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Effects of grazing on soil seed bank dynamics: An approach with functional groups

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Abstract. The relationship between intensity and timing of cattle grazing on changes in the size and composition of the soil seed bank were investigated in a 3-yr study in a Mediterranean grassland in northeastern Israel. Treatments included manipulations of stocking rates and of grazing regimes, in a factorial design.

The retrieved soil seed bank community was rich in species, with 133 species accounting for 80% of the 166 species recorded at the site. Within the seed bank, 89% of the species were annuals. Seed bank dynamics was analysed in terms of plant functional groups and germination strategies. In terms of total seed bank density and including all functional groups, 42% of the seeds present in the soil did not germinate under watering conditions. The dormancy level differed greatly among functional groups. The seed bank of annual legumes, crucifers, annual thistles and annual forbs had a large fraction of non-germinated seeds and characterized areas grazed early in the growing season under high and very high grazing intensity. These functional groups were considered to have a higher potential for persistent seed banks production. In contrast, short and tall annual grasses and tall perennial grasses, that were dominant in ungrazed or moderately grazed paddocks, generally had seed banks with a very small fraction of non-germinated seeds. Seed bank densities varied widely between grazing treatments and years. Under continuous grazing, heavy grazing pressure reduced seed bank densities of grasses and crucifers in comparison to moderate grazing. The greatest reduction on the seed bank densities resulted from heavy grazing concentrated during the seed-set stages.

Keywords: Cattle; Dormancy; Germination; Management; Mediterranean; Persistence; Rangeland; Regeneration strategy.

Nomenclature: Feinbrun-Dothan & Danin (1991).

Introduction

Domestic livestock have grazed Mediterranean ecosystems, and particularly those of the Middle East, for more than 7000 yr (Noy-Meir & Seligman 1979; Edelstein & Milevski 1994). This long history of grazing has been a major factor in determining the structure and organization of plant communities in these ecosystems (Noy-Meir et al. 1989; Seligman 1996).

Annual species are a major component of Mediterranean grasslands. Their persistence under grazing is dependent upon the development and maintenance of considerable soil seed banks. Grazing can reduce seed production of annuals by affecting the allocation of plant resources for reproduction due to reduction of photosynthetic surface and by the direct removal of flowers and seeds. Under heavy grazing, the removal of reproductive structures may lead to situations in which seed banks become a limiting factor for recovery or persistence of the palatable vegetation (O'Connor & Pickett 1992). However, it is not clear whether grazing alone can deplete the seed bank of annual species, causing long-lasting negative effects on the biological diversity and production potential of grasslands (Russi et al. 1992; Meissner & Facelli 1999). Only few studies have dealt with this question, but in different ecosystems (Akinola et al. 1998; Meissner & Facelli 1999). In Mediterranean grasslands grazing can have a large impact on their vegetation (Montalvo et al. 1993; Seligman 1996; Lavorel et al. 1999; Sternberg et al. 2000), however the soil seed bank may buffer inter-annual differences in the extent of this impact (Russi et al. 1992; Ortega et al. 1997). It is generally assumed that the Mediterranean annual plant populations show adaptive responses to the unpredictability of their environment by an escape strategy based on the production of dormant seeds that persist during periods of limited resource supply (Shmida & Ellner 1984; Thompson 1992; Lavorel et al. 1993; Perevolotsky & Seligman 1998). Thus, a persistent soil seed bank acts as a long-term refuge for annual plant populations in the highly variable environments typical of the Mediterranean region (Kigel 1995). Our working hypothesis is that the soil seed bank is an effective stabilizing mechanism in the maintenance of productivity and plant species diversity in Mediterranean grasslands that should be taken into account in grazing management decisions. Thus, the aims of the present research were (1) to investigate the effects of cattle grazing management on soil seed bank dynamics in a Mediterranean herbaceous community; and (2) to study the germination strategies of the main plant functional groups in the community. Studies carried out in these communities have shown that the responses of the vegetation to grazing are associated with plant vegetative traits, such as growth form, height, palatability and spininess (Gómez Sal et al. 1986; Noy-Meir et al. 1989; Lavorel et al. 1999; Sternberg et al. 2000). The relationships between these plant traits and grazing responses were studied by focusing on plant functional groups, in which species with similar biological traits and presumably similar responses to grazing were grouped together (Gitay & Noble 1997; Lavorel et al. 1997). However, species traits related to seed bank dynamics and germination responses have been little studied within the plant functional type context, even though these traits are most relevant for the persistence of herbaceous species under grazing. The specific objectives of our research were: (1) to determine the composition and density of the soil seed bank under different grazing management practices, (2) to study changes of specific plant functional groups in the soil seed bank in response to variation in the timing and intensity of grazing, (3) to determine patterns of seed germination in species and functional groups as an indication to their potential for producing transient or persistent seed banks.

Material and Methods

The study site

The study was conducted at the Karei Deshe Experimental Farm, located in northeastern Israel (32°55' N, 35°35' E, altitude 150 m a.s.l.; for full details of the site characteristics, see Sternberg et al. 2000). The site has a Mediterranean climate, characterized by rainy, mild winters with mean minimum and maximum temperatures of 7 °C and 14 °C, respectively. The mean annual rainfall is 570 mm, falling mostly in winter. The rainy season begins in October-November and normally ends in April. Summers are dry and hot, with mean minimum and maximum temperatures of 19 °C and 32 °C, respectively. During at least five months, there is no rainfall in the region (Gutman 1978). The growing season of the vegetation is closely associated with the distribution of rainfall. Germination of annuals and re-growth of most perennials occurs soon after the first rains.

