



## Effects of cattle grazing timing and intensity on soil seed banks and regeneration strategies in a Mediterranean grassland

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**Abstract:** The relationship between the soil seed bank at the onset of the growing season and the structure of the ensuing vegetation under grazing was investigated in an eastern Mediterranean grassland. Species responses to two contrasting cattle grazing regimes were studied through plant trait analyses. Traits included plant size, phenology, seed size and germination fraction. Changes in species composition of the soil seed bank and the vegetation were analyzed using a plant functional group approach. The results showed that seed bank and relative cover of tall annual and perennial grasses increased when grazed late in the growing season. The opposite was noted for short annual grasses, annual legumes, annual thistles, annual crucifers and other annual forbs. Grazing treatments little affected plant cover of herbaceous perennials. Tall annual and tall perennial grasses have large seeds and germination rates over 90%. Short annual grasses showed similarly high germination rates but with smaller seeds. Annual legumes were characterized by medium size seeds and lower germination fractions (<50%). Tall annual grasses showed high competition capabilities at late grazed paddocks due to a combination of regeneration traits that included: high germination fraction, larger seed and seedling size, and inflorescence with morphological defenses. It is proposed that in addition to plant size and palatability, regeneration traits such as seed dormancy, seed and seedling size play an important role in determining the vegetation structure under different grazing regimes, thus contributing to the high plant species diversity characteristic to Mediterranean grasslands.

### Introduction

In Mediterranean grasslands grazing is essential for maintaining primary productivity and the characteristically species-rich community composition (Noy-Meir et al. 1989, Peco et al. 1998, Sternberg et al. 2000, Noy-Meir and Oron 2001). However, improper management such as overgrazing, can lead to degradation processes with the consequent decrease in productivity and biodiversity of the grassland (Perevolotsky and Seligman 1998). In Mediterranean grasslands, annual plants are a dominant component of the vegetation and the main forage producer consumed by the livestock (Seligman 1996). Thus, the structure of this type of vegetation is largely dependent upon the density and species composition of the soil seed bank, as well as on the germination fraction and on seedling competitive success during plant establishment, after the onset of the rainy season (Kemp 1989, Young and Evans 1989, Lavorel and Lebreton 1992, Kigel 1995, Azcarate et al. 2002, Peco et al. 2003, Sternberg et al. 2003). High grazing pressure may lead to situations in which the seed bank of palatable species becomes a limiting factor (O'Connor and Pickett 1992). Grazing pressure and timing are critical elements in range management. Consequently, grazing during the flowering and seed-set periods of the main species can be critical for building up the seed bank,

potentially leading to its gradual depletion, particularly in grasslands with dominance of annual species (Ramirez 1984, Noy-Meir and Briske 1996). The species-specific regeneration strategies (i.e., transient vs. persistent soil seed banks) (Thompson 2000) can also be responsible in shaping the response of annual plants to grazing (Ortega et al. 1997, Sternberg et al. 2003). It is conceivable that maintenance of a minimal level of seed production in association with a persistent seed bank, may buffer against the impact of early grazing on plant abundance and climatic variability. Moreover, seed size can affect the competitive ability of the species during the seedling stage, by determining seedling potential for establishment (Marañón and Grubb 1993, Westoby et al. 1996, Turnbull et al. 1999, Kidson and Westoby 2000, Azcarate et al. 2002). These seed bank characteristics may differ between annual and perennial plants, since maintenance of a large and more persistent seed bank is less crucial for perennial species, which also rely on vegetative reproduction and dormant perennating structures (Kigel and Koller 1985, Rice 1989, Rees 1996).

We argue that a better understanding of the relationships between species responses to grazing vs. plant structure, seed size and regeneration strategies of annual and perennial plants is required for the rational and sustainable management of Mediterranean grasslands. This is reinforced when

we consider the characteristic mixed composition of annual and perennial species (mainly hemicryptophytes) in these communities. The seed bank in these grasslands represents the potential species composition of the ensuing vegetation and, therefore, may determine their productivity. However, there is no general consensus about the relationship between seed bank characteristics and vegetation structure, since it can vary across plant communities, according to present local environmental conditions, land use and long-term history of disturbances (Ortega et al. 1997, Marañón 1998, Jutila 1998, Egan et al. 2000). Studies in Mediterranean grasslands have shown that responses of the vegetation to grazing are frequently associated to plant traits (*e.g.*, life-cycle, growth form, height, palatability, morphological and chemical defenses) (Gomez Sal et al. 1986, Noy-Meir et al. 1989, Lavorel et al. 1999, Sternberg et al. 2000). However, few studies have focused on the relationships between species response to grazing and reproduction traits, such as timing of flowering and seed-set, seed size and germination fraction, even though Mediterranean grasslands have a large component of annual plants that depend on these traits for regeneration (Peco 1989, Noy-Meir and Briske 1996, Azcárate et al. 2002, Diaz et al. 2007). In the present work we studied the relationships between grazing, timing of flowering and seed traits (*i.e.*, seed size, germination fraction in the field), using a plant functional group approach based on life-form, plant size, palatability and taxonomic affiliation (Noy-Meir et al. 1989, Gitay and Noble 1997, Lavorel et al. 1999, Diaz and Cabido 2001). These relationships were examined in a Mediterranean grassland in northeastern Israel, under two contrasting cattle grazing systems. They were characterized by very heavy stocking rates, early onset of grazing vs. heavy grazing pressure, but late in the grazing season (Sternberg et al. 2000).

