

Recovery of plant species composition and ecosystem function after cessation of grazing in a Mediterranean grassland

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Abstract Short- and long-term changes in species composition, plant biomass production, and litter decomposition after cessation of grazing were examined in a Mediterranean grassland with high dominance of annual species and strong seasonality in biomass production. Short-term changes were assessed during three consecutive years in plots previously exposed to different grazing pressures and compared to plots in long-term (30–40 years) exclosures. Short-term cessation of grazing led in the short-term to an increase in relative biomass of annual crucifers and tall annual and perennial grasses, while biomass of annual legumes, annual thistles and short annual grasses decreased. Consequently, similarity

increased between vegetation recently excluded from grazing and vegetation in long-term protected plots. Our research showed that in systems with high dominance of grasses and annual species, the rapid changes in plant species composition that occur after grazing cessation were associated with a fast recovery of the potential for biomass production to levels found in long-term protected plots, while litter decomposition rate did not change even after long-term cessation of grazing. Moreover, previous history of grazing did not affect plant litter decomposition, despite higher litter quality in grazed treatments. This study provides new insights about the processes involved in the diverse responses of ecosystem functions resulting from shifts in species composition associated with grazing cessation and land use change in Mediterranean grasslands.

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Introduction

In recent years much research effort has focused on the effects of land-use change on ecosystem function (Garnier et al. 2007; Hooper et al. 2005; Lavorel et al. 1997; Peco et al. 2005). An understanding of ecosystem responses to land-use change is vital for the formulation of management plans for today's

ever-changing agricultural landscapes, in particular those which are managed for grazing (Hopkins and Holz 2006; Quetier et al. 2007). Economic pressures have led, in some instances, to intensification, while in others, to widespread abandonment of livestock grazing, across Europe and around the world (Hopkins and Holz 2006; Lavorel et al. 1998; Marriott et al. 2004; Peco et al. 2005, 2006).

Grazing is a key factor affecting ecosystem functions in grasslands (Altesor et al. 2005; Noy-Meir et al. 1989; Perevolotsky and Seligman 1998), particularly primary productivity and nutrient cycling (Altesor et al. 2005; Marriott et al. 2004; Olofsson et al. 2004). Grazing effects on these functions may be positive or negative in different ecosystems (Augustine and McNaughton 2006). In Mediterranean regions with seasonal herbaceous pastures, i.e. where the growing season is limited to the rainy winter months, and the vegetation completely dries up during the summer months, grazing generally reduces plant biomass by reducing leaf area and light interception during the growing season (Perevolotsky and Seligman 1998). In other systems grazing may actually increase plant biomass production in plant communities where re-growth potential is high (Noy-Meir and Briske 1996; Olofsson and Oksanen 2002), as in perennial grasslands (Jacobs and Schloeder 2003; Loeser et al. 2004), or in plant communities with a long evolutionary history and low productivity (Milchunas and Lauenroth 1993).

A main mechanism by which grazing affects ecosystem function is through the modification of species composition (Altesor et al. 2005; Milchunas and Lauenroth 1993; Semmartin et al. 2004; Sternberg et al. 2000). In Mediterranean pastures the frequency of tall perennial and annual grasses, which contribute most to primary productivity and are also the most palatable for the grazers, is consistently reduced by grazing compared to other, shorter species which are less accessible to them (Noy-Meir et al. 1989; Osem et al. 2004; Sternberg et al. 2000). This grazing-mediated change in species composition may alter not only the primary productivity of the community, but also the composition and chemical properties of the plant litter, thus affecting the quality of the plant litter for decomposers (Henry et al. 2005; Olofsson and Oksanen 2002; Semmartin et al. 2004) and, consequently, the rate of nutrient cycling (Bakker et al. 2004; Garnier et al. 2007; Quetier et al. 2007). Plant litter quality is known to strongly influence litter

decomposition rate (Carrera et al. 2008; Gartner and Cardon 2004; Henry et al. 2005; Lodge et al. 2006; White et al. 2004). In this context, lignin and lignin:N ratios have been widely used as indicators of plant litter quality for decomposition (Cornelissen et al. 1999; Gartner and Cardon 2004; Quetier et al. 2007; Wardle et al. 2002; Wedderburn and Carter 1999). In pastures subject to continuous grazing, short grasses and herbaceous forbs with lower investment in structural components (e.g. lignin) are generally more common (Noy-Meir et al. 1989; Osem et al. 2004; Peco et al. 2005; Sternberg et al. 2000), since they avoid grazing by virtue of their low stature, and thrive in open patches left after grazing (Osem et al. 2004; Perevolotsky and Seligman 1998). Plant litter from these shorter species should be of a higher quality, decomposing at a faster rate to release vital nutrients to the ecosystem (Lodge et al. 2006). An additional source of high-quality plant litter is the re-growth of grazed plants, which maintains a larger proportion of younger tissues with increased nitrogen content (Henkin et al. 2007; Olofsson and Oksanen 2002; Semmartin and Ghera 2006). When grazing pressure is reduced or eliminated, taller species become dominant, forming a relatively closed canopy in which competition for light is high (Noy-Meir et al. 1989; Osem et al. 2004; Sternberg et al. 2000). Under these conditions, increased plant height requires a higher investment in structural components rich in lignin, and lower investment in fast-growing tissues with high nitrogen content. Thus, in the absence of grazing the resulting plant litter from taller vegetation should be of a lower quality, with a potentially lower rate of decomposition.

