

# Vegetation response to grazing management in a Mediterranean herbaceous community: a functional group approach

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## Summary

1. A 4-year study was conducted in a Mediterranean herbaceous community in north-eastern Israel to investigate the effects of cattle grazing management on the structure and composition of the community. Understanding the effects of grazing on the dynamics of Mediterranean herbaceous communities is important in formulating rational management plans for both conservation and sustainable animal production.

2. The relationships among plant functional groups were studied in the context of inter-annual variation in rainfall. Treatments included manipulations of stocking rates (moderate, heavy and very heavy) and grazing regimes (continuous vs. seasonal), in a factorial design.

3. The herbaceous community was rich in species, with 166 species recorded at the site, of which 74% were annuals. Plant cover was dominated by 10 species that accounted for 75% of the total cover.

4. Inter-seasonal rainfall variation was a dominant factor in the expression of different grazing treatments on the structure of the plant community. Grazing effects were stronger in wet years than in dry years.

5. Paddocks under continuous grazing were higher in number of species compared with paddocks subjected to seasonal grazing, independently of grazing intensity.

6. Functional group analyses showed that reduction in cover of tall grasses was correlated with an increase in cover of prostrate annual legumes and less palatable groups such as annual and perennial thistles, crucifers and forbs.

7. Cover of functional groups composed of hemicryptophytic species was less variable (lower coefficient of variation) in response to grazing treatments and inter-annual variation in climatic conditions compared with functional groups with annual species.

8. The persistence of the dominant species and the relatively small amplitude of change in plant cover of the functional groups suggest that the community was rather stable in spite of wide variation in grazing regimes and climatic conditions. East-Mediterranean grasslands appear to be adapted to grazing due to their long history of human association.

*Key-words:* cattle, persistence, plant community dynamics, plant functional types, species richness.

*Journal of Applied Ecology* (2000) **37**, 224–237

## Introduction

The impact of grazing on community structure and ecosystem functioning is a key issue for range management as well as for nature conservation. Range managers, on the one hand, emphasize the long-term sustainable maximization of livestock production and profitability of the operation, while conservationists seek to maintain high biodiversity (Tilman, Wedin & Knops 1996; Noy-Meir 1998).

Most studies on grazing management strategies have been conducted in temperate ecosystems (Sheath & Clark 1996). In the Mediterranean region, there is no consensus on rangeland management (Seligman 1996). Mediterranean ecosystems are distinguished by high seasonality in resource availability, great inter-annual rainfall variability, a large component of annual plants in the floristic composition and a long history of grazing and disturbance. Domestic livestock have grazed Mediterranean ecosystems, and particularly those of the Middle East, for more than 5000 years (Noy-Meir & Seligman 1979; Edelstein & Milevsky 1994). It is therefore not unusual to find many species well adapted to grazing, expressing a high degree of resilience following defoliation (Perevolotsky & Seligman 1998).

Grazing can influence the structure and organization of plant communities in different ways (Crawley 1983; Noy-Meir, Gutman & Kaplan 1989). The direct effect of herbivory occurs by the selective and differential removal of plant tissues or species. Indirect effects on botanical composition and species diversity can occur when selective grazing on dominant species reduces their vigour and presence, thus favouring the spread of less competitive but more grazing-tolerant plants.

In grasslands of the northern region of Israel, cattle grazing management is commonly conducted as continuous grazing at moderate stocking rates (0.5 cow ha<sup>-1</sup> year<sup>-1</sup>), with supplementation during periods of low forage quality or forage scarcity. Results from recent studies (Gutman *et al.* 1990; Gutman, Seligman & Noy-Meir 1990) suggest that animal production in this region can be increased substantially by using higher stocking rates in association with deferred grazing. However, the long-term effects of this intensive grazing management on the vegetation is not fully known.

The aim of the present study was to evaluate the responses of species, functional groups and the plant community to different management regimes of cattle grazing in a Mediterranean herbaceous community, especially at high stocking rates. Previous research in these communities has suggested that the responses of vegetation to grazing are associated with plant growth form, mainly plant height, and to a lesser extent with palatability and spininess (Noy-Meir, Gutman & Kaplan 1989). In our study, the relationships among these attributes and grazing

responses were studied by a functional group approach, in which species with similar biological traits resulting in similar responses to grazing were grouped together (Gitay & Noble 1997). Specific objectives of our research were to: (i) study variation in the structure of the herbaceous community resulting from changes in grazing management practice; (ii) analyse the responses of plant functional groups to changes in the timing and intensity of grazing; and (iii) evaluate the effects of the amount and seasonal distribution of rainfall on the structure of the herbaceous community under different grazing regimes. A better understanding of the effects of grazing on the dynamics of Mediterranean herbaceous communities will provide valuable tools for rational management of these areas for both conservation and sustainable animal production.

## Materials and methods

### THE STUDY SITE

The experiment was conducted at the Karei Deshe Experimental Farm, located in the north-eastern part of Israel (latitude 32°55'N, longitude 35°35'E, altitude 150 m a.s.l.). The topography is hilly, with slopes generally less than 10%. Soils are brown basaltic protogrumosols (Dan *et al.* 1970) with variable depth, but rarely deeper than 60 cm, and with a rock cover of about 30%. The site has a Mediterranean climate, characterized by wet and mild winters with mean minimum and maximum temperatures of 7°C and 14°C, respectively. The average seasonal rainfall is 570 mm, falling mostly in winter. The rainy season begins in October–November and ends in April. Summers are dry and hot, with mean minimum and maximum temperatures of 19°C and 32°C, respectively. At least 5 months of dry weather characterize this area (Gutman 1978). The growing season of the vegetation is closely associated with the distribution of rainfall. Germination of annuals and regrowth of most perennials happens soon after the first rains. Growth is rather slow during the winter months of December–January, but the vegetation is usually well established by mid–end January. Growth is rapid in spring and peak growth, coinciding with seed set, occurs in March–April. By mid-May, most of the herbaceous vegetation is dry and most seeds have been dispersed. The forage quality decreases at the beginning of the long dry summer.

### EXPERIMENTAL DESIGN

A grazing experiment was established in 1993 in an area of 250 ha, comprising two blocks of four fenced paddocks each. The average paddock size was 28 ha

(range 21.5–33.8 ha). Grazing treatments comprised two stocking rates, with and without subdivision of the grazing area, in a factorial arrangement yielding four grazing systems. Each grazing system was allocated to one paddock in a randomized block design with two replicates per treatment.

The stocking rates were approximately 0.55 and 1.1 cow ha<sup>-1</sup> year<sup>-1</sup>, designated M (moderate) and H (heavy), respectively. In treatments without subdivision (designated C, continuous), animals were given continuous access to the entire paddock during all of the grazing season, from January until October. In treatments with subdivision (designated S, seasonal), the cows were concentrated on half of the paddock during the beginning of the grazing season (designated E, early) and then moved to the other half of the paddock until the end of the grazing trial (designated L, late). The subdivision of the paddocks was intended to maximize forage use. The experiment was run for 4 years and the allocation of the paddocks to the various systems was unchanged throughout the experimental period.