## Methods

### Study site

The study was carried out at the Karei Deshe Experimental Farm, located in north-eastern Israel (32°55'N, 35°35'E, average altitude 150 m a.s.l., for full details of the site characteristics, see Sternberg et al. 2000). The region has a Mediterranean-type climate with winter rain, occurring during October–April. Long-term average annual precipitation (1964–2006) is 570 mm (CV 29%). At the 1998/9 and 1999/2000 growing seasons, when the present study was carried out, total annual rainfall was relative low with 312 and 484 mm, respectively. Soils are brown basaltic protogregginsols. The Experimental Farm is a 1,400 ha commercially run farm, with about 800 cattle heads (Brahman, Hereford and Simmental breeds). Rocks cover about 35% of the area. Thus, grazing is the only possibility of farming, and has been implemented here since historical times.

### Experimental design

A set of experiments was initiated in 1993 in an area of 250 ha, to study the effects of grazing intensification on the

productivity and plant diversity of these managed grasslands (Sternberg et al. 2000). Stocking rate was raised from 0.55 cow ha<sup>-1</sup> yr<sup>-1</sup>, the standard rate in this region for continuous grazing regime (January to September), to 1.1 and 2.2 cow ha<sup>-1</sup> yr<sup>-1</sup> in a seasonal grazing regime. In the seasonal regime the cattle is shifted from early to late grazed paddocks, when the forage is consumed in the respective paddocks subjected to early grazing. These grazing regimes were implemented during 10 years before the current study. Dates of onset and end of the grazing periods and shifts from early to late paddocks are determined according to the onset of the rains, forage availability and cattle weight gain. The experiments were carried out with cows and their first yearlings.

In this study, two contrasting grazing treatments were compared (for full details see Sternberg et al. 2000 and 2003):

1. Very heavy seasonal stocking rates of 2.2 cow ha<sup>-1</sup> yr<sup>-1</sup> and early onset of grazing, from mid January/early February until the end of March (designated as **Very Heavy Early** treatment - **VHE**).
2. Heavy seasonal stocking rates of 1.1 cow ha<sup>-1</sup> yr<sup>-1</sup> and late onset of grazing, from mid May to September/October (designated as **Heavy Late** treatment - **HL**).

Each treatment had two large replicated paddocks of 13–17 ha with a mean density of 15–40 cows, accordingly. In the season 1999/2000, grazing commenced on February 8 (due to late onset of rains) until April 15 in the VHE treatment, and from May 15 to September 21, in the HL treatment.

The selected treatments were chosen as they represented the two extremes along a gradient of grazing intensity during the growing season and served as a good case for testing the effects of grazing management on vegetation structure.

### Sampling of soil seed banks, seedling density and seed mass

Density of the seed bank (*i.e.* seedlings + non-germinated viable seeds) was determined on January 17, 2000, about 4 weeks after the onset of rains effective for germination (up to 210 mm of accumulative rainfall at sampling time) and before the cattle started grazing. The uppermost 5 cm soil layer including surface litter, where most seeds are located, was randomly removed from ten 25 × 25 cm quadrats in each replicate paddock, adding up a total of 20 samples per treatment. Seedlings were separated immediately after soil collection and kept in a freezer for later identification and counting. To retrieve and count the non-germinated seeds, the soil was washed away using 5 and 0.35 mm sieves that retained the wet seeds and dispersal units of the species making a significant contribution to the vegetation and biomass production in this grassland (Sternberg et al. 2003). The retrieved seeds and organic matter were dried for 24 h under 60°C, and then separated from each other manually under a microscope binocular. Seeds were identified and counted. Undamaged, full and firm seeds were considered as viable seeds. The sum of seed-

lings and viable seeds was regarded as the total soil seed bank. Considering that no additional seedlings emerged in the field after the sampling date, the remaining non-germinated seed fraction assessed the potential carry-over to the next growth season (i.e., potential for persistent seed bank production).

For monitoring seedling cover, permanent 40 × 40 cm quadrats were randomly placed in non-rocky herbaceous gaps, adjacent to areas where the soil samples were collected (5 quadrats per paddock, total of 10 per treatment). Seedling emergence started by the end of December, after the first effective rain. Relative plant cover (%) by grass and forb seedlings was determined three times until the cattle were driven into the paddocks (Jan 13, Jan 30 and Feb 17). Most seedlings emerged by early January in one main germination wave, and very few seedlings emerged afterwards despite continued rains. No seedling death due to drying was noted during this period.

Seed mass of air-dried seeds collected in the field was determined by weighing seeds individually (ca. 20 seeds) or in five small samples of 5-20 seeds, according to their size using an analytical balance ( $\pm 0.01$  mg). Seeds were separated from dispersal and other covering structures before weighing.