We examined these hypotheses in a Mediterranean grassland community characterized by seasonal vegetation due to rain seasonality, and high dominance of annual species and hemicryptophytes (Sternberg et al. 2000). Effects of reduced grazing pressure and cessation of grazing on productivity and nutrient cycling were assessed using peak biomass production and plant litter decomposition, as proxies for these two ecosystem functions. We asked whether relationships observed in grasslands dominated by perennials (Altesor et al. 2005; Semmartin et al. 2004) are similar to grasslands dominated by annuals, such as Mediterranean grasslands which have been barely studied in this context. We examined these relationships using the functional group approach. Responses of vegetation to changes in

grazing conditions are often related to growth form, mainly plant height, as well as to palatability and spininess (Noy-Meir et al. 1989). The functional group approach, in which species with similar biological traits resulting in similar responses to grazing are grouped together (Diaz et al. 2007; Gitay and Noble 1997), allows us to analyse the relationships among these attributes and grazing responses. We hypothesized that a reduction in grazing pressure, and in particular, complete cessation of grazing, should lead to a change in the relative contributions of different functional groups, with higher dominance of taller species, resulting in increased biomass production. In addition, we hypothesized that higher litter quality (due to a lower proportion of taller species with greater structural tissues) in treatments with a recent history of grazing would result in less litter accumulation and faster litter decomposition. We also examined short- and long-term successional trends after cessation of grazing, that are relatively rapid in plant communities with high dominance of annuals (Perevolotsky and Seligman 1998). To this end, we monitored changes in relative biomass of the different species and functional groups during 3 years after grazing exclusion, and compared the vegetation to plots which had been protected for 30–40 years (long-term grazing protection).

Materials and methods

Site description

The research was carried out at the Karei Deshe Experimental Range Station (lat. 32° 55'N, long. 35° 35'E, elevation 150 m a.s.l., 567 mm mean annual rainfall), in the northeast Galilee region of Israel. The vegetation is classified as Mediterranean semi-steppe batha (Zohary 1973), dominated by grasses and forbs. The dominant perennial species are the hemicryptophytes *Bituminaria bituminosa*, *Echinops gaillardotii*, *E. adenocaulos*, *Ferula communis* and *Hordeum bulbosum*, forming approximately 40% of the cover (Gutman and Seligman 1979; Noy-Meir et al. 1989; Sternberg et al. 2000). Most other species are annuals, including grasses (*Avena sterilis*, *Alopecurus utriculatus*, *Bromus* spp.), legumes (*Medicago* spp., *Trifolium* spp.), composites, crucifers and umbellifers. Growth and development of the vegetation depends almost entirely on seasonal rainfall, from mid-October/late-November

to late-April/early-May. During the summer the vegetation dries out. Productivity is strongly dependent on the amount and distribution of the rainfall. During the 3 years of the research seasonal rainfall was 754 mm (2002–3), 665 mm (2003–4) and 395 mm (2004–5), referred in the following as 2003, 2004 and 2005.

Experimental treatments

The rangeland at the station is grazed by cattle under a controlled grazing system (Sternberg et al. 2000). The three experimental treatments used included two grazing treatments—continuous heavy (CH), and continuous moderate (CM), with 1.1 and 0.55 cows ha⁻¹ year⁻¹, respectively, for 10 years prior to the onset of the experiment (Sternberg et al. 2000), and a treatment with grazing exclusion for 30–40 years (long-term protection, LP). The cows grazed for approximately 7 months during each year of the research, from mid-January to late August. Deferment of grazing after onset of the rainy season in late-autumn allows establishment and early growth of the pasture. Each experimental treatment included two replicate plots (in different parts of the farm) making a total of six plots. The grazed plots are larger than the protected (ungrazed) plots (ca. 20–30 ha vs. 0.4–2 ha). The actual sampled area, however, was similar between treatments and shares similar habitats. Within each grazed plot, five 10×10 m exclosures were established in February 2003, separated by 50–100 m. Exclosures were established for sampling the vegetation in the absence of the cattle, and for determining potential biomass production under grazing conditions. In the smaller, long-term protected plots, five 2.5-metre-long stakes were placed randomly (separated by at least 30 m) within each plot, marking the centre of the 100 m² area for sampling. All vegetation sampling was therefore conducted in grazing-excluded areas and represents potential biomass production.

Sampling and analysis of herbaceous vegetation

The herbaceous vegetation was sampled at peak biomass in mid spring (April) of 2003, 2004 and 2005, from five 25×25 cm quadrats randomly placed in each exclosure in the grazed plots and in the sampling areas in the protected plots. Since all the herbaceous vegetation dries out during the summer, biomass at peak season in the spring is a good proxy

for annual aboveground productivity of the herbaceous vegetation. Quadrat positioning avoided rocks and large perennial hemicryptophytes (i.e. *Echinops* spp., *F. communis*, *B. bituminosa*), but included the perennial grass *Hordeum bulbosum*. *H. bulbosum*, the dominant grass species, is a hemicryptophyte, i.e. the perennial organs (corms) are belowground, and the foliage dies off at the end of each growing season, such that measurements of aboveground biomass are not confounded by previous years' growth. All aboveground plant material within the quadrats was removed, plants were sorted to species level, identified (Feinbrun-Dothan and Danin 1991), counted and dried at 70°C for 48 h. Plant species were categorized into functional groups (Noy-Meir et al. 1989; Sternberg et al. 2000): annual crucifers (AC), annual forbs (AF), annual legumes (AL), annual thistles (AT), annual umbellifers (AU), short annual grasses (SAG), tall annual grasses (TAG), short perennial grasses (SPG), tall perennial grasses (TPG), perennial forbs (PF), perennial thistles (PT), geophytes (G). Functional group composition was determined at the quadrat scale. The full species list including percent biomass production per species per treatment in 2003 is presented in Appendix 1. Analyses of the responses to grazing cessation were conducted on the eight functional groups that contributed at least 2% of the total biomass production (AC, AF, AL, AT, AU, SAG, TAG and TPG).