From the point of view of grazing impact on the vegetation, areas grazed at the beginning (E) and at the end (L) of the grazing season in treatments with subdivision must be studied separately. Thus, the four grazing systems imposed a total of six vegetation treatments, defined by the combination of animal density, duration of grazing and season of grazing. The designations of treatments with continuous grazing systems were CM and CH for moderate and heavy stocking rates, respectively. In subdivided systems the treatment designations were S-HE and S-VHE for the heavy and very heavy early grazed areas, and S-HL and S-VHL for the heavy and very heavy late grazed areas. In the subdivided paddocks, the stocking density during the grazing period was double that in the undivided paddocks. The stocking densities in the subdivisions of the moderate and heavy stocking densities were thus heavy (H) and very heavy (VH), respectively.

The continuous moderate treatment (CM) represented the normal grazing regime for the region, and was considered as the control treatment.

#### GRAZING MANAGEMENT

Animals were drawn from a large beef herd that had grazed the station for over 20 years. The herd was composed of Simmental, Brahman and Hereford cows bred to Charolais bulls. The cows assigned to each paddock were randomly assigned each year, to avoid any treatment effect on cattle growth.

The grazing season commenced soon after the green standing herbaceous biomass exceeded 500 kg dry matter (DM) ha<sup>-1</sup>. From previous experience, it was known that below this amount the quantity

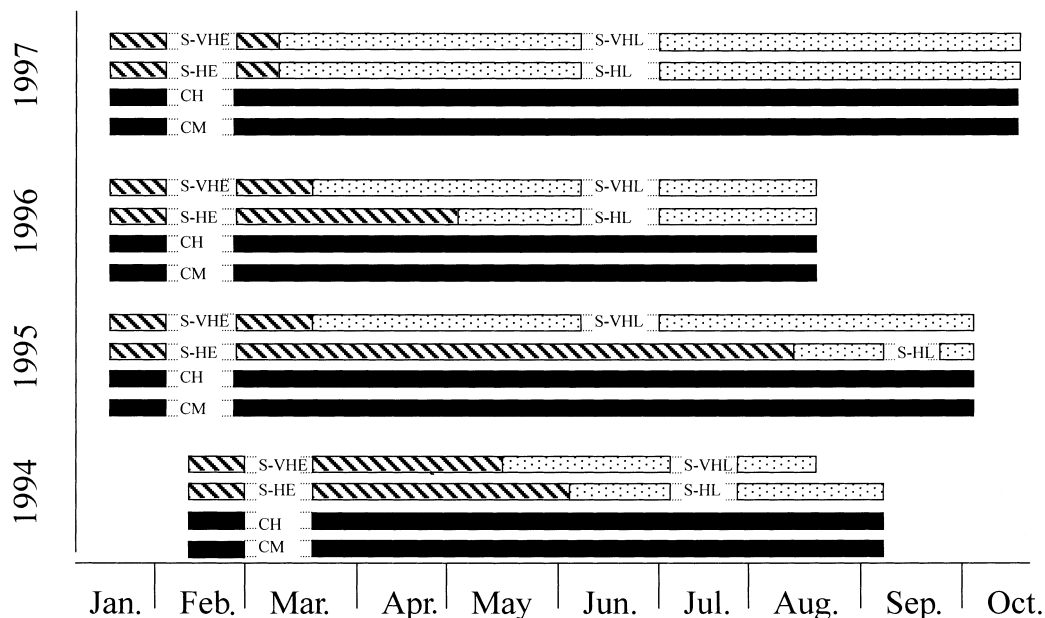
of forage ingested by the cows was very low, usually less than 2 kg DM cow<sup>-1</sup> day<sup>-1</sup>. Animals entered the paddocks on the same date in all grazing systems, although this date differed between years. Grazing commenced on 16 February in 1994 (a dry year), and 13, 15 and 19 January in 1995–97, respectively.

The date of transfer from the early season to the late season areas in the grazing system with subdivision tended to be earlier in the very heavy early treatments (S-VHE) than in heavy early (S-HE) because of more rapid depletion of forage. The average transfer date for the S-VHE treatments was 1 April, while the average date for S-HE was 22 May.

Grazing was terminated in the late summer, when a declining trend in average animal live weight was detected. In 1995, 1996 and 1997 all grazing systems were terminated on the same date (7 October, 10 August and 21 October, respectively). At termination, the herd was kept in corrals outside the paddocks until the following grazing season, and fed with barley grain, wheat straw and poultry litter. Figure 1 shows the grazing periods implemented according to grazing system and year.

#### SAMPLING

The vegetation was monitored in spring (early to mid-April), during the peak season of primary production. Plant cover and species composition were estimated using the step-point method (Mueller-Dombois & Ellenberg 1974), along permanent transects, 500–700 m long, that traversed the paddocks from fence to fence. Every two steps, a thin stick was placed vertically in the vegetation. The uppermost species in contact with the recording stick were sampled. Bare ground and rock cover were recorded where no vegetation was encountered. The vegetation was classified into 10 functional groups according to life cycle, plant height, palatability and taxonomy (for terminology on species traits see Noy-Meir, Gutman & Kaplan 1989): tall perennial and tall annual grasses (> 50 cm at maturity); short annual grasses (< 50 cm); perennial and annual legumes; perennial and annual thistles (composites plus one prickly umbellifer species, *Eryngium* spp.); geophytes; crucifers; and 'forbs' (all other dicots). The crucifers were recorded separately because of their low palatability due to chemical compounds, and occasional dominance in the vegetation. Species richness was calculated as the mean number of species per paddock, independently on the size of the paddocks. Relative cover (%) was calculated from total plant cover, excluding rock and bare ground cover. Species nomenclature follows Feinbrun-Dothan & Danin (1991).



**Fig. 1.** Grazing periods according to grazing system and year. Continuous moderate (CM) and continuous heavy (CH) (solid bars); seasonal heavy early (S-HE) and seasonal very heavy early (S-VHE) (hatched bars); seasonal heavy late (S-HL) and seasonal very heavy late (S-VHL) (stippled bars).

#### STATISTICAL ANALYSIS

Analysis of variance (ANOVA) techniques were used to analyse the randomized block design at individual sampling dates. Species relative cover data (%) were transformed by the arcsine square-root transformation (Sokal & Rohlf 1995). The multi-year data were analysed using the repeated measures ANOVA procedure of the SAS general linear model (GLM; SAS Institute Inc., Cary, NC, USA, 1996) to estimate overall significance of treatment effects. Factors examined in the model were: block, treatment, year and their interaction. The CONTRAST procedure (SAS Institute Inc., Cary, NC, USA, 1996) was used within the repeated measures framework to test differences between grazing regimes. Contrasts included were: continuous vs. seasonal grazing, stocking rates and their interactions. Within the seasonal regime, the analysis included additional contrasts: timing (early vs. late grazing), stocking rates and their interaction. Coefficient of variation (CV) for the cover of each functional group was calculated from all paddocks for the 4-year period (Sokal & Rohlf 1995). Pearson's pair-wise correlation analyses were performed to study co-variation of relative plant cover among the 10 functional groups, in responses to differences in timing and intensity of grazing (Ludwig & Reynolds 1988). Tests for significant differences between CVs were carried out according to Sokal & Braumann (1980).