Experimental design

A grazing experiment was established in 1993 in an area of 250 ha, comprising two blocks, each one with four fenced paddocks. 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 designated M (moderate) and H (heavy), with ca. 0.55 and 1.1 cow.ha^{-1}.yr^{-1}, respectively. In treatments without subdivision (designated C, continuous), animals were given continuous access to the entire paddock during the whole 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 aimed to maximize forage use.

From the point of view of grazing impact on the seed bank and vegetation, areas grazed at the beginning (E) and at the end (L) of the grazing season in treatments with subdivision, were studied separately. Thus, the four grazing systems imposed a total of six grazing treatments, defined by the combination of animal density, duration of grazing and season of grazing. The designations of treatments with continuous grazing systems are CM and CH for moderate and heavy stocking rates, respectively. 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, 1.1 cow.ha^{-1}) and very heavy (VH, 2.2 cow.ha^{-1}), respectively. In these systems the treatment designations for the early heavy and early very heavy stocking rates are S-HE and S-VHE, respectively and S-HL and S-VHL for the heavy and very heavy, late grazed areas. The continuous, moderate treatment (CM) represents the standard grazing regime for the region, and was considered as the control treatment. The grazing season started soon after the standing green herbaceous biomass exceeded 500 kg-dry-matter.ha^{-1} (Sternberg et al. 2000).

Sampling

Soil samples were collected in late October 1995, 1996 and 1997, before the winter rains and onset of germination. The seeds present in these soil samples were exposed for at least five months to local climatic conditions since seed set and the following shedding

(March/April). In each treatment, 32 soil samples were taken (16 per paddock) from open spaces between rocks outcrops along transects similarly used for vegetation sampling (Sternberg et al. 2000). The plant litter and soil within a 25 cm × 25 cm quadrat were collected to a depth of 5 cm. Each soil sample was thoroughly mixed and vegetation, stones and coarse roots were removed. A half litre sample representing about 100 cm^2 of soil surface was placed in plastic trays (20 cm × 20 cm) in a layer 1-2 cm deep. These samples were germinated in an unheated shadehouse in winter (January) under frequent watering and natural light and temperature conditions. Emerged seedlings were counted and removed as soon as they could be identified. Seedling emergence was monitored during three months, until no more seedlings emerged from the soil samples. The soils from each germination tray was then washed away, first through a coarse sieve (4 mm mesh) and then through a fine sieve (0.4 mm mesh). From previous measurements it was noted that the seed size of wet seeds of the large majority of the species in the experimental site was bigger than 0.4 mm. This was confirmed by the fact that 132 of a total of 166 species (80%) were retrieved by the sieving procedure. Most of the remaining species (34 spp.) were rare species or growing within rock outcrops where soil sampling was not carried out. The sieving fraction containing the seeds was dried in an oven at 65 °C for two days. Non-germinated seeds were retrieved, identified and counted under a binocular. Seeds were opened under the binocular and decayed and broken seeds, as well as seeds with damaged embryos were discarded as non-viable for germination. The total seed bank estimation per tray included the germinable seed bank (emerged seedlings) and the non-germinated seeds; these are the basic data.

Seed bank functional groups

Species present in the established vegetation and in the corresponding soil seed bank were categorized into 11 functional groups according to life cycle, plant height, palatability and taxonomy (Sternberg et al. 2000; see Noy-Meir et al. 1989 for terminology on species traits): tall perennial and tall annual grasses (> 50 cm at maturity), short annual grasses (< 50 cm), perennial and annual legume species, perennial and annual 'thistles', annual crucifers, perennial and annual 'forbs' (all other dicots) and geophytes. The tall perennial grass group was predominantly *Hordeum bulbosum*. Perennial legumes were also represented by a single species, *Bituminaria bituminosa*. The crucifers were recorded separately because of their low palatability due to chemical compounds, and occasional dominance in the vegetation.

Dormancy levels of seed banks of different species were evaluated from the proportion of germinable seeds from total seed bank. The potential for producing transient and persistent seed banks (i.e. inter-annual seed carry-over in the seed bank) was evaluated according to seed germinability under optimal climatic conditions (irrigated soils during winter, the natural germination season). Species present in the soil seed bank, that showed low germination fraction (i.e. high dormancy) under these conditions, were considered as having the potential to produce a persistent seed bank, while species showing high germination fraction (i.e. low dormancy) were considered as having the potential of producing transient seed banks. Thus, we differentiated between actual persistency of seed bank in the field due to innate and enforced seed dormancy, and the potential of these species for producing a persistent seed bank.

Statistical analysis

In this study, none of the species data counts complied with the assumptions of parametric tests, so the dependent variables were rank-averaged transformed and tested for homogeneity of variance before analysis (Conover & Iman 1981). Analysis of variance (ANOVA) techniques were used to analyse species and functional group densities in a randomized block design at individual sampling dates (Sokal & Rohlf 1995). The multi-year data were analysed using the repeated measures ANOVA procedure of the SAS General Linear Model (GLM; Anon. 1996) to estimate overall significance of treatment effects. Factors examined in the model were: block, treatment, year and their interactions. The CONTRAST procedure (SAS Institute Inc., version 1996) was used within the repeated measures framework to test differences between grazing regimes. Contrasts included: (1) stocking rates under continuous grazing; (2) within the seasonal regime: timing (early versus late grazing), stocking rate and their interaction.