Species similarity between treatments, as well as within and among years for each treatment, was assessed using Sorensen's quantitative similarity index:

$$C_N = 2jN / (aN + bN)$$

where aN is the total biomass in treatment a, bN is the total biomass in treatment b and jN is the sum of the lower of the two abundances, for each species present in both treatments (Magurran 1988). This index takes into account both qualitative and quantitative changes in species composition. All similarity values were calculated at the enclosure scale. Similarity values between treatments/years were calculated for all pairs of enclosures between treatments/years.

Soil sampling and analysis

Sampling and analysis of the basaltic soil was conducted in October 2003, before the winter rains.

Five soil cores from the 0–10 cm soil layer were sampled next to each enclosure in the grazed plots, and near to each sampling area in the long-term protected plots. Plant material on the soil surface was removed before sampling the soil. Soil cores from each enclosure were bulked before soil analyses, for a total of ten replicates per treatment. Soil samples were analyzed at the 'Laboratoire d'Analyses de Sols' of the National Institute for Agronomic Research (INRA, 62000 Arras, France). Soil texture was analysed by sedimentation. Soil moisture was determined gravimetrically by drying at 105°C for 48 h. Soil C and N were determined by the Dumas method (combustion). Soil pH was measured by the electrometric method at 20°C. Soluble phosphorus was determined by Olsen's method. The above parameters did not differ among treatments as follows: soil moisture (61.5±1.8%), clay content (61.1±1.9%), silt content (34.4±0.9%), sand content (4.8±0.3%), C (23.0±0.9%), N (1.99±0.082%), pH (7.27±0.03), P (119±16 ppm) and C:N ratio (11.6±0.1).

Plant litter accumulation

We assessed accumulation of the standing dry herbaceous vegetation (plant litter) before the onset of the rains, at the end of September 2004. Plant litter was sampled from five 25×25 cm quadrats randomly placed within enclosures to measure accumulation after 1 year in the absence of grazing, and outside enclosures to measure accumulation under grazing. Sampling was carried out in each enclosure in the grazed plots and within each sampling area in the protected plots. Litter samples were dried at 70°C for 48 h and weighed.

Plant litter decomposition experiment

During the summer (July) of 2003, a mixture of standing dry herbaceous vegetation ("native plant litter") was collected separately from a 1 m² area in the centre of each enclosure in the grazed plots and each sampling area in the long-term protected plots. Plant litter was bulked for each plot, and seeds, fruits and roots were removed. Stems were cut to a length of 5–10 cm, depending on their thickness, to maximize mixing of the different plant species in the litter samples. Samples of 4.0±0.1 g from the mixed litter were placed in 15×15 cm nylon litter bags with mesh size of 1.1 mm (Quested et al. 2007). This mesh size was deemed optimal for minimizing loss of plant

litter from the bags while allowing most microbiota and mesofauna to enter the bags, although some groups of larger mesofauna, e.g. carabid larvae, may be excluded. Fifteen replicate bags were placed in each enclosure/sampling area within the experimental plots. Additional plant litter bags were prepared from standard green hay (“standard plant litter”) obtained from Sweden (Quested et al. 2007), in order to rule out differences in the conditions of the microenvironment in the different plots. Eight replicate bags were placed in each enclosure/sampling area.

Determination of the initial chemical properties of the native and standard plant litters was carried out using Near-Infra-Red Spectroscopy (NIRS), at CEFE, CNRS, in Montpellier, France (Fortunel et al. 2009). Plant litter was analysed for (percentage by mass): ash, cellulose, hemicellulose, nitrogen and lignin. Lignin:N ratios were calculated.

Plant litter bags were placed in the field in September 2003 before the onset of the rains. Native plant litter bags were placed in the treatments from which the litter had been collected, together with standard plant litter bags. Standing plant material and seeds were cleared from the soil surface; the bags were positioned on the soil and secured with nails. After the first wave of germination, and subsequently throughout the growing season, we removed seedlings which sprouted beneath the litter bags in order to maintain constant contact between litter bags and soil. In addition, a clear area was maintained around the litter bags, to minimise effects from the surrounding vegetation (shading, moisture, nutrients etc), and thus maintain similar conditions for decomposition in the different plots. Plant litter bags were collected at the end of two (standard litter) or three (native litter) consecutive growing seasons (June 2004, May 2005 and May 2006), since most litter decomposition takes place during the wet months of the winter and spring. Between three and five replicate bags were retrieved from each enclosure/sampling area per collection date. The bags were carefully lifted from the soil, large clods of soil were removed, and the bags were put into paper bags for transport to the laboratory. In the laboratory, soil aggregates, seeds and new plant material were removed from litter samples before weighing (± 1 mg).

Organic matter content of plant litter (i.e. the combustible portion of the litter) was determined for the litter bags collected from the field, and for reference samples of initial plant litter that were used

for calculating initial organic matter content of litter samples. The plant litter was ground to 2 mm before combustion at 500°C for 4 h. Organic matter content of litter samples was determined as the combusted portion of the litter samples. Initial organic matter content of recovered litter samples was calculated according to the organic matter content of the reference litter samples. Organic matter loss (i.e. reduction in organic matter content) from recovered litter samples was determined according to their calculated initial organic matter content.