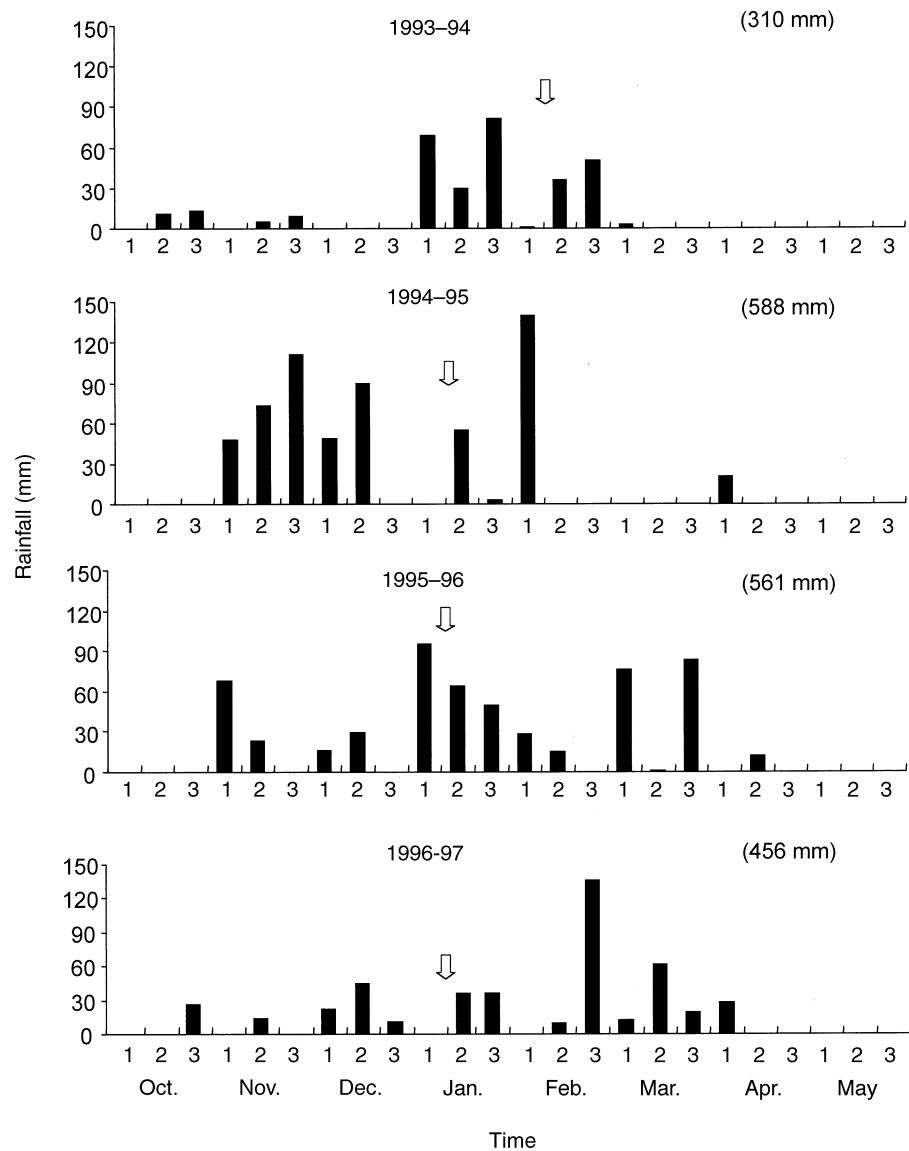
#### Results

##### RAINFALL DISTRIBUTION AND GRAZING

The inter-annual and within-season rainfall during the research period are presented in Fig. 2. The first season (1994) was relatively dry; onset of the rains was late and total rainfall amounted to 46% of the long-term annual average for the site. Vegetation did not begin new growth until January 1995. Consequently, the cattle were introduced in the paddocks relatively late (16 February), when the available green forage exceeded the 500 kg DM ha<sup>-1</sup>. In the following seasons, effective rain for germination fell during November, when the total rainfall was average (1995 and 1996) or 20% lower (1997), and grazing started by mid-January, the usual date for effective grazing. Whereas the total annual rainfall in these three seasons was similar, distribution of rainfall was quite different, with 63%, 41% and 26% of total rainfall occurring before the onset of grazing in 1995–97, respectively.

##### VEGETATION CHARACTERISTICS AT THE SITE

During the experiment a total of 166 species was recorded at the site, 74% of which were annuals. Average percentage plant cover in all the paddocks across the 4-year study was dominated by 10 species, which accounted for almost 75% of total plant



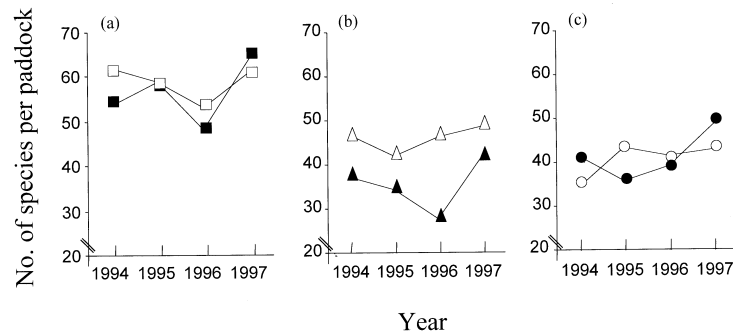
**Fig. 2.** Precipitation distribution at 10-day intervals at the experimental site during the rainfall seasons 1993-94, 1994-95, 1995-96 and 1996-97. Arrows indicate the start of grazing. In parentheses, total rainfall for the season.

cover. These comprised four grasses (37%), two thistles (14%), two legumes (15%), one crucifer (6%) and one forb (3%). About half of the relative plant cover comprised annual species and the other half perennial species, mostly hemicryptophytes. Palatable species (grasses, annual legumes and several dicots) represented close to 55% of the total plant cover. Tall grasses were the main palatable plants (37%) and included the perennial grass *Hordeum bulbosum*, the most abundant species (23%), and three annual grasses, *Avena sterilis* (6.7%), *Hordeum spontaneum* (3.9%) and *Triticum dicoccoides* (3.5%). Other important, but less palatable, species were the perennial legume *Bituminaria bituminosa* (9.4%), the annual thistle *Scolymus maculatus* (5.8%), the perennial thistle *Echinops adenocaulos*

(7.9%) and the annual crucifer *Rapistrum rugosum* (6.2%). The most common annual legume was the prostrate *Trifolium pilulare* (6%), while the less palatable *Echium* spp. were the most abundant annual forbs (3.8%). The main geophyte present at the site was *Asphodelus ramosus* (0.8%), an unpalatable plant with tuberous roots.