Results

Soil seed bank characteristics

During the 3-yr sampling a total of 133 species were identified in the retrieved soil seed bank (App. 1). This represented 80% of the total number of species recorded in the established vegetation at the site (166 spp.; Sternberg et al. 2000). Of the 133 species identified, 112 species were represented in the germinable seed bank, while 21 species (ca. 16%) were present in the seed bank but did not germinate under watered conditions. Seeds from ungerminated species constituted only 5% of the

Table 1. Soil seed bank composition by main functional groups in the grazing treatments. Data is averaged (mean ± standard error) for three years of data (1995-1997) and is the sum of germinated and non-germinated seeds. The relative proportion of each funtional group within each treatments is presented. Treatments: CM = continuous moderate; CH = continuous heavy; S-HE = seasonal heavy early; S-HL = seasonal heavy late; S-VHE = seasonal very heavy early; S-VHL = seasonal very heavy late.

Plant functional groups	CM		CH		S-HE		S-HL		S-VHE		S-VHL	
	Density (m^{-2})	Prop (%)	Density (m^{-2})	Prop (%)	Density (m^{-2})	Prop (%)	Density (m^{-2})	Prop (%)	Density (m^{-2})	Prop (%)	Density (m^{-2})	Prop (%)
Short annual grasses	4354 ± 269	42.7	1277 ± 93	18.6	2307 ± 220	34.4	5478 ± 371	61.5	4664 ± 291	40.9	1591 ± 88	32.7
Tall annual grasses	405 ± 31	3.9	198 ± 17	2.8	180 ± 20	2.1	896 ± 70	10.1	361 ± 25	3.2	149 ± 12	3.1
Tall perennial grasses	182 ± 9	1.8	74 ± 4	1.1	177 ± 13	2.1	213 ± 23	2.4	136 ± 12	1.1	166 ± 7	3.4
Annual legumes	1160 ± 78	11.4	1069 ± 60	15.5	1801 ± 145	21.4	949 ± 47	10.5	2043 ± 140	17.9	575 ± 35	11.8
Annual thistles	164 ± 29	1.6	280 ± 64	4.0	107 ± 14	1.3	59 ± 4	0.5	163 ± 21	1.4	40 ± 11	0.8
Crucifers	1989 ± 171	19.5	609 ± 46	8.8	1957 ± 246	23.2	381 ± 32	4.3	1294 ± 161	11.4	1121 ± 79	23.0
Annual forbs	1932 ± 107	19.1	3378 ± 375	49.1	1298 ± 91	15.3	926 ± 61	10.3	2722 ± 216	23.9	1219 ± 117	25.1
Total	**10176**	**100**	**6885**	**100**	**7827**	**100**	**8902**	**100**	**11383**	**100**	**4861**	**100**

total seed bank abundance. During the 3-yr study, the seed bank in all paddocks was dominated by 12 species that accounted for 72% of the total soil seed bank (App. 1). Annuals were 89% of the retrieved species. The overall density of the seed bank averaged over all treatments was composed of 38% short annual grasses, 5% tall annual grasses, 2% tall perennial grasses, 24% annual forbs, 15% annual legumes, 15% annual crucifers, and 2% annual thistles. Seeds of perennial non-grass species (legumes, thistles, crucifers, forbs and geophytes) were less than 1% of the total seed bank density. As to the seeds, *Hordeum bulbosum* was the dominant perennial grass, with almost 2% of the seed bank. The short annual grass seed bank included three *Bromus* species (16%) (*B. alopecuros, B. lanceolatus***,** *B. madritensis* and *B. scoparius* were pooled together since their seeds could not be differentiated), *Alopecuros utriculatus* (7%) and *Lolium rigidum* (6%). The seed bank of tall annual grasses was dominated by *Avena sterilis* (3%) and *Hordeum spontaneum* (2%), while main annual legumes were *Trifolium pilulare* (8%) and *T. argutum* (4%). Annual crucifers included *Rapistrum rugosum* (12%) and *Ochthodium aegyptiacum* (2%), while main annual forbs were *Stellaria media* (9%) and *Hedypnois cretica* (3%).

Overall effects of grazing on seed bank density

The effects of grazing on the seed bank resulted from interactions among the grazing regime, intensity of grazing and the onset of grazing (Table 1). Seed bank density varied widely between grazing treatments, from 1383 seed.m^{-2} under seasonal very heavy early grazing (S-VHE) to 4861 seed.m^{-2} under seasonal very heavy late grazing (S-VHL). Seasonal grazing at equivalent stocking rates (CH vs. S-HE and S-HL) increased the total seed bank, especially in the late grazing treatment (6885 vs. 7827 and 8902 seed.m^{-2}, respectively), mainly due to larger seed banks of all functional groups including grasses, with the exception of annual forbs. Effects of stocking rate were dependent on the grazing regime (continuous vs. seasonal) and, within the seasonal regime, on the timing of grazing onset (early vs. late). Under the continuous grazing regime, increasing grazing pressure from moderate (CM) to heavy (CH) reduced the size of the seed bank by 32%. This was mainly due to the reduction of grasses (69%) and crucifers (69%), while annual thistles and forbs increased by 71% and 75% respectively under continuous heavy grazing. Under the seasonal grazing regime, effects of timing (early vs. late grazing) on the size and composition of the seed bank were dependent on the stocking rate and were larger under very heavy stocking rate. Total seed bank density was reduced by 57% by seasonal very heavy late grazing (S-VHL) compared to very heavy early grazing (S-VHE). This large difference was mainly due to a decrease in the seed bank of short annual grasses (66%), annual legumes (72%) and annual forbs (55%) following late onset of grazing. Under lower grazing pressure, on the other hand, late onset of grazing resulted in a small increase (12%) in the seed bank density (Table 1). Despite this small effect, large differences between these two treatments appeared at the functional group level. Under seasonal heavy early grazing (S-HE), the proportion of annual grasses in the seed bank was reduced and accounted for 37% compared to 72% under seasonal heavy late grazing (S-HL), while the relative proportion of tall perennial grasses did not change (ca. 2%). In contrast, the relative proportions of crucifers and annual legumes in the seed bank were increased under seasonal heavy early grazing.