#### Vegetation survey

Time course of flowering was recorded for the most common species during the growing season. A vegetation survey was carried out in both treatments between March 27 and April 17, by the table-method of Braun-Blanquet (Knapp 1984). The minimal quadrat size for sampling, containing 80% of the species, was 16 m<sup>2</sup>. Twenty quadrats were recorded in each treatment within patches of vegetation homogeneously structured (total of 40 vegetation records: 10 replicates × 2 paddocks × 2 treatments). Nomenclature follows Feinbrun-Dothan and Danin (1991).

#### Plant functional groups

Species were categorized into plant functional *a priori* groups, according to life-cycle, plant height at flowering, palatability and taxonomy (Noy-Meir et al. 1989, Sternberg et al. 2000): perennial tall (PTGR) and annual tall grasses (ATGS, >50 cm), annual short grasses (ASGR, < 50 cm), perennial (PLEG) and annual legumes (ALEG), perennial (PTHI) and annual thistles (ATHI), annual crucifers (ACRU), and annual “forbs” (AFOR, all other dicots) and geophytes (GEOP). Crucifers were grouped separately due to their relative low palatability.

#### Data analysis

Differences between treatments were tested by a one-way analysis of variance (ANOVA) by means of the JMP 5.01 software (SAS Institute Inc.). A square root transformation was used to normalize counts of seeds and seedlings. Average germination fraction was computed as GF (%) =

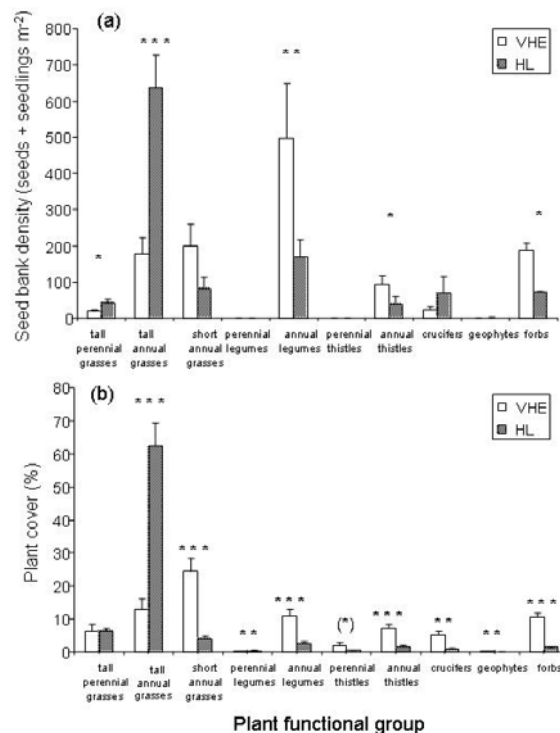
100 × (seedlings/ seeds + seedlings), taking together values from all soil samples, since no differences were found between treatments. For the vegetation analysis, frequency data obtained by the Braun-Blanquet method were converted into percent values, and average relative cover (%) was determined (Knapp 1984).

## Results

### Seed bank response to grazing

Very heavy early grazing (VHE) resulted in a significantly bigger seed bank compared to the heavy late grazing pressure (HL): 1,661 ± 55 vs. 1,174 ± 29 seeds m<sup>-2</sup>, respectively ( $p=0.05$ ). In these two contrasting grazing regimes, the seed bank at the onset of the growing season was mostly composed of seeds from annual species (98.2 and 96.2% for VHE and HL, respectively). Very few seeds of the common perennials were found in either of the treatments, e.g., the thistles *Echinops adenocaulus*, *E. gaillardotii* and *Eryngium creticum*, the legume *Bituminaria bituminosa*, and the umbellifer *Ferula communis* (5 and 2 seeds m<sup>-2</sup> in VHE and HL grazing, respectively). The main exception was the perennial tall grass *Hordeum bulbosum* with a seed bank ranging between 19-43 seeds m<sup>-2</sup>.

The grazing regimes resulted in significant differences in the seed bank density in plant functional groups with higher seed abundance (Fig. 1a, Table 1). Early grazing at very



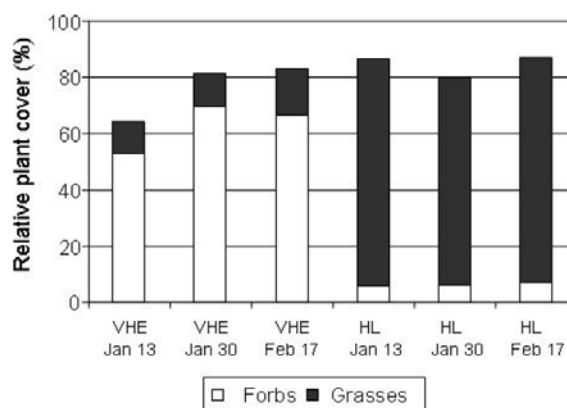
**Figure 1.** Seed bank (a) and relative cover (b) of different functional groups. Seed bank is total sum of seedlings and non-germinated seeds. Significant differences at (\*) 0.05, (\*\*) 0.01 and (\*\*\*) 0.001 levels. VHE: Very heavy early treatment, HL: Heavy late treatment.