#### EFFECTS OF GRAZING TREATMENTS ON SPECIES RICHNESS

The grazing treatments had a significant effect on species richness in 1994, 1995 and 1996 ( $F_{1,5} = 13.3$ ,  $P = 0.007$ ;  $F_{1,5} = 12.9$ ,  $P = 0.008$ ;  $F_{1,5} = 7.33$ ,  $P = 0.027$ , respectively; Fig. 3). Results from the repeated measures ANOVA showed significant differ-



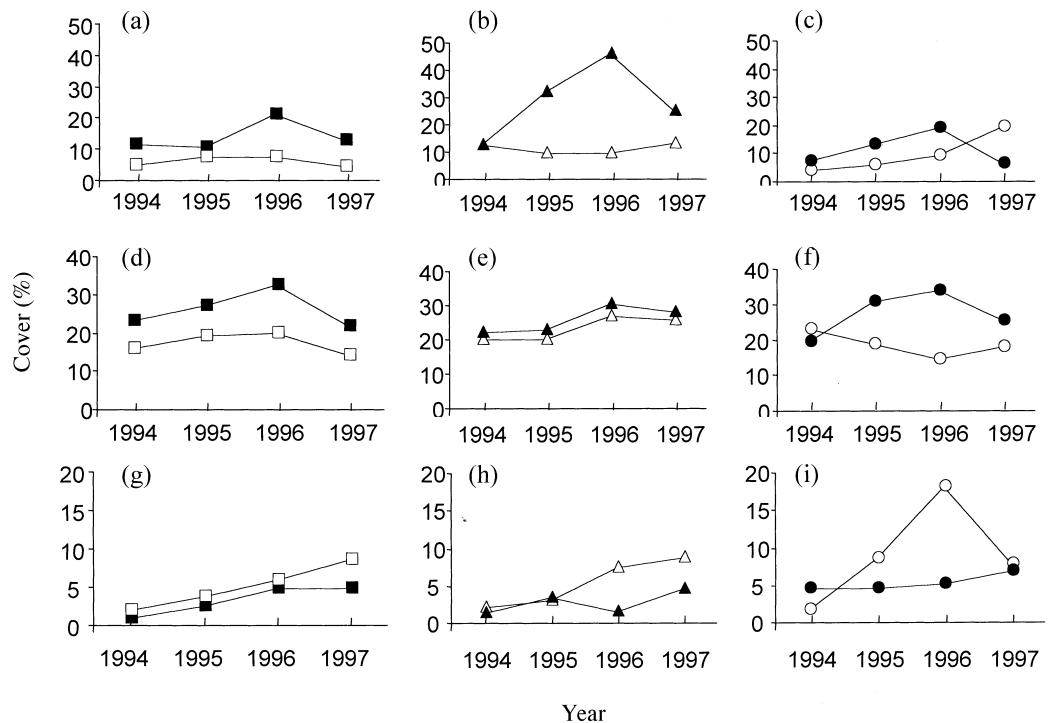
**Fig. 3.** The effects of grazing treatments on species richness in continuous (a) and seasonal regimes (b and c). Treatments: continuous moderate, CM (black squares); continuous heavy, CH (white squares); seasonal heavy early, S-HE (white triangles); seasonal heavy late, S-HL (black triangles); seasonal very heavy early, S-VHE (white circles) and seasonal very heavy late, S-VHL (black circles).

ences in species richness between treatments over time ( $F_{5,5}=7.73$ ,  $P=0.014$ ), with higher values in continuous grazing treatments (CM and CH). Differences among years and their interaction with treatments were also significant ( $F_{3,5}=22.7$ ,  $P=0.002$ ;  $F_{15,15}=28.4$ ,  $P=0.0019$ , respectively). Species richness was greater in paddocks under continuous grazing, in contrast with plots with seasonal grazing ( $F_{1,5}=25.3$ ,  $P=0.005$ ). Lowest species richness was noted in paddocks with the heavy late (S-HL) treatment, which remained practically ungrazed during the growing season and at the time of the vegetation sampling. In contrast to the differences in

species richness among grazing treatments, no pattern of increase or decrease in richness was found within each treatment during the 4-year study (Fig. 3).

#### EFFECTS OF GRAZING TREATMENTS ON FUNCTIONAL GROUPS

Tall annual and perennial grasses were the main contributors to the palatable biomass consumed by the cattle, and were similarly affected by the grazing treatments. Tall annual grasses were sensitive to grazing manipulations (Fig. 4a–c and Table 1) and

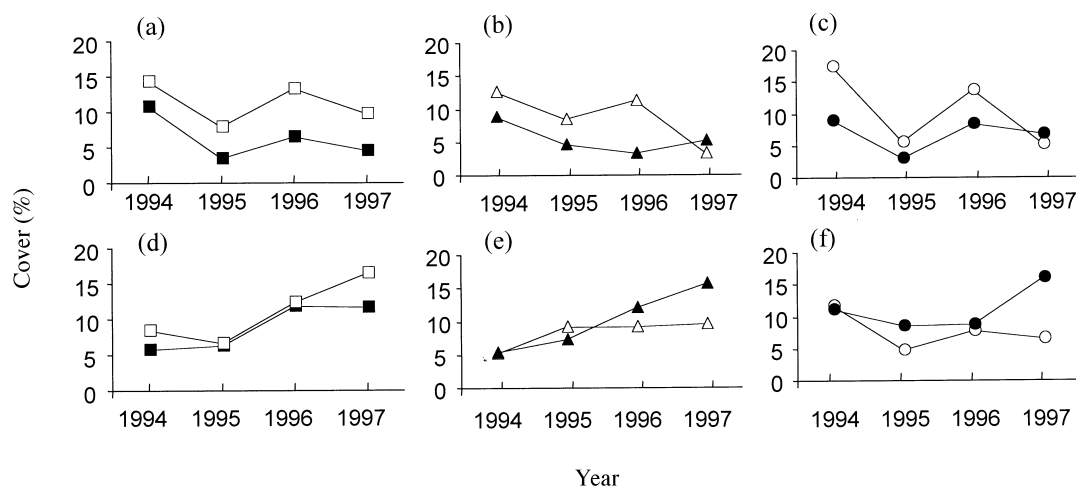


**Fig. 4.** The effects of grazing treatments on functional group cover. Tall annual grasses (a–c); tall perennial grasses (d–f); short annual grasses (g–i). Key for grazing treatments as in Fig. 3.