Grazing treatments and seed bank functional groups

Differential effects of timing and intensity of grazing on the seed bank and interactions with year conditions were analysed for the different functional groups. Grazing significantly affected the seed bank of short and tall annual grasses during the three research seasons, while seed bank of tall perennial grasses (mainly *H. bulbosum*) was affected only in 1996 (Table 2 and Fig. 1). Under continuous grazing, the seed bank of the three grass functional groups was smaller under a higher stocking rate (CH vs. CM). These differences were significant for short annual grasses and tall perennial grasses, but not for tall annual grasses (Table 2). Under the seasonal regime, grazing pressure interacted strongly with the timing of grazing (early vs. late) in determining the size of the seed bank of short and tall annual grasses, i.e. early grazing reduced the seed bank of both functional groups at the lower stocking rate (S-HE vs. S-HL), but increased it at the higher stocking rate (Timing × SR, Table 2). On the other hand, increasing the stocking rate augmented the density of their seed banks in early grazing, but diminished it in late grazing. Seed bank of perennial grasses under seasonal grazing was not affected either by timing of grazing nor by stocking rate (Table 2).

The response of annual thistles to grazing treatments was significant in 1996 and 1997 (Table 2, Fig. 2a-c). Contrast analysis showed differences in seed bank densities when comparing different grazing intensities under continuous grazing (SR continuous) and duration (continuous vs. seasonal). The latter was mainly due to a higher seed bank density found in 1997 under the continuous heavy treatment (CH, Fig. 2a).

Annual crucifers were well represented in the seed bank, and grazing manipulations had significant effects on their densities (Fig. 2d-f, Table 2). Differences between treatments were significant during the 3-yr study, particularly when comparing the low number of seeds in paddocks that were grazed after seed set (S-HL, Fig. 2e), with those grazed before it (S-HE and CM, Fig. 2d). These differences are also evident in the contrast analyses of grazing timing (early vs. late grazing) and its interaction with stocking rate (SR) in the seasonal regime (Table 2).

Seed bank of annual forbs was composed by a heterogeneous group of annual dicots (mainly composites, umbellifers and caryophylls). In general, forbs were sensitive to grazing manipulations: as a general trend, density increased with increasing grazing intensity (Table 2 and Fig. 2 g-i). Furthermore, early grazing significantly favoured seed bank density of this functional

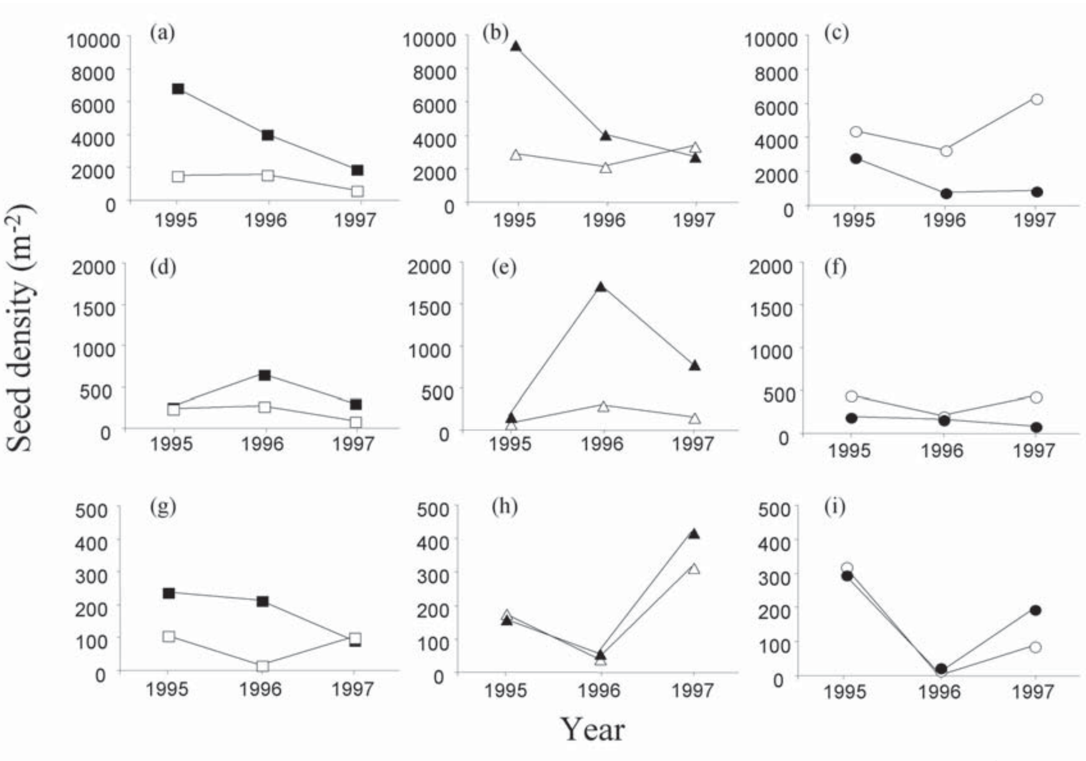

Fig. 1. Effects of grazing on seed density of functional groups. Short annual grasses (**a-c**); tall annual grasses (**d-f**); tall perennial grasses (**g-i**). Treatments: CM = continuous moderate (■); CH = continuous heavy (□); S-HE = seasonal heavy early (Δ); S-HL seasonal heavy late (▲); S-VHE = seasonal very heavy early (○); S-VHL = seasonal very heavy late (●).