**Table 1.** Effects of grazing treatments (VHE vs. HL) on the density of the total seed bank (seedlings + non-germinated seeds) and on the relative cover of dominant herbaceous species by functional groups. PTGR- perennial tall grasses, ATGR- annual tall grasses, ASGR- annual short grasses, ALEG- annual legumes, ACRU- annual crucifers, AFOR- annual forbs, ATHI- annual thistles. Values are averages  $\pm$  SE. P: level of significance, n.s.: non-significant difference ( $P>0.05$ ). (\*) Plants already dead and undetectable at time of vegetation survey. (\*\*) Seedlings could not be differentiated at germination time, species were pooled together.

Functional groups and species	Total seed bank density (seeds + seedlings)/m <sup>2</sup>			Relative cover (%)		
	VHE	HL	P	VHE	HL	P
PTGR						
<i>Hordeum bulbosum</i>	18.6 $\pm$ 5.1	42.1 $\pm$ 8.6	0.017	6.3 $\pm$ 2.0	6.1 $\pm$ 1.0	n.s.
ATGR						
<i>Avena sterilis</i>	159.7 $\pm$ 40.7	351 $\pm$ 68.1	0.001	11.5 $\pm$ 3.3	11.3 $\pm$ 4.6	n.s.
<i>Hordeum spontaneum</i>	11.2 $\pm$ 4.8	226.1 $\pm$ 52.9	0.001	1.4 $\pm$ 0.7	50.6 $\pm$ 8.4	0.001
<i>Triticum dicocoides</i>	6.9 $\pm$ 2.7	57.4 $\pm$ 25.7	0.003	0.1 $\pm$ 0.0	0.6 $\pm$ 0.5	n.s.
ASGR						
<i>Alopecurus utricularis</i>	61.1 $\pm$ 25.1	45.7 $\pm$ 23.7	n.s.	7.6 $\pm$ 1.4	2.2 $\pm$ 0.5	0.01
<i>Aegilops</i> spp	16.4 $\pm$ 11.2	2.7 $\pm$ 2.0	n.s.	0.3 $\pm$ 0.2	0.9 $\pm$ 0.9	n.s.
<i>Bromus</i> spp	70.8 $\pm$ 34.8	15.4 $\pm$ 12.5	0.027	5.7 $\pm$ 1.3	0.4 $\pm$ 0.1	0.001
<i>Phalaris</i> spp	46.8 $\pm$ 24.0	22.3 $\pm$ 11.9	n.s.	0.2 $\pm$ 0.1	0.1 $\pm$ 0.1	0.046
ALEG						
<i>Trifolium pilulare</i>	22.3 $\pm$ 7.2	65.9 $\pm$ 23.2	0.003	3.5 $\pm$ 1.1	0.8 $\pm$ 0.2	0.003
<i>Trifolium argutum</i>	367.6 $\pm$ 151	46.8 $\pm$ 25.2	0.001	5.2 $\pm$ 1.3	1.0 $\pm$ 0.5	0.001
<i>Hymenocarpus circinnatus</i>	55.9 $\pm$ 25.0	37.8 $\pm$ 12.6	n.s.	1.8 $\pm$ 0.6	0.5 $\pm$ 0.1	0.012
<i>Medicago</i> spp	45.1 $\pm$ 13.5	15.4 $\pm$ 5.9	0.044	0.1 $\pm$ 0.0	0.0 $\pm$ 0.0	0.034
ATHI						
<i>Carthamus glaucus</i>	73.4 $\pm$ 21.1	39.4 $\pm$ 20.0	0.056	7.2 $\pm$ 1.0	1.2 $\pm$ 0.5	0.001
ACRU						
<i>Ochrodium aegyptiacum</i> and <i>Rapistrum rugosum</i> **	18.6 $\pm$ 6.5	28.7 $\pm$ 12.5	n.s.	3.6 $\pm$ 1.0	0.5 $\pm$ 0.1	0.002
AFOR						
<i>Stellaria media</i>	462.0 $\pm$ 238	68.6 $\pm$ 37.3	0.037	*	*	*
<i>Anagallis arvensis</i>	86.2 $\pm$ 43.5	4.8 $\pm$ 1.5	0.022	0.5 $\pm$ 0.1	0.1 $\pm$ 0.0	0.001
<i>Pimpinella cretica</i> and <i>Ainsworthia trachycarpa</i> **	19.7 $\pm$ 7.1	10.7 $\pm$ 5.6	n.s.	4.6 $\pm$ 0.8	0.3 $\pm$ 0.1	0.001

heavy stocking rate (VHE) reduced by 126% and 255% the seed bank of PTGR (mainly *Hordeum bulbosum*) and ATGR, respectively, compared to heavy late stocking rate (HL). The reduction in the seed bank was significant ( $p<0.01$ ) for each one of the three most abundant tall grasses (*Hordeum spontaneum*, *Avena sterilis*, *Triticum dicocoides*). In contrast, the seed bank of all other functional groups (ASGR, ALEG, ATHI and AFOR) was increased at very early heavy grazing (VHE), compared to late heavy grazing (HL). In ASGR this increase was observed for all species, but was significant only for the pooled *Bromus* species (*B. alopecurus*, *B. lanceolatus*, *B. madritensis*, *B. scoparius*). As for the AFOR, the decline in late grazing treatment (HL) was significant in all species, except the umbellifers. ALEG exhibited opposite responses to the grazing treatments: early, very heavy grazing (VHE) increased the seed bank density in *Medicago* species (66%), *Hymenocarpus circinnatus* (32%) and particularly that of *Trifolium argutum* (87%), but decreased that of *Trifolium pilulare* (by 66%).