Statistical analysis

Data of peak season biomass and plant litter biomass were ln-transformed before analysis. Data expressed as percentages were arcsine-transformed prior to analysis. Mixed, nested ANOVA models were used to analyse 2003 and 2005 functional group species composition, between-years comparisons of similarity, soil properties and plant litter accumulation. Initial chemical composition of plant litter was analyzed using a one-way ANOVA with treatment as the main effect. Within-treatment changes in similarity with time were analysed using a treatment by year factorial design. Changes over time in similarity (between treatments), biomass production and functional group composition were analysed by a mixed model, nested, repeated-measures ANOVA, as were the data from the plant litter decomposition experiment (mass loss and organic matter loss). Year was the response effect. For all analyses, Tukey HSD and Student's *t*-test were used for comparison of means when main effects were significant. All analyses were conducted with JMP IN 7 (SAS Institute Inc., Cary, USA).

Results

Functional group composition

At the time of enclosure establishment in 2003, initial differences were found in the proportions of functional groups, reflecting the effects of previous continuous moderate (CM) and continuous heavy (CH) grazing treatments, and of the long-term protected (LP) treatment on the vegetation (see data in Appendix 2). Among the functional groups, however, only tall perennial grasses (TPG) varied significantly across

treatments ($F_{2,3}=10.4$, $p=0.045$), with higher representation in LP compared to CM and CH. Short annual grasses (SAG) showed an opposite, marginally significant trend ($F_{2,3}=7.43$, $p=0.069$). The other functional groups of annual species showed high spatial variation in their contribution to total biomass, but no significant treatment effects were observed, due to the high heterogeneity of the vegetation at the plot level.

Functional group composition changed rapidly and significantly between 2003 and 2005, after cessation of grazing (Fig. 1). These changes mirrored the initial differences in functional group composition between treatments in 2003, when exclosures were established (Appendix 2a). The proportion of annual crucifers (AC) increased significantly with time ($F_{2,288}=29.4$, $p<0.0001$), primarily between 2003 (0–4%) and 2004

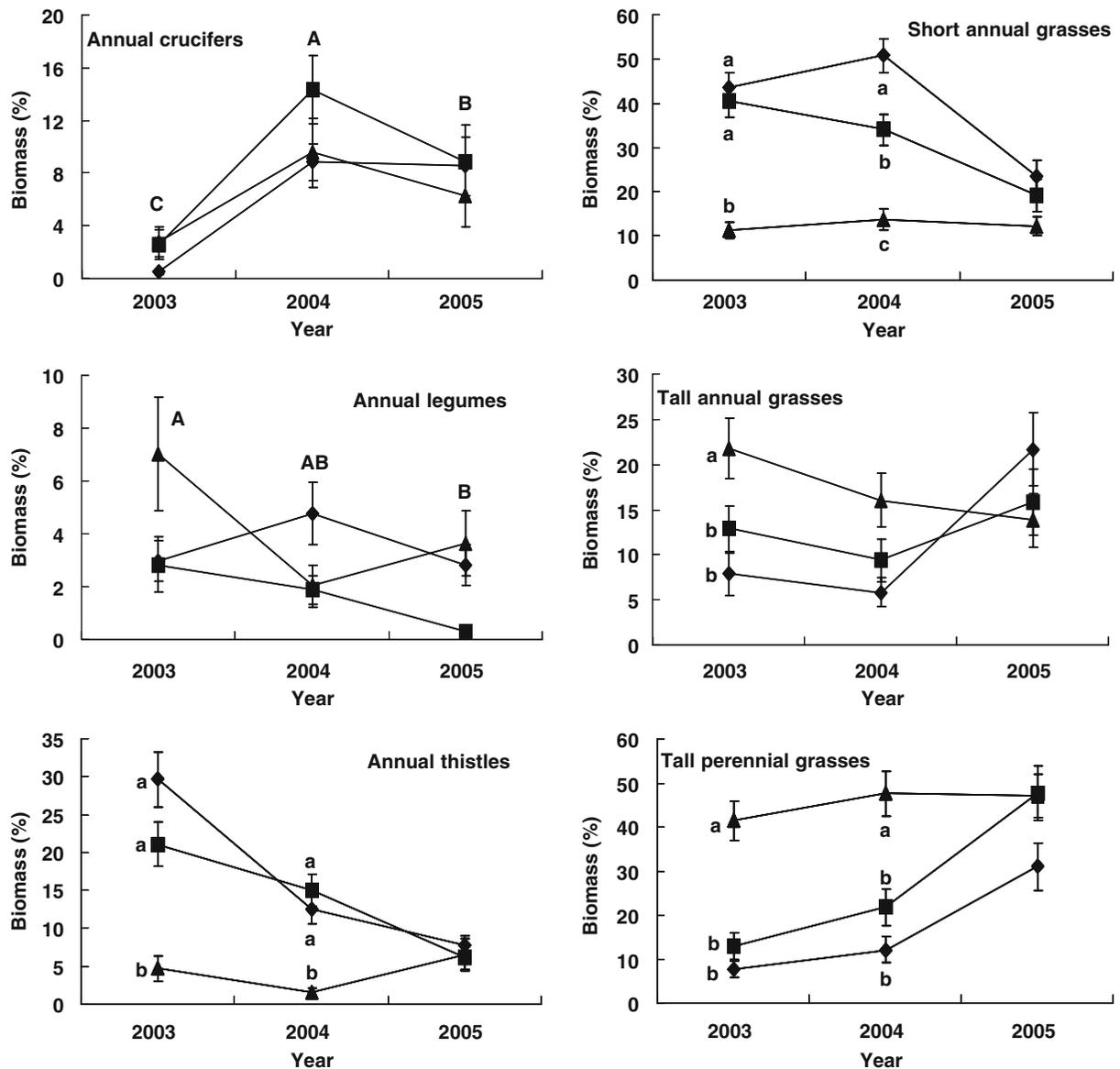


Fig. 1 Changes in proportional biomass (mean \pm standard error) of six functional groups for 3 years from the onset of grazing exclusion. Treatments: CH heavy grazing (diamonds), CM moderate grazing (squares), LP long-term protection from

grazing (triangles). Years with different uppercase letters are significantly different according to Tukey HSD ($\alpha=0.05$). Data points within years with different lowercase letters are significantly different according to Tukey HSD ($\alpha=0.05$)