Table 2.Results of two-way and repeated measures ANOVAs for functional groups over the 3-yr study. Bold numbers indicate significant differences between treatments. Stocking rate (SR), continuous vs. seasonal (C. vs. S).

			Short annual grasses		Tall annual grasses		Tall perennial grasses		Annual legumes		Annual thistles		Crucifers		Annual forbs	
Effect	Year	d.f.	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Treatment	1995	1,5	**13.7**	**0.019**	**6.79**	**0.044**	0.43	0.824	**34.1**	**0.002**	0.72	0.608	**13.9**	**0.011**	**6.82**	**0.041**
Treatment	1996	1,5	**9.46**	**0.026**	**35.1**	**< .001**	**7.43**	**0.034**	**36.2**	**<.001**	**11.2**	**0.023**	**23.7**	**0.004**	**17.1**	**0.008**
Treatment	1997	1,5	**33.8**	**0.002**	**11.3**	**0.022**	1.67	0.141	**25.1**	**0.004**	**15.2**	**0.016**	**12.4**	**0.020**	**36.8**	**< 0.001**
Overall analysis																
Treatment		5,5	**6.59**	**0.031**	**7.32**	**0.021**	**5.27**	**0.042**	**16.2**	**0.004**	**15.0**	**0.004**	**13.5**	**0.008**	**16.5**	**0.003**
Year		2,10	1.77	0.170	**8.40**	**0.007**	**28.9**	**<. 001**	**32.4**	**<.001**	**4.75**	**0.009**	**6.40**	**0.002**	**31.3**	**< 0.001**
Treat. × Year		10,10	1.45	0.152	**4.86**	**0.010**	**3.70**	**0.027**	1.34	0.205	**5.82**	**0.006**	**3.91**	**0.018**	1.21	0.276
Contrasts																
Timing (*early vs. late*)		1,5	0.11	0.739	**9.17**	**0.028**	0.01	0.937	**10.5**	**0.024**	2.16	0.166	**18.9**	**0.006**	**22.5**	**0.005**
SR (*seasonal*)		1,5	1.92	0.190	**15.5**	**0.015**	0.52	0.483	**17.6**	**0.007**	2.12	0.171	0.06	0.803	**16.3**	**0.010**
Timing × SR		1,5	**14.4**	**0.019**	**20.9**	**0.007**	2.17	0.166	0.62	0.444	0.29	0.595	**16.3**	**0.010**	**7.42**	**0.038**
SR (*continuous*)		1,5	**11.0**	**0.026**	3.26	0.096	**9.35**	**0.030**	1.13	0.307	**8.45**	**0.040**	**9.44**	**0.026**	**7.41**	**0.039**
Length (C. vs. S.)		1,5	**8.43**	**0.039**	**9.42**	**0.026**	1.94	0.189	0.45	0.512	**13.7**	**0.019**	3.85	0.073	**73.2**	**< 0.001**

[1]Results for block and interactions in the overall analysis were not significant and were not included for clarity of the table presentation.

group. Similarly to annual thistles, the contrast analysis showed differences in seed bank density when comparing grazing duration (continuous vs. seasonal), particularly due to high seed bank densities found in 1997 under the continuous heavy treatment (CH, Fig. 1g).

Seed bank of annual legumes was significantly affected by grazing treatments and year conditions (Table 2, Fig. 3a-c). Significant differences between treatments were observed in 1995 to 1997 (Table 2). The contrast analysis showed that early grazing in the growing season at heavy and very heavy stocking rates resulted in a significant increase in the density of annual legumes in the seed bank (Table 2). On the other hand, effects of grazing duration (continuous vs. seasonal) and stocking rate under continuous grazing were not significant.

The complex responses of the different functional groups to the grazing treatments can be summarized as follows: 1. Under the seasonal grazing regime, early grazing generally increased the seed bank density of annual legumes, annual crucifers and annual forbs com-