**Table 1.** Results of two-way and repeated measures ANOVAs for functional groups over the 4-year study. Bold numbers indicate significant differences between treatments. Stocking rate (SR), continuous vs. seasonal (C vs. S). Coefficient of variation (CV) in per cent\*

Effect	Year	d.f.	Short annual grasses			Tall annual grasses			Tall perennial grasses			Annual legumes			Perennial legumes			Annual thistles			Perennial thistles			Crucifers			Geophytes			Forbs		
			F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P		
Treatment	1994	1,5	0.69	0.655	2.06	0.22	0.55	0.736	0.39	0.841	0.66	0.672	1.45	0.346	0.77	0.611	0.76	0.617	2.48	0.171	0.17	0.963										
	1995	1,5	<b>5.94</b>	<b>0.036</b>	<b>11.9</b>	<b>0.008</b>	0.69	0.653	1.06	0.475	0.37	0.849	1.50	0.335	<b>7.54</b>	<b>0.022</b>	2.16	0.209	1.51	0.332	0.18	0.959										
	1996	1,5	3.06	0.123	<b>9.05</b>	<b>0.015</b>	<b>8.21</b>	<b>0.018</b>	2.70	0.149	0.32	0.881	<b>21.2</b>	<b>0.002</b>	1.31	0.386	4.78	0.055	0.91	0.540	0.36	0.858										
	1997	1,5	0.99	0.506	<b>7.40</b>	<b>0.023</b>	3.03	0.124	1.45	0.346	1.13	0.448	<b>11.7</b>	<b>0.009</b>	0.67	0.663	3.93	0.079	1.26	0.404	0.85	0.568										
<b>Overall analysis</b>																																
Treatment		5,5	2.48	0.171	<b>10.5</b>	<b>0.011</b>	2.65	0.154	1.43	0.351	0.22	0.937	<b>24.7</b>	<b>0.002</b>	1.47	0.342	<b>8.36</b>	<b>0.018</b>	1.28	0.395	0.09	0.990										
Year		3,15	<b>16.3</b>	<b>0.001</b>	<b>11.3</b>	<b>0.001</b>	2.57	0.093	<b>5.63</b>	<b>0.009</b>	<b>23.5</b>	<b>0.001</b>	<b>11.1</b>	<b>0.001</b>	<b>11.8</b>	<b>0.001</b>	0.64	0.601	1.73	0.204	<b>24.4</b>	<b>0.001</b>										
Treatment × year		15,15	1.91	0.113	<b>4.26</b>	<b>0.004</b>	1.25	0.336	0.65	0.797	<b>5.00</b>	<b>0.002</b>	0.69	0.756	1.33	0.293	0.95	0.535	1.56	0.201	2.14	0.076										
CV			83.3		75.1		29.2		66.6		51.1		73.9		49.9		59.3		92.7		40.4											
<b>Contrasts</b>																																
Timing (early vs. late)		1,5	4.74	0.081	<b>15.4</b>	<b>0.011</b>	4.66	0.083	3.25	0.131	0.67	0.449	<b>54.1</b>	<b>0.001</b>	3.64	0.115	2.31	0.189	0.20	0.675	0.01	0.920										
SR (seasonal)		1,5	5.15	0.072	<b>15.6</b>	<b>0.011</b>	0.41	0.552	0.53	0.499	0.01	0.963	<b>32.5</b>	<b>0.002</b>	0.96	0.373	<b>7.15</b>	<b>0.044</b>	3.03	0.142	0.25	0.638										
Timing × SR		1,5	0.03	0.874	<b>7.26</b>	<b>0.043</b>	1.33	0.301	0.02	0.892	0.19	0.681	0.01	0.927	2.53	0.173	<b>13.7</b>	<b>0.014</b>	0.39	0.561	0.01	0.918										
SR		1,5	1.40	0.290	2.46	0.178	0.80	0.411	0.14	0.727	0.07	0.805	<b>11.2</b>	<b>0.021</b>	1.12	0.339	0.91	0.384	0.84	0.401	0.03	0.871										
C vs. S		1,5	1.11	0.341	5.98	0.058	0.84	0.402	0.56	0.468	0.11	0.754	<b>31.8</b>	<b>0.002</b>	0.01	0.973	<b>14.1</b>	<b>0.013</b>	2.04	0.213	0.01	0.932										
SR × C vs. S		1,5	5.10	0.073	<b>21.4</b>	<b>0.006</b>	5.63	0.064	3.19	0.134	0.08	0.788	<b>26.5</b>	<b>0.004</b>	0.04	0.850	<b>10.8</b>	<b>0.021</b>	2.95	0.146	0.39	0.558										

\*Results for block and interactions in the overall analysis were not included for clarity of the table presentation, as no significant differences were found.



**Fig. 5.** The effects of grazing treatments on functional group cover. Annual legumes (a–c); perennial legumes (d–f). Key for grazing treatments as in Fig. 3.

the three main species in this group (*Avena sterilis*, *Hordeum spontaneum* and *Triticum dicoccoides*) had similar patterns of change. Their cover showed a general trend of reduction with increase of grazing intensity ( $F_{5,5} = 10.5$ ,  $P = 0.011$ ), and was affected by differences in growth conditions between years ( $F_{3,15} = 11.3$ ,  $P = 0.001$ ). The reduction of cover by grazing was stronger in rainy years (1995 and 1996; Table 1) than in the dry year (1994) (treatment  $\times$  year,  $F_{15,15} = 4.26$ ,  $P = 0.004$ ), particularly when compared with the high cover in the S-HL treatment in which the paddocks were not under grazing at the time the vegetation was recorded. Indeed, when contrasting timing (early vs. late grazing), cover was higher in the late treatments ( $F_{1,5} = 15.4$ ,  $P = 0.011$ ), particularly S-HL. When comparing stocking rates (SR) in the seasonal regime (1.1 vs. 2.2 cow ha<sup>-1</sup> year<sup>-1</sup>), a reduction in cover was noted with the increase in grazing pressure ( $F_{1,5} = 15.6$ ,  $P = 0.011$ ). However, the reduction in cover was dependant on the season of grazing ( $F_{1,5} = 7.26$ ,  $P = 0.043$ ), mainly due to the S-HL treatment.