Grazing regime also changed the relative proportion of grasses and forbs in the seedling population, as measured before onset of grazing. Effects of previous years of late and heavy grazing pressure (HL) increased the cover of grass seedlings compared to that of forbs (63.2 vs. 13.2%,  $p<0.005$ ) (Fig. 2). In contrast, early and very heavy grazing pressure (VHE) resulted in a lower cover by grass compared to forb seedlings (6.4 vs. 78.1%,  $p<0.001$ ). The differences in cover between grass and forb seedlings were relatively constant during the early stages of establishment (Jan. 13 to Feb. 17, Fig. 2). Among the dicots that were taxonomically identified at the seedling stage, density of *Carthamus glaucus* seedlings was significantly higher in the very heavy early



**Figure 2.** Relative plant cover (%) of grass and forb seedlings at the onset of the growth season. VHE: Very heavy early treatment, HL: Heavy late treatment.

grazing treatment compared to the late heavy treatment ( $p<0.001$ ), while the densities of other common species *Hymenocarpus circinnatus*, *Rapistrum rugosum* and *Echium palaestinum* were similar in both treatments (results not shown).

#### Vegetation responses to grazing

Changes caused by grazing regimes in the relative cover of the different functional groups in the ensuing vegetation were generally similar to the trends observed for their seed banks (Fig. 1b, Table 1). Thus, late grazing at the lower grazing pressure (HL) increased significantly the relative cover of ATGR and PLEG, and reduced that of ASGR, ALEG, PTHI, ATHI, and AFOR. However, in contrast to the seed

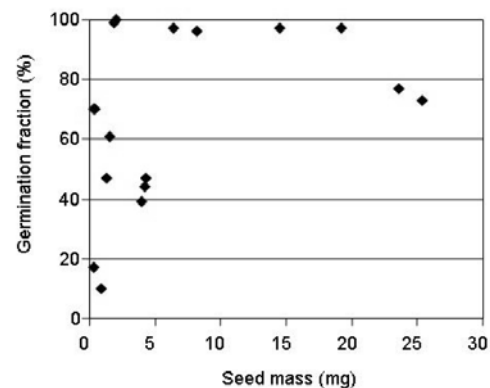
**Table 2.** Germination fraction and seed mass and under natural conditions in the field and under irrigation in a screen-house, for dominant herbaceous species (nethouse data from Sternberg et al. 2003). PTGR- perennial tall grasses, ATGR- annual tall grasses, ASGR- annual short grasses, ALEG- annual legumes, ACRU- annual crucifers, AFOR- annual forbs, ATHI- annual thistles. \* Seedlings could not be differentiated at germination time in the field and species were pooled together.

Functional groups and species	Germination rate (%)		Seed mass (mg)
	Field	nethouse	
PTGR			
<i>Hordeum bulbosum</i>	95.6	98.9	8.20
ATGR			
<i>Avena sterilis</i>	90.7	83	14.46
<i>Hordeum spontaneum</i>	97.1	97	19.24
<i>Triticum dicoccoides</i>	76.9	65	23.60
ASGR			
<i>Alopecurus utricularis</i>	97.5	99.0	2.01
<i>Aegilops</i> spp	97.2	-	6.70
<i>Bromus</i> spp	99.4	98	1.88
<i>Phalaris</i> spp	46.6	59	1.33
ALEG			
<i>Trifolium pilulare</i>	39.2	31	4.02
<i>Trifolium argutum</i>	10.3	8	0.89
<i>Hymenocapus circinnatus</i>	43.9	28	4.17
<i>Medicago polymorpha</i>	47.4	43	4.25
ATHI			
<i>Carthamus glaucus</i>	73.1	57	25.4
<i>Scolymus maculatus</i>	-	27	3.5
ACRU			
<i>Ochtodium aegyptiacum</i> and <i>Rapistrum rugosum</i>	69.1	19 13	3.55 1.50
AFOR			
<i>Stellaria media</i>	17.2	12	0.29
<i>Anagallis arvensis</i>	0	33	0.38
<i>Pimpinella cretica</i> ,		77	0.29
<i>Ainsworthia trachycarpa</i> *	60.9	30	0.36

bank, it did not affect the cover of the PTGR and reduced the cover of the ACRU. At the species level, the increase in cover of the ATGR in HL treatment was mostly due to an increase in *Hordeum spontaneum*, the wild barley. In ASGR, ALEG and ATHI, the concomitant reduction in cover was observed in most species of each group. In the tall perennial *Hordeum bulbosum* and annual *Avena sterilis*, the relative cover was similar in both grazing treatments in spite of a 126% and 119% increase, respectively, in their seed bank in the heavy late (HL) grazing treatment. Other exceptions were the crucifers (mainly *Rapistrum rugosum*), whose relative cover increased five times in the very heavy early grazing treatment, while their seed bank did not differ between treatments. Although GEOP cover was relative low in the whole study area, their cover significantly increased under very heavy grazing pressure (VHE).