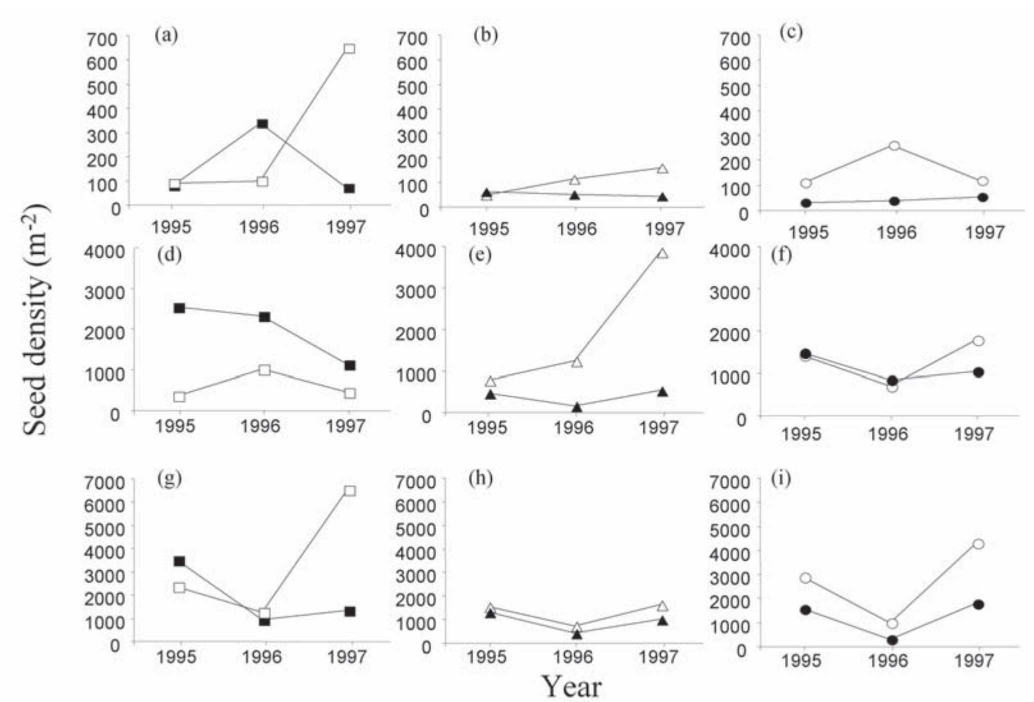

Fig. 2. Effects of grazing treatments on seed density of functional groups. Annual thistles (**a-c**); Annual crucifers (**d-f**); Annual forbs (**g-i**). Key for grazing as in Fig. 2.

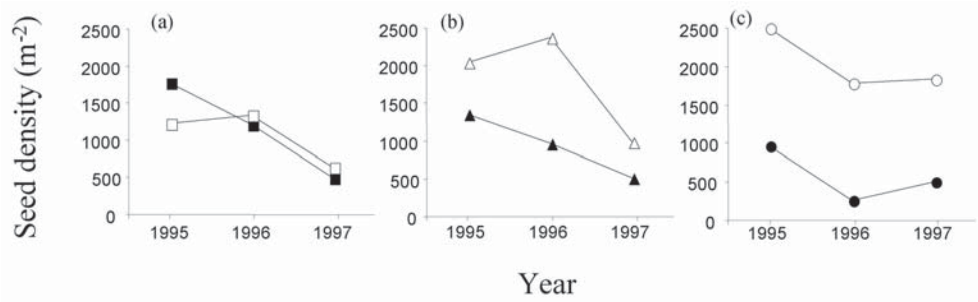

Fig. 3. Effects of grazing treatments on seed density of annual legumes (**a-c**). Key for grazing as in Fig. 2.

pared to late grazing, under both high and very high grazing pressure. In contrast, it reduced the seed bank of short and tall annual grasses under heavy grazing, but increased them under very heavy grazing. Timing and intensity of grazing did not affect the seed bank of tall perennial grasses. 2. Under continued grazing, increasing stocking rate generally reduced the seed bank of all grass functional groups and crucifers. In the seasonal regime, very heavy grazing early in the season increased the seed bank of short and tall annual grasses and annual forbs. In contrast, in the late grazing treatment, very heavy grazing strongly reduced the seed bank of short and tall annual grasses, but had small or inconsistent effects in the other functional groups. In the annual legumes, the seed bank was little affected by grazing pressure in the continuous grazing regime. Seasonal, very heavy late grazing caused the lowest seed bank density found in the whole experiment (S-VHL, Table 1).

Seed dormancy in seed banks

In terms of total seed bank density and including all functional groups, 42% of the seeds present in the soil did not germinate under watering conditions, during the natural germination season. Dormancy levels varied among species and functional groups. Most seeds of short and tall annual grasses germinated in the shadehouse (96% and 87%, of the total seed bank respectively, Table 3). Moreover, *H. bulbosum*, representing tall perennial grasses, showed 100% of germination, as no ungerminated seed was found in the germination trays after washing and sieving the soil. This high germination fraction suggests low potential for persistent seed bank in these functional groups. However, short annual grasses such as *Phalaris* spp. (*P. paradoxa* and *P. media* were pooled together since their seeds could not be differentiated) and the tall annual *T. dicoccoides* were exceptions to this trend, showing lower germination rates (59% and 65%, Table 3). In contrast to the grasses, annual legumes, annual crucifers and annual forbs showed much lower seed germination (24%, 24% and 30%, respectively, Table 3), indicating higher potential for persistent seed banks production. Annual thistles, represented mainly by *Carthamus* spp. (*C. tenuis* + *C. glaucus*) and *Scolymus maculates,* showed a mixed germination strategy (51%, Table 3), but with a trend of

Table 3. Mean germination percentage (%) of main and all species by plant functional groups. Data for all treatments is pooled and averaged for three years of data (1995-1997).

Short annual grasses		Tall annual grasses		Tall perennial grasses		Annual legumes		Annual thistles		Crucifers		Annual forbs	
Species	%	Species	%	Species	%	Species	%	Species	%	Species	%	Species	%
Alopecuros utriculatus	100	*Avena sterilis*	83	*Hordeum bulbosum*	100	*Medicago polymorpha*	43	*Carthamus* spp.	57	*Brassica nigra*	39	*Anagallis arvensis*	33
Brachypodium distachyon	100	*Hordeum spontaneum*	97			*Hymenocarpos circinnatus*	28	*Scolymus maculatus*	27	*Ochthodium aegyptiacum*	19	*Beta vulgaris*	34
Bromus spp.	98	*Triticum dicoccoides*	65			*Trifolium argutum*	8			*Rapistrum rugosum*	13	*Hedypnois cretica*	11
Lolium rigidum	92					*Trifolium pilulare*	31					*Malva nicaeensis*	36
Phalaris spp.	59					*Trifolium purpureum*	15					*Stellaria media*	12
All species	96		87		100		24		51		24		30

producing persistent seed banks, particularly in *S. maculatus* (27%).