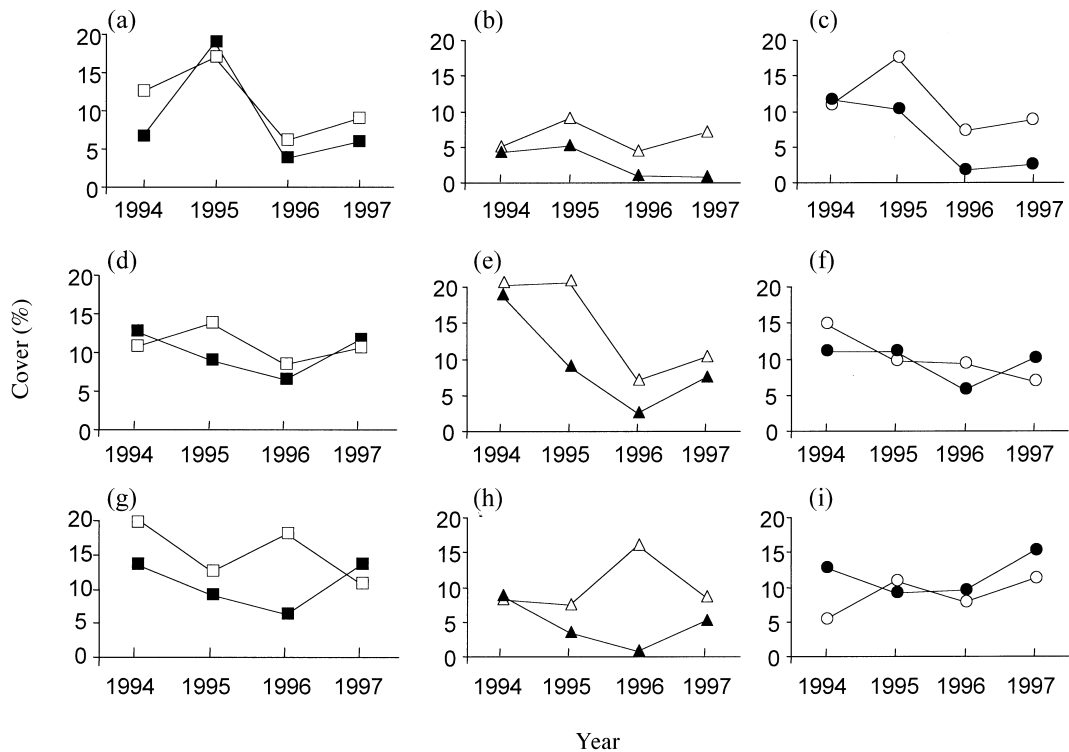
Cover of tall perennial grasses (mostly *Hordeum bulbosum*) was consistently higher in paddocks with continuous grazing at lower pressure (moderate vs. heavy) as well as in treatments with late grazing, as found for tall annual grasses (Fig. 4d–f). However, the overall analysis showed that grazing treatments, differences between years and contrasts, had no effect on cover of perennial grasses (Table 1). Cover of tall perennial grasses was significantly affected by the grazing treatment only in 1996 (Table 1), the relatively wet year, with the largest differences occurring between treatments CM and S-VHE.

Short annual grasses showed a small but significant trend of increase in cover from year to year

(2.1–6.4%, average for all treatments,  $F_{3,5} = 16.3$ ,  $P = 0.001$ ) but their cover was not influenced by grazing treatments and regimes (Fig. 4g–i and Table 1). In contrast, cover of annual legumes decreased with time, specially in the CH and S-VH treatments ( $F_{3,5} = 5.63$ ,  $P = 0.009$ ). However, no significant differences between grazing treatments were found, as observed for the short annual grasses, even though a trend of higher cover occurred under CH and early grazing treatments (Fig. 5a–c and Table 1).

Perennial legumes were represented by a single species, *Bituminaria bituminosa*. Its cover was not affected by grazing treatments (Fig. 5d–f and Table 1) but increased from year to year, principally in the treatments with continuous and S-HL grazing ( $F_{3,5} = 23.5$ ,  $P = 0.001$ ), while in other treatments cover remained unchanged (treatment  $\times$  year,  $F_{15,15} = 5.00$ ,  $P = 0.002$ ).

Annual thistles tended to show opposite patterns of response compared with tall grasses, as their cover increased with the severity of the grazing treatment (Fig. 6a–c). Changes in cover were related to yearly conditions and grazing treatment ( $F_{3,5} = 11.1$ ,  $P = 0.001$ ;  $F_{5,5} = 24.7$ ,  $P = 0.002$ , respectively). In 1996 and 1997, thistle cover values were lower in paddocks that were grazed late than in those that were grazed early in the season at high stocking rates (S-HL vs. S-VHE) ( $F_{1,5} = 21.2$ ,  $P = 0.002$ ;  $F_{1,5} = 11.7$ ,  $P = 0.009$ , respectively). Indeed, contrast analysis of the seasonal regime showed that early grazing (HE and VHE treatments) increased annual thistle cover ( $F_{1,5} = 54.1$ ,  $P = 0.001$ ), and that this increase was greater at the highest stocking rate (2.2 vs. 1.1 cow ha<sup>-1</sup> year<sup>-1</sup>) ( $F_{1,5} = 32.5$ ,  $P = 0.002$ ). Furthermore, cover of



**Fig. 6.** The effects of grazing treatments on functional group cover. Annual thistles (a–c); perennial thistles (d–f); crucifers (g–i). Key for grazing treatments as in Fig. 3.

annual thistles was higher in the continuously grazed paddocks when contrasted with the seasonal regime plots, and this trend was dependent on stocking rate intensities (SR  $\times$  continuous vs. seasonal,  $F_{1,5} = 26.5$ ,  $P = 0.004$ ).

Perennial thistle cover varied according to differences in growth conditions between years, with the lowest cover in 1996 ( $F_{3,5} = 11.8$ ,  $P = 0.001$ ), a relatively rainy season in which tall grasses reached a high cover (Fig. 6d–f). In 1995, cover was lower in paddocks that were late grazed compared with those grazed early in the season with high stocking rates (S-HL vs. S-HE,  $F_{1,5} = 7.54$ ,  $P = 0.022$ ). However, the overall analysis showed that cover of perennial thistles was not affected by grazing treatments (Table 1).

Cover of crucifers, all annual species hardly consumed by the cattle, tended to be higher with higher stocking rates ( $F_{5,5} = 8.36$ ,  $P = 0.018$ ; Fig. 6g–i). In the seasonal grazing treatments, the contrast analysis showed that cover was significantly higher when the stocking rate was double (1.1 vs. 2.2 cow  $\text{ha}^{-1} \text{year}^{-1}$ ,  $F_{1,5} = 7.15$ ,  $P = 0.044$ ), particularly when grazing started early in the season ( $F_{1,5} = 13.7$ ,  $P = 0.014$ ). Furthermore, as observed for annual thistles, cover of crucifers in paddocks that were grazed late in the season (S-HL) was lower than in continuously grazed paddocks (CH). Differences

between continuous vs. seasonal regimes were dependent on the intensity of grazing ( $F_{1,5} = 14.1$ ,  $P = 0.013$ ;  $F_{1,5} = 10.8$ ,  $P = 0.021$ , respectively).

Cover of geophytes, mainly the non-palatable *Asphodelus ramosus*, was low (general mean cover of 0.8%) and showed no significant changes due to grazing treatments and year conditions (Table 1). Furthermore, even the heaviest grazing pressure treatment applied in this study did not increase cover of this unpalatable monocot, commonly dominant in overgrazed Mediterranean environments.

Forbs was a heterogeneous group including low-cover dicots that did not share clear trends of response to the grazing treatments. Most species in this group were less palatable annual composites (2.2%), annual umbellifers (2.3%), perennial umbellifers (e.g. the toxic tall *Ferula communis*, 0.6%) and the less palatable annual *Echium* spp. (3.8%), with a total cover close to 9%. Forb cover was affected by differences in growth conditions between years, but not by grazing treatments (Table 1).