#### Germination fraction and seed weight

In general, grasses showed a high germination fraction in the field (90-97%), compared to legumes (10-47%), forbs (17-70%), crucifers (61%) and annual thistles (73%) (Table 2). These trends found in the field correspond with trends previously reported by Sternberg et al. (2003) for soil samples kept outdoors in a nethouse under continued irrigation. In both situations, most grasses show a high germinability. Exceptions to the low dormancy trend observed in most grasses were *Phalaris* spp. with 47% germination and, to a less extent *Triticum dicoccoides* with 77% germination. In



**Figure 3.** Relationship between seed size and germination fraction. Each symbol represents a dominant species.

contrast annual legumes, annual crucifers and other forbs showed intermediate or low germination in the field, as well as under irrigated conditions.

Large differences in seed weight were observed between species (0.29 to 25.4 mg), even within functional groups. The relationship between seed weight and germination fraction of the seed bank was examined in Fig. 3. All species with seeds heavier than 5 mg showed a high germination fraction (>75%). In contrast, germination fraction of medium and small sized seeds was more variable and ranged between 10 and 99%.

**Table 3.** Time of flowering and seed set of dominant species by functional groups. Gray: flowering period, Black- onset diaspore dispersal period. PTGR- perennial tall grasses, ATGR- annual tall grasses, ASGR- annual short grasses, ALEG- annual legumes, ACRU- annual crucifers, AFOR- annual forbs, ATHI- annual thistles, PTHI- perennial thistles. Numbers indicate decades in each month.

Funct. group	Species	Decade	February			March			April			May			June			July		
			1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
PTGR	<i>Hordeum bulbosum</i>								█	█	█	█								
ATGR	<i>Avena sterilis</i>								█	█	█	█								
	<i>Hordeum spontaneum</i>								█	█	█	█								
	<i>Triticum dicoccoides</i>											█	█	█	█					
ASGR	<i>Alopecurus utricularis</i>					█	█	█	█	█	█									
	<i>Phalaris paradoxa</i>					█	█	█	█	█	█									
	<i>Bromus alopecurus</i>					█	█	█	█	█	█									
	<i>Aegilops peregrina</i>					█	█	█	█	█	█									
ALEG	<i>Medicago polymorpha</i>								█	█	█	█								
	<i>Hymenocarpus circinnatus</i>								█	█	█	█								
	<i>Trifolium argutum</i>								█	█	█	█								
	<i>Trifolium pilulare</i>								█	█	█	█								
ACRU	<i>Ochrodium aegyptiacum</i>		█	█	█	█	█	█	█	█	█									
	<i>Rapistrum rugosum</i>		█	█	█	█	█	█	█	█	█									
	<i>Brassica nigra</i>											█	█	█	█					
AFOR	<i>Stellaria media</i>		█	█	█															
	<i>Scandix iberica</i>					█	█	█	█	█	█									
	<i>Ainsworthia trachycarpa</i>					█	█	█	█	█	█									
	<i>Pimpinella cretica</i>								█	█	█	█								
ATHI	<i>Scolymus maculatus</i>											█	█	█	█					
	<i>Carthamus glaucus</i>											█	█	█	█					
PTHI	<i>Echinops gaillardotii</i>											█	█	█	█					
	<i>Echinops adenocaulus</i>											█	█	█	█					

#### Timing of flowering and seed dispersal

Timing of flowering, seed-set and dispersal differed among the main species and had important consequences in determining the grazing effects on species composition and abundance (Table 3). Ephemeral, small species like *Stellaria media* were the first to flower and disperse seeds. Most species flowered during April. However, wide variation in flowering time was observed within each family and functional group. Among the most abundant crucifers, *Ochrodium aegyptiacum* started flowering in mid February, followed by *Rapistrum rugosum* in mid March and by the late flowering *Brassica nigra* in early May. Other crucifers that were less abundant (*Isatis lusitanica*, *Biscutella didyma*) or had a patchy distribution (*Ricotia lunaria*) also showed early flowering during February (results not shown). Among the umbellifers, *Scandix iberica* flowered first (end March), succeeded by *Ainsworthia trachycarpa* (mid April) and *Pimpinella cretica* (early May). The most abundant, prostrate annual legumes showed a more synchronic flowering that culminated during April, but continued to flower during the period of fruit maturation and dispersal, particularly *Trifolium pilulare*. Short grasses flowered and dispersed seeds earlier than tall grasses, particularly *Alopecurus utricularis*

and *Phalaris paradoxa*. Among the larger grasses, *Aegilops peregrina*, a medium size grass, as well as the dominant tall annual and perennial grasses started to flower in early April. The perennial *Hordeum bulbosum* and the annual *Hordeum spontaneum* flowered and dispersed seeds at the same time. In contrast, *Triticum dicoccoides* was the last tall grass to flower and disperse seed (May to mid June). Annual and perennial thistles were the latest species to flower and disperse seed, when most of the vegetation was already dry, with *Carthamus glaucus* flowering by the end of June-early July.