Discussion

Seed bank density and species richness

Seed bank density at the onset of the growing season ranged widely between years and treatments. The lowest seed densities were found in 1996 at the seasonal very heavy grazing treatment with 2935 seed.m^{-2}, while the highest were present in 1995 at the continuous moderate grazing treatment with 15384 seed.m^{-2}. The large difference between treatments clearly reflects the effects of grazing intensity on seed production. This range soil seed density is relatively low compared to other studies in Mediterranean herbaceous communities, e.g. 67 000 seed.m^{-2} (Bartolome 1979), 6000 -35 000 seed.m^{-2} (Russi et al. 1992), 20000-40000 seed.m^{-2} (Levassor et al. 1990) and 110000 seed.m^{-2} (Ortega et al. 1997). This wide variation in seed bank densities probably reflects differences in vegetation characteristics, grazing systems and climatic conditions.

Another peculiarity of Mediterranean annual grasslands is their relative high species richness (di Castri 1981). Previous studies in seed banks of Mediterranean annual communities in California and Spain have reported high species richness (Marañon 1998; Marañon & Bartolome 1989; Ortega et al. 1997). Indeed, the 133 species determined in this study represent a high number of species and strengthen the importance of considering in seed bank studies, both the germinable and non-germinable seeds. Studies where only germinable seed banks were assessed may underestimate total seed abundance and provide biased estimates of composition due to seed dormancy and/or quiescence. The risk for biased estimates is shown by this study when considering that 42% of the total seed bank remained dormant under watering conditions and that species differ strongly in their dormancy. Furthermore, the addition of species that were present in the soil seed bank and did not germinate, although mostly representing rare annual forbs species, are important when considering grazing effects on biodiversity in a broader context and strengthen the germination methodology used in this study (Tilman et al. 1996; Meissner & Facelli 1999; Tracy & Sanderson 2000).

Seed banks and functional groups

A particularly clear-cut trend that characterizes the studied Mediterranean grassland is the extremely small seed bank (ca. 3%) produced by all the perennial species (mostly hemicryptophytes) that, in average, share 50% of the relative plant cover in the site (Sternberg et al. 2000). Apparently, lack of seed production is not the main constraint, since dominant perennials such as *Bituminaria bituminosa* (9% cover), *Echinops* spp. (8% cover), and *Ferula communis* (4% cover) flowered profusely and set seeds. These perennials have low palatability due to spininess or chemical defences. In contrast, the highly palatable tall perennial grass *H. bulbosum,* consistently produced a non-dormant seed bank that was relatively small (ca. 2%) compared to the average relative plant cover of this species at the site (23%) (Sternberg et al. 2000). This seed bank, albeit small and non-dormant, together with the regeneration buds associated with the basal corm characteristic to this species, probably counterbalances the lack of herbivory defences in this palatable perennial grass. The trend for establishing small seed banks in the dominant herbaceous perennial species was also evident when analysed at the functional group level, by comparing seed bank densities of perennials vs. annuals within the grasses, legumes, umbellifers and composite thistles. In all these functional groups, the perennials had less than 1-2% of the seed bank. One explanation to this phenomenon could be related to differential resources partitioning priorities between perennial and annual plants (Garnier et al. 1997). Annuals relay only on seeds for reproduction, whereas perennials (mostly hemicryptophytes in this community) divide the reproductive biomass between seeds and perennating buds located on storage structures (e.g. corms, rhizomes, roots), generally favouring the latter (Gutman et al. 2002). Exploiting such an option by these perennials can be advantageous only if the species can withstand grazing as well as a long, dry and hot summer, and recurrent fires. The wide distribution, dominance and persistence of hemicryptophytes such as *H. bulbosum, B. bituminosa, Echinops adenocaulus* and *F. communis* in eastern Mediterranean grasslands are an indication of the success of this partitioning strategy (Seligman 1996; Noy-Meir & Sternberg 1999; Sternberg et al. 2000). The contrasting resource allocation patterns in annuals and perennials are particularly evident when comparing responses to defoliation in tall annual (*Triticum dicoccoides* and *Avena sterilis*) and perennial (*H. bulbosum)* grasses. After defoliation annual grasses showed a greater allocation to re-growth and seed production than perennial grasses (Noy-Meir & Briske 1996; Briske & Noy-Meir 1998; Gutman et al. 2002), and this is probably reflected in the larger seed banks of these species.

Seed banks and germination strategies

A wide spectrum of seed germinability (i.e. dormancy) levels was found in the different species and functional groups. Annual legumes, annual crucifers, annual thistles (except *Carthamus* spp., 57% germination) and annual forbs showed in general a high seed dormancy (less than 43% germination), while grasses (all functional groups, except *Phalaris* spp. and *T. dicoccoides* with 59 and 65% germination, respectively) showed very low dormancy (Table 3). These dormancy trends indicated high and low potential, respectively, for producing persistent seed banks in these functional groups. These results are consistent with other studies from the Mediterranean region that showed that legumes and forbs formed persistent seed banks, while grasses have little seed carry-over between years (Russi et al. 1992; Peco et al. 1998). It is remarkable that most species included in each functional group showed similar trends in seed dormancy. Taxonomic similarities in seed morphology (e.g. seed coat impermeability in legumes) or physiological mechanisms of germination control may explain the homogeneity in dormancy trends within each group. However, the fact that even in the taxonomically heterogeneous annual forb group most species showed high seed dormancy (Table 3), provides further support to our assumption that seed bank traits can be used in the characterization of plant response groups to grazing.