#### LIFE FORMS AND VARIATION IN RELATIVE PLANT COVER

The degree of variation in relative plant cover among functional groups differed due to year and treatment effects, as expressed by the coefficient of

variation (CV in Table 1). Species in the functional groups showed a rather patchy distribution, reflecting the spatial heterogeneity in growing conditions. Functional groups including annual species had higher CVs compared with groups with perennial (hemicryptophytic) species. This trend was particularly evident when comparisons were carried out between annual and perennial functional groups belonging to the same taxonomic category (grasses and legumes) or possessing similar morphological characteristics (thistles): (i) 29% in perennial grasses vs. 75% and 83% in short and tall annual grasses, respectively ( $P < 0.05$ ); (ii) 51% in perennial vs. 66% in annual legumes ( $P = \text{NS}$ ); and (iii) 49% in perennial vs. 73% in annual thistles ( $P < 0.05$ ). Furthermore, annual crucifers had a relatively high CV of 59% compared with perennial functional groups. On the other hand, the relatively low CV of the forbs (40%) was probably due to the inclusion in this heterogeneous group of species with different life forms and contrasting responses to grazing. The particularly high CV of geophytes was probable due to their low cover and sampling limitations.

#### CO-VARIATION OF FUNCTIONAL GROUPS IN RESPONSE TO GRAZING

Co-variation in relative cover of the 10 different functional groups in response to grazing was analysed, and the correlation matrix is presented in Table 2. A positive correlation ( $P < 0.01$ ) was observed between the cover of tall annual and perennial grasses (i.e. reduction in grazing pressure increased their cover). Similarly, positive correlations ( $P < 0.05$ ) were found between the less palatable groups, forbs vs. annual and perennial thistles (Table 2), as their cover increased with grazing intensity. Opposite trends (negative correlations) were found when comparing the palatable, tall, annual and perennial grasses with less palatable groups, annual and perennial thistles, forbs and crucifers. Dominant annual legumes were prostrate species and were negatively correlated with tall annual and perennial grasses.

#### Discussion

##### RAINFALL PATTERNS, GRAZING SYSTEMS AND PLANT COMMUNITY STRUCTURE

A major finding in this study was that the vegetation structure at the experimental site was strongly affected by the inter-annual climatic conditions compared with the grazing treatments. The cover of most functional groups was influenced by annual rain conditions, with the notable exceptions of tall perennial grasses, crucifers and geophytes (Table 1). In relatively wet seasons, grazing treatments had significant effects on the cover of functional groups

**Table 2.** Correlation analysis between functional groups. Bold numbers indicate significant correlation between groups: \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$  and NS, not significant. (+) or (-) indicates positive or negative correlation

	Short annual grasses		Tall annual grasses		Tall perennial grasses		Annual legumes		Perennial legumes		Annual thistles		Perennial thistles		Crucifers		Geophytes		Forbs		
	$R^2$	$P$	$R^2$	$P$	$R^2$	$P$	$R^2$	$P$	$R^2$	$P$	$R^2$	$P$	$R^2$	$P$	$R^2$	$P$	$R^2$	$P$	$R^2$	$P$	
Short annual grasses																					
Tall annual grasses	0.047	NS	0.101	NS	0.002	NS	0.011	NS	0.001	NS	0.001	NS	0.087	NS	0.008	NS	0.051	NS	0.038	NS	
Tall perennial grasses			<b>0.270</b>	** (+)	<b>0.275</b>	** (-)	0.003	NS	<b>0.289</b>	NS	<b>0.241</b>	* (-)	<b>0.445</b>	** (-)	<b>0.445</b>	** (-)	0.032	NS	<b>0.281</b>	** (-)	
Annual legumes					<b>0.219</b>	* (-)	0.018	NS	<b>0.176</b>	NS	<b>0.171</b>	* (-)	0.136	NS	0.136	NS	0.056	NS	<b>0.402</b>	** (-)	
Perennial legumes							0.001	NS	0.001	NS	0.125	NS	0.119	NS	0.119	NS	0.007	NS	0.007	NS	
Annual thistles									<b>0.178</b>	* (-)	0.097	NS	0.048	NS	0.001	NS	0.078	NS	<b>0.157</b>	NS	
Perennial thistles									0.048	NS	0.048	NS	0.002	NS	0.065	NS	0.048	NS	<b>0.186</b>	* (+)	
Crucifers															0.002	NS	0.123	NS	<b>0.271</b>	** (+)	
Geophytes																	0.029	NS	<b>0.032</b>	NS	
Forbs																			<b>0.098</b>	NS	

with tall species. However, the lack of grazing impacts on all functional groups during the dry season 1994 indicates that drought had a major effect on the dynamics of the plant community, with grazing playing a secondary role. These results are consistent with observations from other studies that have attempted to relate changes in vegetation to rainfall and grazing intensity (Lauenroth & Sala 1992; Biondini, Patton & Nyren 1998; Koukoura, Tsiouvaras & Papanastasis 1998).

In Mediterranean grazing systems, the seasonal pattern of rainfall is a major constraint dictating the timing of grazing (Pineda *et al.* 1987; O'Connor & Roux 1995). In our experiment, onset of deferred grazing was determined by the timing of the first effective rains (Fig. 2). In the seasonal grazing regimes, timing of transfer in spring between early and late grazing treatments was dictated by plant biomass availability that, in turn was dependent on both the amount and distribution of rainfall and on grazing pressure. Finally, the timing of the last effective rains and grazing pressure determined the end of the grazing period. Thus, as a result of variation among years in the timing of these events, due to difference in rainfall patterns and to the different grazing regimes (e.g. continuous vs. seasonal), the vegetation was subjected to grazing at different phenological stages, i.e. plant establishment, flowering, seed set and seed dispersal. The effects of grazing at different phenological stages probably affected the regrowth capabilities of the dominant palatable species. In addition, grazing during seed set will potentially reduce soil seed banks of the edible species, with the consequent reduction of their presence in the ensuing vegetation. It is probable that, in Mediterranean grasslands, gradual accumulative changes in the vegetation due to different grazing regimes are masked, on a short time scale, by the large inter-annual fluctuations in rainfall patterns.

Species richness was consistently higher in paddocks under continuous grazing compared with those under the seasonal regime (Fig. 3). The differential effects of grazing systems on species richness can be explained by the combined effects of repeated vertical differential defoliation, horizontal disturbance and grazing history (Noy-Meir, Gutman & Kaplan 1989). The vertical defoliation imposed by cattle on tall plants (dominants), associated with the opening of gaps by biomass removal, trampling and wallowing, altered the competitive interactions, enabling the establishment of less competitive species, with the consequent increase in species richness (Grime 1979; Grubb 1986). Paddocks under continuous grazing were more evenly 'disturbed' during the whole grazing season. Thus, several species were able to germinate and establish. The lack of significant difference between moderate and heavy grazing under the continuous regime is explained by the prevailing role of regular opening of sites for establish-

ment in the closed sward, compared with the intensity of grazing. It may also indicate that, apart from the continuous heavy treatment, possible losses of grazing-vulnerable species were still offset by invasion of grazing-tolerant species.