#### Discussion

##### Seed bank size

The size of the seed bank recorded in the 1999/2000 season in the very heavy early and late heavy grazing treatments (VHE and HL) was relatively small (ca. 1200-1700 seeds m<sup>-2</sup>) compared to other studies in Mediterranean grasslands (Bartolome 1979, Young and Evans 1989, Levassor et al. 1991, Russi et al. 1992, Ortega et al. 1997), and to the 3-yr average reported for the 1995-1998 seasons in the same paddocks by Sternberg et al. (2003) using the same technique for the retrieval of non germinated seeds. This important differ-

ence was mainly due to a strong diminution in the seed bank of ASGR and ACRU. The smaller seed bank at the onset of the 1999/2000 season can be attributed to the previous extremely dry growth season in 1998/9 (312 vs. 570 mm yr<sup>-1</sup> long term average), that conceivable resulted in a much reduced seed production. This possibility is supported by the fact that lack of rain after mid February in the 1994/5 season and the subsequent drought during the flowering and seed-set period, also resulted in a relatively small seed bank at the start of the following season (Sternberg et al. 2003). This reduction was of 36% in the very heavy early (VHE) and 30% in the heavy late (HL) treatments, compared to an average rainfall year (Sternberg, unpublished data). However, the fact that ASGR had the largest reduction in seed bank compared to previous seasons, even though they are better adapted to drought through their smaller size, shorter life-cycle with earlier flowering and seed-set, suggests that additional factors may reduce their seed bank in dry years.

#### *Relationships between seed bank and ensuing vegetation*

Closer seed bank-vegetation similarity usually occurs in Mediterranean grasslands with high dominance of annual species (Levassor et al. 1990, Lavorel and Lebreton 1992, Peco et al. 1998). In our research site in which annuals are the main component of the vegetation, early and very heavy grazing resulted in a significant reduction in the cover of tall annual and perennial grasses, and a concomitant increase in cover of short and prostrate species (short annual grasses, annual legumes, and annual forbs), compared to late grazing at lower stocking rate (Sternberg et al. 2000). These response trends in the vegetation were confirmed in the present study. Furthermore, we found a close correspondence between the changes induced by the different grazing regimes in the vegetation and in the seed bank at the functional group level (Fig. 1), but not at the species level (Table 1). It is conceivable that compensatory changes occur within functional groups between species with similar characteristics, competing for similar ecological niche. Thus, in this type of Mediterranean grassland seed banks of functional groups have better predictive value for the structure of the ensuing vegetation than seed banks of individual species.

#### *Life-form and seed bank*

In herbaceous grasslands, perennial species tend to have a smaller seed bank compared to annuals (Rice 1989). Our results give further support to this generalization. Relatively abundant hemicryptophytes typical to this vegetation, such as the thistles *Echinops* spp. and *Eryngium creticum*, the toxic *Ferula communis* and the perennial legume *Bituminaria bituminosa*, had extremely small seed banks (see also Sternberg et al. 2003) and relay on perennating buds and storing roots for seasonal regeneration. *Ferula communis* and *Bituminaria bituminosa* have a fairly abundant production of seeds, but most of them are not incorporated into the seed bank and their fate after dispersal is not clear. In contrast, seed survival in both *Echinops* species present in the site was

very poor due to insect predation on the inflorescences (Kigel, unpublished). Low seed survival due to insect attacks has been observed also in the locally abundant geophyte *Asphodelus ramosus* (Ayal and Izhaki 1993). *Hordeum bulbosum*, on the other hand, was the only perennial at the site producing a considerable seed bank, within the range of tall annual grasses. Moreover, in contrast to other herbaceous perennials at the site, *Hordeum bulbosum* is highly palatable. We suggest that vegetative reproduction from basal corms in *Hordeum bulbosum* is not enough to balance losses due to grazing by the cattle and corm consumption by rodents during the summer (Noy-Meir 1988). The relatively large seed production enables, therefore, its persistence and dispersal in the community, even under heavy grazing pressure. Persistence of the other perennials is most probably based on their morphological and chemical defenses.

#### *Flowering traits*

Flowering time and inflorescence morphology are important factors in the response of tall grasses to grazing. During the early green season all tall grasses are grazed. But after flowering the long and tough awns in the spikes of *H. spontaneum*, *H. bulbosum* and *Triticum dicoccoides* provide a morphological defense and prevent spike consumption by the cattle. However, *Triticum dicoccoides* appears to be the most grazing sensitive grass species (Horovitz 1998, Noy-Meir and Briske 1996), since it is the last to flower within this functional group and remains highly attractive for the cattle when other tall grasses are less consumed. High palatability linked to late flowering and relatively low seed production may explain its low tolerance to grazing and limited presence at the site (<1% cover). In contrast, most abundant non-palatable annual (*Carthamus glaucus*, *Scolymus maculatus*) and perennial thistles (*Echinops* spp) show late summer flowering, when most of the vegetation is already dry. Their late reproductive period is related to a better ability to extract water from the drying soil by deeper roots, as has been shown for *Carthamus tinctorius* (Merrill et al 2002).