Paradoxically, the most palatable functional group, the grasses, had seed banks with the lowest dormancy (Table 3). This trend appears to characterize annual grasses of Mediterranean grasslands (Bartolome 1979; Russi et al. 1992; Ortega et al. 1997; Marañon 1998) and has been found also in semi-arid rangelands in Israel (Y. Osem unpubl.). These grasses probably cope with environment unpredictability and with grazing pressure by greater developmental plasticity and massive production of seeds. Furthermore, the fact that in our research seed bank dormancy levels were determined under conditions favourable for germination (winter low temperatures, irrigation), does not preclude the possibility that under less optimal field conditions enforced dormancy occurs, preventing germination, and allowing inter-annual carry over of a fraction of the seed population. However, recent research at the same site, in which *in situ* germination of the natural seed bank was examined in the field, showed that more than 94% of the seed bank of most species in all grass functional groups germinated by mid-winter (S. Aboling unpubl.).

A possible explanation to the lack of dormancy in grasses is avoidance of seed predation. Several species, particularly tall grasses, have relatively big seeds that enable them to emerge through the litter at the onset of the rainy season, and improve competitiveness of their seedlings during the wave of germination occurring after the first effective rains. Seed granivory by ants, rodents and birds particularly of attractive large seeds, can be an important driving force in this type of environments (Brown & Human 1997; Wolff & Debussche 1999). By germinating soon after the first rains, these species reduce their time of exposure and therefore the risk of being eaten or collected by granivorous agents. However, securing their establishment after simultaneous massive germination also implies high seedling competition, with large numbers of equally well-adapted annual species. In this context, the relatively large seed size and fast emergence in tall grasses is an advantage (Baker 1972). The rapid development of the root system and leaf area associated with larger seed size are a preemptive strategy that competitively eliminates smaller seedlings (Wright & Westoby 2001). This idea is supported by high densities of seeds of annual grasses (more than 70% of relative total seed abundance) found in ungrazed areas during seed set (S-HL treatment, Table 1).

At the species level, the relatively lower germination observed in *T. dicoccoides*, e.g. 65% in irrigated soil samples (Table 3) and 77% *in situ* in the field (S. Aboling unpubl.), was probably related to the fact that in this species two seeds with high and low dormancy, respectively, are normally present in the dispersal unit (Horowitz 1998). Thus, the lower average germination was probably due to less germination of the smaller and more dormant seed. In contrast, the short and tall annual grasses, as well as the tall perennial grass *H. bulbosum,* that showed nearly 100% of germination, had only one seed in their dispersal unit. Multi-seeded dispersal units with graded seed dormancy (*M. polymorpha, Trifolium* spp*., Hymenocarpus circinnatus, Beta vulgaris*) and heterocarpy (*Hedypnois cretica*) are traits frequently found in the Mediterranean vegetation (Kigel 1995).

Grazing, seed banks and unpredictable environments

The herbaceous vegetation at Karei Deshe Experimental Farm can be visualized as a relatively constant matrix consisting of hemicryptophytic species with about 50% relative plant cover and remaining gaps that are available every year for germination of annual plants, the most variable component in the system. In our system, two germination strategies coexist: (1) a low dormancy and massive germination strategy in most grass species, with higher potential for transient seed banks and less carry-over from year to year; (2) a more cautious strategy based on higher dormancy and fractional germination, that characterizes the legumes, and most abundant crucifers, annual thistles and annual forbs, with a higher potential for the formation of persistent seed banks. The effect of the applied grazing treatments on the relative cover of perennial plants was relatively small (Sternberg et al. 2000). In contrast, grazing had a large differential effect on the cover of annual species by selective removal of the palatable, larger and more competitive species (mostly tall grasses), and release of the shorter and prostrate species from competition. The balance between these competing annual plants probably determines their seed production, that in interaction with biotic (e.g. grazing, granivory) and abiotic (e.g. water, light) factors, established the seed bank characteristics for the occupation of the empty gaps at the onset of the rainy season.

It has been postulated that for climatically variable and frequently disturbed environments greater seed dormancy should buffer from the consequences of reproductive failure in unfavourable years (Venable & Brown 1988; Clauss & Venable 2000). Our results support this prediction as the seed bank composition of intensively grazed areas was dominated by a larger fraction of small non-germinated seeds. A dormant seed bank confers the advantage of possible future recruitment following environmental fluctuations and site disturbance (Cohen 1966; Pake & Venable 1996; Davies & Waite 1998; Thompson et al. 1998). Similarly to other studies small seeds from annual legumes, crucifers and forbs were among the dominant fraction of non-germinated seeds (Pagnotta et al. 1997). On the contrary, seed banks of ungrazed or moderate grazed areas (S-HL or CM; Table 1) were characterized by a high proportion of germinable tall grasses species. Indeed, in our case, species with larger seeds (e.g. tall grasses: range 8-24 mg) have higher germination fractions. However, short annual grasses have also a high germination fraction even though they have smaller seeds (e.g. range 0.3-2 mg; S. Aboling unpubl.).

Seed bank and grazing management

The maintenance of Mediterranean species-rich grasslands depends on frequent grazing that prevents the closing of the sward by few dominant tall grass species (Sternberg et al. 2000). Grazing during the growing season allows a more heterogeneous seed bank composition and structure, increasing chances to achieve sustainability in Mediterranean grasslands (Seligman 1996). However, the significant detrimental impact of grazing on seed banks of annuals, particularly at very heavy grazing pressure during flowering and seed set (S-VHL treatment), indicates that these effects can be minimized by grazing management decisions. Grazing deferment in heavily grazed paddocks particularly in the period of seed set could be enough to preserve a more diverse seed bank composition, including the maintenance of seed banks of valuable forage species such as tall grasses (Noy-Meir & Briske 1996). Reducing grazing pressure during the reproductive stage could prevent seed bank dominance of less palatable or less nutritious species such as thistles, crucifers and forbs.

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