Partitioning the effects of plant biomass and litter on Andropogon gerardi in oldfield vegetation. Ecology 78: 2091-2104.

Foster, B.L. and Gross, K.L. 1998. Species richness in successional grassland: effects of nitrogen enrichment and plant litter. Ecology 79: 2593-2602.

Fowler, N.L. 1986. Microsite requirements for germination and establishment of three grass species. American Midland Naturalist 115: 131-145.

Gibbens, R.P. and Lenz, J.M. 2001. Root systems of some Chihuahuan desert plants. Journal of Arid Environments 49: 221-263.

Goldberg, D.E. and Werner, P.A. 1983. The effects of size of opening in vegetation and litter cover on seedling establishment of goldenrods (Solidago spp.). Oecologia 60: 149-155.

Hairston, N.G., Smith, F.E. and Slobodkin, L.B. 1960. Community structure, population control and competition. American Naturalist 94: 421-425.

Hamrick, J.L. and Lee, J.M. 1987. Effect of soil surface topography and litter cover on the germination, survival, and growth of musk thistle (Carduus nutans). American Journal of Botany 74: 451-457.

Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. Annual Review of Ecological Systems 22: 477-503.

Jarman, P.J. 1974. The social organization of antelope in relation to their ecology. Behaviour 48: 215-267.

Johnston, A., Dormaar, J.F. and Smoliak, S. 1971. Long-term grazing grazing effects on fescue grassland soils. Journal of Range Management 24: 185-188.

Knapp, A.K. and Seastedt, T.R. 1986. Detritus accumulation limits productivity of tallgrass prairie. BioScience 36: 662-668.

Laca, E.A. and Demment, M.W. 1996. Foraging strategies of grazing animals. In: Hodgson, J. And Illius, A.W. (eds.), The Ecology and Management of Grazing Systems. CAB International, Wallinford, pp. 137-158.

Lecompte, F., Ozier-Lafontaine, H., Pages, L. 2001. The relationships between static and dynamic

variables in the description of the root growth. Consequences for field interpretation of rooting variability. Plant and Soil 236: 19-31.

Leetham, J.W. and Milchunas, D.G. 1985. The composition and distribution of soil microarthropods in the shortgrass steppe in relation of soil water, root biomass, and grazing by cattle. Pedobiologia 28: 311-325.

Maarel, E. and Titlyanova, A.A. 1989. Above-ground and below-ground biomass relations in steppes under different grazing conditions. Oikos 56: 364-370.

Marañon, T. 1986. Plant species richness and canopy effect in the savanna-like "dehesa" of S.W. Spain. Ecología Mediterránea 12: 131-141.

McNaughton, S.J. 1984. Grazing lawns: animals in herds, plant form, and co-evolution. American Naturalist 124: 863-886.

McNaughton, S.J., Banyikwa, E.F. and McNaughton, M.M. 1998. Root biomass and productivity in a grazing ecosystem: the Serengeti. Ecology 79: 587-592.

Milchunas, D.G., Sala, O.E. and Lauenroth, W.K. 1988. A generalized model of the effects of grazing by large herbivores on grasslands community structure. American Naturalist 132: 87-106.

Milchunas, D.G. and Lauenroth, W.K. 1989. Three-dimensional distribution of plant biomass in relation to grazing and topography in the shortgrass steppe. Oikos 55:82-86.

Milchunas, D.G. and Lauenroth, W.K. 1993. Quantitative effects of grazing on vegetation and soil over a global range of environments. Ecological Monographs 63: 327-366.

Muñoz-Goyanes, G. 1960. Anverso y reverso de la mixomatosis (Madrid: Dirección General de Montes, Caza y Pesca Fluvial).

Naeth, M.A. 1988. The impact of grazing on litter and hydrology in mixed prairie and fescue grassland ecosystem of Alberta. PhD University of Alberta, Canada.

Nicholson, I.A., Patterson, I.S. and Currie, A. 1990. A study of vegetation dynamics: selection by sheep and cattle in Nardes pasture. In: Watson, A. (ed.), Animal Populations in Relation to Their Food Resource. British ecological Society Symposium 10. Blackwell Scientific Publishers, Oxford, UK, pp. 129-143

Nie, Z.N., Mackay, A.D., Valentine, I., Barker, D.J. and Hodgson, J. 1997. Influence of pastoral fallow on plant root growth and soil physical and chemical characteristics in a hill pasture. Plant and Soil 197: 201-208.