#### *Seed weight and germination fraction*

Seed weight and germination fraction are important traits in terms of competition and recruitment (Westoby et al. 1996, Rees 1996, Peco et al. 2003, Moles et al. 2004, Diaz et al. 2007). Relatively large seed weight and "mass germination" characterize the tall grasses in the study area. These traits are probably part of a preemptive strategy in the competition with shorter grasses and forbs during seedling establishment. In the treatment with late onset of grazing, in which tall grasses were dominant, seedlings of tall grasses reached 70% cover, ca. 3-4 weeks after the onset of the rainy season. Furthermore, since larger seeds produce larger seedlings, tall grasses are able to emerge in sites with a deep cover of plant litter, a situation occurring where tall grasses are dominant and grazing pressure is low (Young and Evans 1989, Facelli and Pickett 1991, Onodi et al. 2006). In the case of short annual grasses, small size, early flowering and large output of

small seeds might function as an escape strategy, thus balancing their high germination fraction, high palatability and low competitive ability. This strategy probably does not work in the case of tall annual grasses that are more accessible to the cattle, flower later and are less able to maintain their reproductive capacity when grazed early (Noy-Meir and Briske 1996).

Species with relatively large seeds (> 5 mg) consistently had a high germination fraction in the field as well as under irrigated conditions (i.e., low dormancy) (Table 2, Fig. 3). It can be argued that larger seed size is associated with increased establishment success (Marañón and Grubb 1993, Kidson and Westoby 2000, Moles et al. 2004), but also with increased levels of seed predation (Thompson 2000). These trends should reduce expected levels of dormancy (Venable and Brown 1987, Volis et al. 2004). Rodent and particularly ant granivory were frequently observed during the summer at the study site. As in other Mediterranean grasslands, ants preferentially remove large seeds and dispersal units (Detrain and Pastels 2000, Ascarete and Peco 2006), as those produced by tall grasses, and may represent an important factor selecting for lower dormancy in species with large seeds. In contrast, smaller seeds may escape granivory through cracks in the soil surface and soil burial, thus selecting for germination controlling mechanisms leading to higher dormancy (e.g., light-dependent germination) (Kigel 1985).

#### *Plant traits, seed traits and response to grazing*

Plant size, seed size and germination fraction appear to be main factors determining vegetation structure in the different grazing regimes. However, different trait combinations occur in the different functional groups. Tall grasses, the most palatable species, have the highest germination fraction (i.e., lowest potential for producing a persistent seed bank). This trait can be problematic in dry years and may lead to seed bank depletion, especially when rains effective for germination occur early in the season and drought reduces seed production later in the season. However, the long-term records (13 years) at Karei Deshe Range Farm show that, despite wide fluctuations in the cover of tall grasses, they always represent a high proportion of the vegetation, even after dry years (Sternberg, unpublished). This suggests, that enough seeds are produced to regenerate the population of grass species even in dry years, and they do not rely on persistent seed banks. Furthermore, natural refuges in which these palatable species are protected from grazing (e.g., among rocks), ensure continued seed production in the landscape scale. In the case of *Hordeum bulbosum*, the relatively high cover is maintained across seasons by corms with perennating buds that develop at the base of the flowering tillers (Ofir 1981). It is proposed that tall annual grasses are highly competitive species that became dominant under late grazing, due to a combination of regeneration traits, i.e., high germination fraction, large seeds producing large, competitive seedlings, and inflorescences with morphological defenses (e.g., long tough awns) that deter grazing and allow

seed production. Shorter grass species probably persist by escaping grazing due to their smaller size and by greater production of smaller seeds, but their abundance in the plant community may fluctuate widely due to high germination fraction (i.e., low potential for persistent seed banks), and to the lower competitive ability of their seedlings. Forbs display various combinations of plant traits. Small forbs, like *Stellaria media*, are poor competitors. They persist due to their prostrate habit, extremely early flowering (i.e., January, before canopy closure), and by producing many small dormant seeds without dispersal means, leading to a local, persistent seed bank. The most abundant annual legumes (e.g., *Trifolium pilulare*) have a prostrate habit enabling escape from grazing and produce relatively small seeds with a low germination fraction (Russi et al. 1992, Sternberg et al. 2003). They flower during April and have a prolonged period of seed production due to their indeterminate growth pattern, ending when the soil is dry. Thus, the less competitive short and prostrate species are maintained in the grassland through production of persistent seed banks, and their cover increases under grazing regimes that prevent dominance by tall grasses. Dominant annual thistles, umbellifers and crucifers are relatively more competitive, taller species that may flower either early or late during the season. They usually have dormant seeds, keeping about one-third of non-germinating seeds. Some of these forbs have small seeds (*Pimpinella cretica*, *Ainsworthia trachycarpa*), while others like *Carthamus glaucus* have large seeds that produce large seedlings, able to compete with the seedlings of tall annual grasses. The fact that in the study year, a relative large proportion of forbs seeds did not germinate even after 4 weeks of ample rainfall in early winter (i.e., 210 mm rainfall), is a further indication of the potential of these species to produce a persistent seed bank, in contrast to the high germination fraction in most grass species.

Finally, our findings support the assumption that the high plant diversity characteristic to Mediterranean grasslands is partly due the large number of annual species that are adapted to the prolonged dry summer season and persist under grazing during the growth season. Persistence is carried out through different combinations of plant and regeneration traits, including plant size, inflorescences and mature dispersal units with morphological defenses, germination strategy (low vs. high germination fraction), seed size and ensuing seedling competitive ability. Low potential for persistent seed bank production is probably balanced by massive production of small seeds (as in short annual grasses), or by producing unpalatable inflorescences, large seeds and highly competitive seedlings (as in tall grasses). The diverse vegetation strategies reflect the long co-evolutionary process of grazing in this type of ecosystem.

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