(9–14%). Annual legumes (AL) were relatively more abundant in LP in 2003 (8%), but decreased in 2004 and 2005 (2%), compared to a decrease from 2% to <0.5% in CM, and relative constancy in CH (treatment by year [TxY] interaction: $F_{4,288}=2.69$, $p=0.031$). Annual thistles (AT) decreased strongly with time in CM and CH from 20–30% to 5%, while they remained low (1–5%) in LP (TxY interaction: $F_{4,288}=14.1$, $p<0.0001$). Similarly, short annual grasses (SAG) also showed a large decrease between 2004 and 2005 in CM (35 to 10%) and CH (50 to 20%), but they remained low (10%) in LP (TxY interaction: $F_{4,288}=7.82$, $p<0.0001$). In contrast, tall annual grasses (TAG) were more abundant in LP compared to CM and CH in 2003 (20% vs. 8–14%) and 2004 (15% vs. 7–12%), and increased for CM and CH in 2005, although this was significant only for CH (interaction TxY $F_{4,288}=4.82$, $p=0.001$). In LP, TAG decreased gradually from 2003 to 2005. Similarly to TAG, TPG was relatively higher in LP (45%) compared to CM and CH (10–20%) in 2003 and 2004, and increased in CM and CH in 2005 by 40–55% relative to 2003 and 2004 (T × Y interaction: $F_{4,288}=4.64$, $p=0.001$). TPG remained high in LP from 2003 to 2005.

Due to the above changes, no significant differences were found in 2005 between treatments in the proportions of functional groups after 3 years of grazing cessation (Appendix 2b). Furthermore, due to the decrease in relative biomass of three groups of annuals (AF, AL, AU), only five functional groups

(AC, AT, SAG, TAG and TPG) contributed at least 2% to total biomass production in 2005.

Similarity

Sorensen's quantitative similarity index (i.e. similarity) of species composition between grazed (CM, CH) and ungrazed (LP) plots (Fig. 2) increased significantly from 2003 (0.15–0.21) to 2005 (0.42–0.43). In addition, similarity of vegetation between CM and CH increased from 0.39 to 0.46 during the same time period (interaction between treatment-comparison and year; $F_{4,882}=16.3$, $p<0.0001$). Indeed, similarity between CM and CH was higher than that between LP and CM or CH in 2003 and 2004, but not in 2005 (Fig. 2).

Plant biomass production

Peak plant biomass production (Fig. 3a) was higher in LP compared to CM and CH in 2003 and 2004, but was similar in 2005 due to an increase in CM and CH biomass (TxY interaction; $F_{4,288}=9.84$, $p<0.0001$). Biomass production ranged from 298 g m⁻² (CM in 2003) to 678 gm⁻² (LP in 2003).

Plant litter accumulation

Plant litter accumulation prior to the onset of the rainy season was assessed in 2004. Litter accumulation in LP was higher than that measured outside of exclosures in both CM and CH ($F_{2,24}=26$, $p<$