Noy-Meir, I. 1998. Effects of grazing on Mediterranean grasslands: the community level. In: Papanastasis, V.P. and Peter, D. (eds.), Ecological Basis of Livestock Grazing in Mediterranean Ecosystems.. European Comission Science, Research and Development, Brussels, pp. 312-317.

Olff, H., De Leeuw, J., Bakker, J.P., Platerink, R.J., Van Wijnen, H.J. and De Munck, W. 1997. Vegetation succession and herbivory in a salt marsh: changes induced by sea level rise and silt deposition along and elevational gradient. Journal of Ecology 85: 799-814.

Olff, H., Brown, V.K. and Drent, R.H. 1999. Herbivores: Between Plants and Predators. Blackwell Science Ltd., Oxford, England.

Osem, Y., Perevolotsky, A. and Kigel, J. 2004. Site productivity and plant size explain the response of annual species to grazing exclusion in a Mediterranean semi-arid rangeland. Journal of Ecology 92: 297-309.

Peco, B., Sánchez, A.M., Azcárate, F.M. 2006. Abandonment in grazing systems: Consequences for vegetation and soil. Agriculture, Ecosystems and Environment 113: 284-294.

Pineda, F.D., Nicolas, J.P., Peco, B., Ruiz, M. & Bernáldez, F.G. 1981. Succesion, diversité et amplitude de niche dans les pâturages du centre de la Péninsule Ibérique. In : Poissonet, P., Romane, F., Austin, M.P., van der Maarel, E., & Schmidt, W. (Eds.). Vegetation dynamics in grasslands, heathlands and Mediterranean Ligneous Formations. Dr. W. Junk Publish, The Hague, pp. 267-278.

Prins, H.H.T. and Olff, H. 1998. Species-richness of African grazer assemblages: towards a functional explanation. In: Newbery, D.M., Prins, H.H.T & Brown, N. (eds.), Dynamics of Tropical Communities. Blackwell Science Ltd, Oxford, pp. 449-490

Ritchie, M.E. and Olff, H. 1999. Herbivore diversity and plant dynamics: compensatory and additive effects. In: Olff, H., Brown, R.H. and Drent, R.H. (eds.), Herbivores: Between Plants and Predators. Blackwell Science Ltd, Oxford, pp 175-204.

Rodríguez, M.A., Brown, V.K. and Gómez-Sal, A. 1995. The vertical distribution of below-ground pasture biomass in five community types subjected to different grazing regimes. Journal of Vegetation Science 6: 63-72.

Rogers, P.M. 1979. Ecology of the European wild rabbit, *Oryctolagus cuniculus* (L.) in the Camargue, Southern France. PhD Thesis. University of Guelph, Canada.

Rosenzweig, M.L. 1973. Exploitation in three trophic levels. American Naturalist 107: 275-294.

Rossiter, R.C. 1966. Ecology of the Mediterranean annual-type pasture. Journal of Agronomy and Crop Science 18:1-56.

Titlyanova, A.A., Romanota, I.P., Kosykh, N.P. and Mironychera-Tokareva, N.P. 1999. Pattern and process in above-ground and below-ground components of grassland ecosystems. Journal of Vegetation Science 10: 307-320

Sims, P.L. and Singh, J.S. 1978. The structure and function of the western North American grasslands. III. Net primary production, turnover and efficiencies of enery capture and water use. Journal of Ecology 66: 573-597.

Soriguer, R.C. 1983. Consideraciones sobre el efecto d los conejos y los grandes herbívoros en los pastizales de la Vera de Doñana. Doñana, Acta Vertebrata, 10: 155-168.

van de Koppel, Huisman, J., van der Wal, R. and Olff, H. 1996. Patterns of herbivory along a productivity gradient: an empirical and theoretical investigation. Ecology 77: 736-745.

Vogt, K.A., Vogt, D.J., Palmiotto, P.A., Boon, P., O´Hara, J. and Asbjornsen, H. 1996. Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. Plant and Soil 187: 159-219.

Willms, W.D., Smoliak, S. and Baily, A.W. 1986. Herbage production following litter removal on Alberta native grasslands. Journal of Range Management 39: 536-540.