Under the seasonal grazing regime, the combined effects of timing, intensity of grazing and the phenological status of the vegetation during grazing determined a more complex pattern of plant community richness. The lowest number of species was observed in plots under heavy late grazing (S-HL). These paddocks were not grazed at all during the growing period, as the cattle were moved to the plots in May, after seed production and dispersal. At the time of vegetation sampling (April), the cattle had consequently not yet grazed in these plots. As a result of the late grazing, dominant species were able to close the vegetation matrix, preventing the establishment of less competitive species. Competition effects were clear in the 1996 season, when substantial March rainfalls resulted in a closed sward with less species in the S-HL paddocks. In contrast, paddocks with early grazing treatments (S-HE and S-VHE) showed a higher number of species, probably due to a reduction in competition and the consequent high establishment of species less sensitive to grazing. It is important to mention that the recording technique may have enhanced grazing effects on species richness. Recording by the step-point method probably resulted in a subtle bias towards the tall species and an underestimation of the short prostrate species, particularly in the late grazed paddocks.

It has been proposed that several hypotheses relating grazing intensity and biodiversity (Connell 1978; Grime 1979; Grubb 1986) converge in the context of a general 'dominance-disturbance theory' (Noy-Meir 1998). This theory predicts a hump-shaped response to grazing, in which low and high intensity of grazing reduce diversity, while grazing at intermediate intensity increases it. Our data on the relationship between grazing regimes and species richness generally support this theory. Species richness increased from the less grazed plots (S-HL) to the continuously grazed ones (CM and CH), and was reduced by treatments with very heavy grazing (S-VHE and S-VHL). Our findings also emphasize the impact that grazing regime has on species richness (continuous vs. seasonal, early vs. late), in addition to grazing intensities.

#### RELATIONSHIPS BETWEEN GRAZING AND PLANT LIFE-HISTORY TRAITS

A particular characteristic of the structure of this Mediterranean herbaceous community was the presence of few (1–3) dominant species in each functional group. Thus variation in relative cover of the

functional groups reflected patterns of variation of these dominant species.

Life history and plant morphology of the dominant species are important attributes in the responses of the community to grazing intensity and timing (Noy-Meir, Gutman & Kaplan 1989; Diaz, Acosta & Cabido 1994; McIntyre, Lavorel & Tremont 1995; Lavorel *et al.* 1997). The functional group analysis showed that the reduction in cover of tall annual grasses was a key factor in shaping the responses of the community to grazing (Table 2). In the continuously and early heavy grazed paddocks this reduction led to a compensatory increase of short-stature, prostrate and rosette-forming species (Table 2). Similar results were observed in Spanish Mediterranean annual grasslands (Fernandez-Ales, Laffarga & Ortega 1993). In contrast, hemicryptophytic species, such as *Hordeum bulbosum* (grass), *Echinops adenocaulos* (thistle) and *Bituminaria bituminosa* (legume), and geophytes such as *Asphodelus ramosus*, were less affected by grazing. They appear to be adapted to survive under heavy and very heavy grazing pressure, as their perennating buds are buried near the soil surface and most of their shoots desiccate in summer. Their persistence is also associated with the development of physical or chemical defences, such as spikes with rigid awns (*Hordeum bulbosum*), spiny leaves (*Echinops adenocaulos*) and secondary chemical compounds (*Bituminaria bituminosa* and *Asphodelus ramosus*). They are also less dependent on seed production compared with annual species. This hemicryptophytic strategy and associated morphology allows fast growth and early establishment after the first rains, and a higher tolerance of grazing. Furthermore, patches occupied by hemicryptophytic species were densely covered by litter (e.g. desiccated leaves) and by the basal parts of the plant where the perennating buds are located (e.g. corms in *Hordeum bulbosum*). It is conceivable that seedling establishment of annual species within these patches is difficult and their further development is constrained by the fast initial growth of the hemicryptophytes. These characteristics probably contribute to a greater constancy of cover of these species on a time scale and in response to grazing, as expressed by their lower CV (Table 2). In contrast, cover of annual species was more variable (greater CV) from year to year and among grazing treatments, as germination and seedling establishment were strongly affected by inter-annual climatic fluctuations and competition. Even though hemicryptophytes are better buffered against climatic vagaries and grazing disturbances than annual species, their relative cover still varies in response to these factors, as well as in response to fire and other disturbances (Noy-Meir 1990, 1995; Noy-Meir & Sternberg 1999). In this context, *Hordeum bulbosum* is an outstanding key species because, in spite of its high palatability, it remained the most abundant

species. Its response to grazing deserves further research.

#### GRAZING AND CONSERVATION MANAGEMENT

Continuous and early cattle grazing greatly increased gap formation, allowing the establishment and development of a more species-rich community. This result has important implications for the conservation management of Mediterranean grasslands using cattle, as a diverse and spatially heterogeneous community could more easily achieve sustainability (Tainton *et al.* 1996). A diverse community also allows a widening of the seasonal forage flow, resulting in a lengthening of the grazing season (Seligman 1996).

The responses of the plant community to grazing can also be considered in relation to predictions of vegetation resistance to disturbance. One important question here relates to whether an increase or reduction in grazing intensity affects persistence of the community? (for terminology see Grimm & Wissel 1997). Our results show that, for a Mediterranean grassland, a more diverse community can be maintained under continuous grazing at both moderate and high intensities. In paddocks that were not grazed during the growing season, under seasonal, heavy late grazing (S-HL), tall annual and perennial grasses appeared to form a stable, close and less diverse community in which they could regenerate themselves annually while effectively preventing the establishment of other species. However, further reduction of grazing intensity may destabilize this community, as observed in ungrazed exclosures, where the complete exclusion of grazing for more than 20 years facilitated repeated vole eruptions with consequent drastic changes in the plant community (Noy-Meir 1988). In addition, the accumulation of large amounts of ungrazed vegetation is conducive to more frequent wild fires during the dry summers. Thus, the exclusion of grazing in areas with a long history of grazing can be considered as a disturbance (Milchunas, Sala & Lauenroth 1988). East Mediterranean grasslands probably evolved to a state of balanced persistence and productivity under intensive grazing. However, under either very heavy grazing pressure or in the absence of grazing, they can change to an alternative, less productive, state (Harrison 1979).

Long-term studies, including grazing effects on seed bank dynamics, in Mediterranean grasslands with their typically high inter- and intra-seasonal variability are necessary to understand species persistence in this community. These studies will inform future management recommendations for conservation and sustainable animal production in Mediterranean grasslands.

## Acknowledgements

The authors would like to thank to Dr Avraham Genizi and Hagit Baram from the Volcani Centre, and Dr Hillary Voet from the Department of Agricultural Economics and Management, Faculty of Agricultural, Food and Environmental Quality Sciences, The Hebrew University of Jerusalem, for their advice regarding the statistical analysis of the results. We also thank Professor Imanuel Noy-Meir and Dr Noam Seligman for helpful comments on an early draft of this manuscript. Valuable comments from Sandra Lavorel and two anonymous referees are acknowledged. Thanks are also extended to the many people who participated in field work through the years. The research was supported by the Agriculture Research Organization, Ministry of Agriculture and Rural Development.

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*Received 9 March 1999; revision received 10 November 1999*