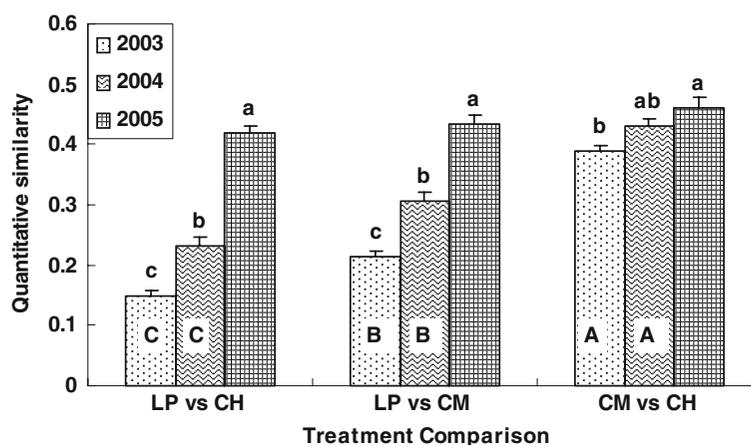
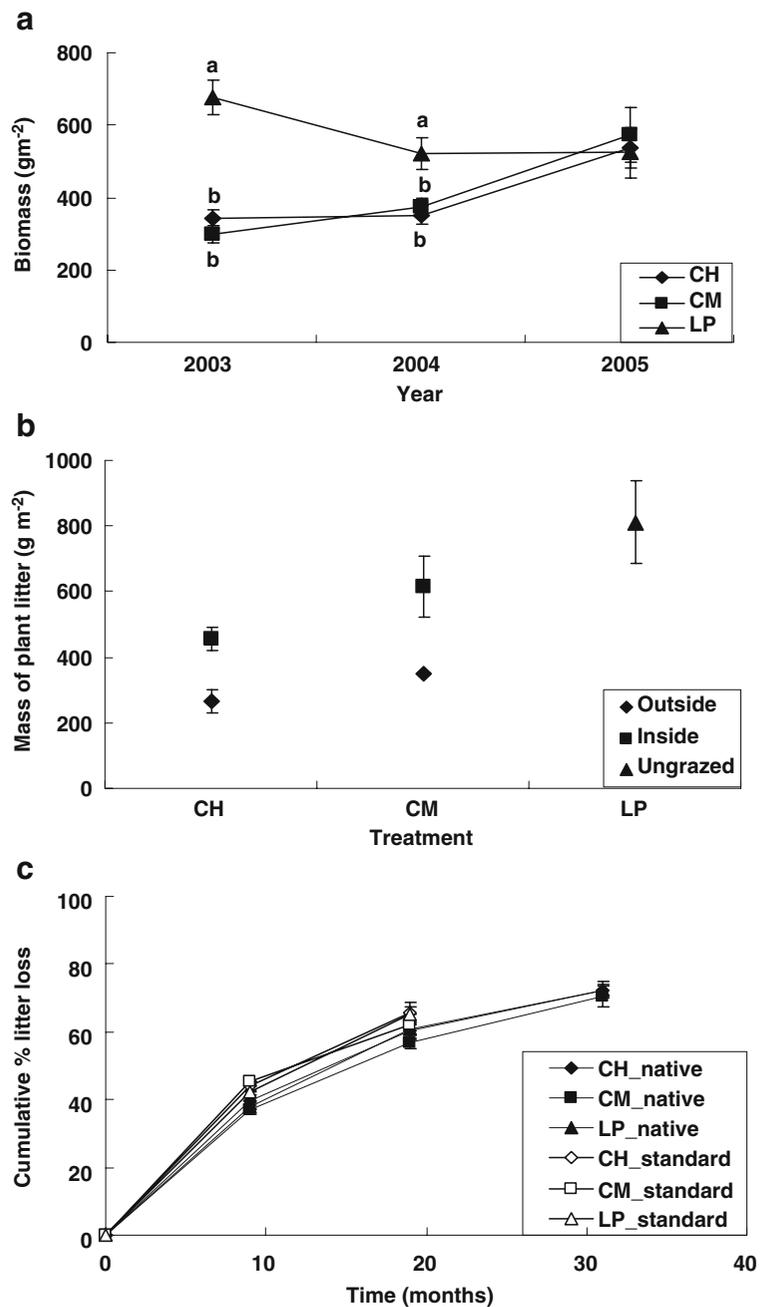


Fig. 2 Changes in similarity of species composition (quantitative Sorensen index) between treatments during secondary succession in exclosures in grazing treatments. Treatments: CH heavy grazing, CM moderate grazing, LP long-term protection

from grazing. Columns with different lowercase letters within categories are significantly different according to Tukey HSD ($\alpha=0.05$); columns with different uppercase letters within years are significantly different according to Tukey HSD ($\alpha=0.05$)

Fig. 3 Aboveground biomass production (a), plant litter accumulation (b) and cumulative mass loss from plant litter bags (c) (mean \pm standard error). a and c Show changes from 2003 to 2005, while b shows 2004 data only. Treatments: CH heavy grazing, CM moderate grazing, LP long-term protection from grazing. In (a), data points within years with different lowercase letters are significantly different according to Tukey HSD ($\alpha=0.05$). For (c), values are means of ten exclosures



0.0001; Fig. 3b). Litter accumulation in LP was higher than in CH inside exclosures but not significantly different from accumulation inside exclosures in CM ($F_{2,24}=13.8$, $p=0.0001$). Significantly more litter accumulated inside exclosures than outside of them ($F_{1,96}=53.5$, $p<0.0001$), and comparison between CM and CH showed that plant litter accumulation was higher overall in CM compared to CH ($F_{1,80}=$

15.4, $p=0.0002$). Plant litter accumulation ranged from 266 gm⁻² (CH outside exclosures) to 811 gm⁻² (LP).

Plant litter decomposition

Several chemical properties of the native plant litter differed between treatments (Table 1). Lignin content

Table 1 Initial chemical composition of litter samples from plots with long-term protection from grazing (LP), and plots under continuous heavy (CH) and continuous moderate (CM) grazing, analyzed by ANOVA. Data are mean

Treatment	Ash %	N %	Lignin %	Lignin:N
CH	8.55 (0.29)	0.67 (0.043)	5.63 b (0.32)	8.46 b (0.39)
CM	7.39 (0.54)	0.58 (0.026)	4.75 b (0.20)	8.17 b (0.042)
LP	6.88 (0.64)	0.63 (0.015)	7.30 a (0.16)	11.62 a (0.35)
<i>F</i>	2.63	2.06	27.6	40.1
<i>P</i>	0.151	0.209	0.0009	0.0003

percent by mass values and standard error (in parentheses). Within columns, values followed by different lowercase letters are significantly different according to Tukey HSD ($\alpha=0.05$). $N=9$; $df=2$

was higher ($F_{2,6}=27.6$, $p=0.0009$) in LP compared to both CM and CH, while nitrogen content did not vary between treatments (average of 0.63% across all treatments). Therefore, the lignin:N ratio was significantly higher ($F_{2,6}=40.10$, $p=0.0003$) in LP compared to CM and CH, due to the higher lignin content in LP. The grazing treatments did not affect ash content (the non-combustible portion of the plant litter), which averaged 7.6% across all treatments. The standard litter contained 0.57% N, 8.59% lignin, and a lignin:N ratio of 15.1 (Fortunel et al. 2009).

Plant litter mass loss in the different grazing treatments during the 3-year experiment was similar and the average litter mass lost each year decreased gradually with time (Fig. 3c). Repeated-measures ANOVA revealed that the only significant factor was time, with significant increases in mass loss between years ($F_{2,47}=306$, $p<0.0001$). Average mass loss after the first, second and third rainy seasons was 38.2%, 21.1% and 12.5%, respectively, with a cumulative loss of 71.8% 3 years after setting the litter bags in the field. For 2004 and 2005, mass loss from standard litter was consistently higher than for native litter ($F_{1,81}=25.0$, $p<0.0001$; Fig. 3c), and averaged 44% and 20.4% after the first and second rainy seasons, respectively. Similarly to plant litter mass loss, organic matter loss from plant litter increased with time ($F_{2,48}=46.8$, $p<0.0001$), primarily between 2004 and 2005, with no differences between treatments (data not shown), and a cumulative average loss of 59.4% after 3 years. For 2004 and 2005, organic matter loss from standard litter was slightly but significantly higher than for native litter ($F_{1,82}=28.7$, $p<0.0001$), with a cumulative average loss of 65% after 2 years compared to 59.3% for native litter.

Discussion

Grazing, vegetation composition and biomass production

The long-term initial grazing treatments resulted in several noticeable differences in functional group composition of the herbaceous vegetation. This was reflected in the differences in the relative biomass distribution among functional groups between treatments in the first season after exclosures were set. Vegetation in the grazed treatments was dominated by short annual grasses and annual thistles, while under long-term protection from grazing tall annual and perennial grasses were dominant. Similar trends were previously found in this system from frequency data (Noy-Meir et al. 1989; Sternberg et al. 2000), as well as in other Mediterranean grazing systems, e.g. dehesa grasslands in Spain (Peco et al. 2005), Mediterranean semi-arid rangeland (Osem et al. 2004). In our system, changes in functional group composition during secondary succession after establishment of the exclosures mirrored the initial differences in functional group composition between long-term protected and grazed plots, with dominance by short annual grasses and annual thistles initially, while after three growing seasons, tall annual grasses and the tall perennial grass, *Hordeum bulbosum* dominated. Most other functional groups comprised less than 10% of the biomass at any one time, with minimal impact on the shift in vegetation structure.

The change in functional group composition after short-term grazing exclusion lead to increased similarity between grazed treatments and protected treatments 3 years after setting the exclosures. Gutman and Seligman (1979) found that after the initiation of the experimental grazing treatments, vegetation

changes occurred over a similar time scale, with the first significant changes in species composition (increase of forbs in CH) occurring after 3 years, while a steady state was reached after 5 years. Such rapid changes in vegetation composition have been documented in other grassland systems rich in annual species (see Marriott et al. 2004 and references therein), probably due to the greater ability of these species to maintain a viable seed bank for regeneration (Aboling et al. 2008; Sternberg et al. 2003).

In our study, the increased dominance of tall grasses after grazing exclusion led directly to increased biomass production in the exclosures which equalled that in the long-term protected plots. Thus, 3 years may be considered sufficient for recovery of biomass production in this system, while species composition requires at least another 2 years (Gutman and Seligman 1979). Such rapid recovery is not uncommon in Mediterranean grasslands with high dominance of annuals, which have evolved under a long history of grazing (Perevolotsky and Seligman 1998), and indicates a high degree of resilience within the system (Sternberg et al. 2000).

Plant litter accumulation was predictably higher in long-term protected plots than in grazed plots, due to increased abundance of tall grasses. Within exclosures and in long-term protected plots, litter accumulation could exceed biomass production, as shown for 2004. This may be attributed to the annual thistles, *Scolymus maculatus* (grazed plots) and *Carthamus glaucus* (protected plots), which reach maturity in May–June (Aboling et al. 2008), up to 2 months after biomass sampling, thus contributing more to litter accumulation than to peak biomass production. In addition, in the absence of grazing, litter accumulates between years. We can probably assume that a significant proportion of the *S. maculatus* litter in grazing exclosures from 2003 was still present in 2004, contributing to the high values of accumulated litter.

Contrary to the rapid and strong recovery of species composition and biomass production after grazing cessation, we found few significant effects of a reduction in grazing intensity on species composition, and no effect on biomass production, despite the large difference in vegetation consumption between the two levels of grazing intensity (31% in CM compared to 65% in CH; C. Golodets, unpublished

data) and the low similarity between them. However, litter accumulation was higher in CM 1 year after establishment of exclosures, reflecting the more rapid recovery of the perennial *H. bulbosum* in this treatment (Appendix 2). Olofsson (2006) found that reduced grazing pressure in heavily grazed areas had little effect on vegetation composition, while a significant change was recorded when grazing pressure was increased in lightly-grazed areas. In a world-wide meta-analysis, Milchunas and Lauenroth (1993) found that differences in biomass production in grazed–ungrazed comparisons were more sensitive to changes in ecosystem variables such as aboveground net primary production (ANPP) and evolutionary history of grazing, than to grazing variables *per se*, such as level of consumption or years of grazing treatment.

Plant litter decomposition

The initial litter chemical composition indicated higher litter quality in grazed plots than in long-term protected plots, due to the lower lignin content, and consequently, lower lignin:N ratio. In our research we focused on the effect of grazing on plant species composition, assuming that plant litter composition reflects the species composition of the plant community. Thus, we can trace litter quality to the species composition of the original plant community (Wardle et al. 2002). Litter quality was higher in grazed plots due to the lower proportions of tall grasses, which are the main contributors of lignin to the plant litter in the studied system. Since high litter quality promotes faster decomposition (Semmartin and Ghera 2006), we expected greater mass loss of plant litter in the grazed treatments, or at least in the heavily grazed treatment (Cornelissen 1996; Quested et al. 2007; Semmartin et al. 2004; Semmartin and Ghera 2006; Wedderburn and Carter 1999). Contrary to our expectations, plant litter mass loss and organic matter loss from the litter were not affected by plant litter quality.

Plant litter decomposition is affected by three main factors: climate, litter quality and the nature and abundance of the decomposer community (Couteaux et al. 1995). We worked in areas of similar topography and rockiness in the different experimental plots, such that abiotic conditions were relatively uniform across plots. Uniformity in soil characteristics and composition among plots and treatments confirms

this assumption. We may therefore assume that the decomposer community is similar between treatments. Li et al. (2005) found significant effects of grazing on nematodes and protozoa in the same experimental site, but these organisms are not critical for decomposition of plant litter (Wardle and Lavelle 1997). It can be argued that differences in the surrounding vegetation caused by grazing in the different treatments may affect plant litter decomposition through changes in in situ litter-bag conditions (e.g. shading, moisture, addition of nutrients to the soil). We can rule out effects of shading or increased moisture in the ungrazed treatment, or in the exclosures in the third year, since the area near the litter bags was kept clear of vegetation. Any effect on soil nutrients (e.g. via fecal returns from herbivores) would have been evident in the initial soil chemistry. However, since the soil is basaltic and rich in nutrients, the potential impact of fecal returns is negligible. Indeed, Li et al. (2005) did not find any differences in soil organic matter or N content between heavily grazed and ungrazed plots at the experimental site. In addition, any herbivore effect on soil nutrients should lead to differences between treatments in litter mass loss (at least for standard litter) in the first year, when vegetation composition between grazed and ungrazed vegetation was least similar. Such differences were not recorded, therefore we can rule out all effects relating to differences in vegetation and soil conditions between the CM, CH and LP treatments. Thus, of the three main factors affecting litter decomposition (i.e. mass loss), plant litter quality remains as the main factor differing between the experimental treatments. The finding that decomposition of the standard litter was faster compared to the native litter despite its lower quality, can be largely explained by the fact that the standard litter comprised mostly thin leaves, while the native litter contained many stems as well as leaves. Therefore, the surface area-to-volume ratio was much higher in the standard litter, allowing greater access to decomposing organisms.

The challenge remains to explain why the difference in native plant litter quality between treatments had no effect on litter mass loss between treatments. Litter decomposition in relation to grazing has not been widely studied in Mediterranean grassland ecosystems with high dominance of annual species. Previous studies which examined this process

reported similar litter mass loss (Cortez et al. 2007; Dukes and Field 2000; Koukoura 1998) and lignin contents (Dukes and Field 2000; Henry et al. 2005) to those found in the current study. Such low lignin levels are typical of herbaceous vegetation (Cortez et al. 2007). Semmartin et al. (2004) concluded that the litter quality effect is largest when the change in species composition involves a change in functional diversity (see also Diaz and Cabido 2001; Henry et al. 2005; Quested et al. 2007; Pérez Harguindeguy et al. 2008; Scherer-Lorenzen 2008). In our plant community, changes in functional diversity between grazing treatments were insufficient to create enough variability in litter quality, and thus affect litter decomposition rates. Differences in functional diversity between treatments were due to changes in dominance of three taxonomically similar functional groups (tall perennial grasses, tall annual grasses and short annual grasses), whereas changes in the natural rangelands of Argentina studied by Semmartin et al. (2004) involved replacement of C₃ and C₄ bunch grasses by C₃ exotic forbs. Considering that the three dominant groups in our system are C₃ species belonging to the same family, with similar chemical composition (Henry et al. 2005), the narrow range in litter quality and uniform rates of litter decomposition across treatments are not surprising. In addition, the significant presence of annual thistles in grazed plots reduced the variability in lignin content between grazed and ungrazed treatments. Thistles are known to contribute considerably to the lignin content of the plant litter, thereby increasing litter lignin content in grazed plots. Thus although grazing led to differences in the ratio between tall and short grasses and improved litter quality, these differences in quality were not expressed in the rate of litter decay.

When plant litter decays, the most easily decomposable compounds are lost first, while the more resistant fractions require more time. Lignin is a complex polymer which is highly resistant to decay, and is the main factor controlling the latter stages of plant litter decomposition (Cortez et al. 2007). Taylor et al. (1989) have shown that for plant litter with a low lignin content and low lignin:N ratio, such as in our experiment, lignin control of litter decomposition begins only after the large pool of labile material (which may be close to 50% mass loss) has been exhausted. Thus the influence of lignin on retarding litter decomposition is relatively weak and late, and

probably did not influence decomposition rates in the time-frame of this experiment (Cortez et al. 2007). Similarly, Henry et al. (2005) found that differences in plant litter quality due to lignin had no significant effect on decomposition rate.

Conclusions

In this research we examined the recovery of species composition after cessation of grazing, and the coupling between species composition, biomass production and litter decomposition. We hypothesized that changes in species composition due to reduced grazing pressure or cessation of grazing would improve biomass production to pre-grazing levels, while species composition of recently-grazed vegetation was expected to improve litter decomposition compared to long-term ungrazed vegetation. We found that small changes in functional group composition led to rapid recovery of biomass production, however a recent history of grazing did not affect litter decomposition.

This research provides new insights into the diverse responses of different ecosystem processes in Mediterranean grasslands to shifts in species composition associated with land-use change, such as grazing cessation. We may conclude that in this ecosystem, with high dominance of annuals and hemicryptophytes, biomass production is a highly sensitive process which recovers within a relatively short time-frame (e.g. 3 years) after cessation of grazing. Conversely, due to the uniformity of chemical composition among the dominant functional groups which are taxonomically similar, and the fact that shifts in litter quality are due to lignin content, the rate of plant litter decomposition is highly stable on a time-scale of at least 30–40 years.

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