Original article

Effects of seasonal grazing and precipitation regime on the soil macroinvertebrates of a Mediterranean old-field

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ABSTRACT

Soil macroinvertebrate communities (SMC) are well known to influence major ecosystem processes, but relatively few investigations have examined the mechanisms and factors involved in SMC regulation. We conducted a factorial experiment with combinations of seasonal grazing by sheep and irrigation (simulating different precipitation regimes) to assess their effects on the SMC of a semiarid Mediterranean old-field. We also analyzed effects on plant species richness, total aboveground biomass, and litter. The data were collected in autumn and spring, the two favorable seasons for SMC and primary production in the region, and season was included as an additional random factor. Main results were: 1) Ungrazed plots accumulated more aboveground plant biomass and litter during spring, providing extra food for soil biota. However, grazing during autumn or spring did not affect SMC characteristics. 2) Reduction of inter-annual precipitation variability in autumn and spring increased the abundance of two decomposer taxa: Oligochaeta and Diplopoda. Additionally, if summer drought was reduced, plant species richness, litter and the abundance of Isopoda were increased. 3) Oligochaeta and Diplopoda increase their abundance in spring, particularly, the most abundant taxon (Oligochaeta). We conclude that inter- and intra-annual variability in precipitation is a key environmental factor for the decomposer soil fauna in Mediterranean ecosystems, modifying the physical characteristics of the soils (humidity, hardness, etc.), as well as affecting the amount or characteristics of plant biomass or litter. The respiration system of the macroinvertebrates (cutaneous, tracheal or branquial) and the capacity to migrate vertically into the soil may determine the decomposers' responses to precipitation.

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1. Introduction

Soil macroinvertebrate communities (SMC) are involved in key processes of terrestrial ecosystems, including soil bioturbation, organic matter turnover and decomposition, and nutrient cycling [4,7,16]. In turn, these are key determinants of ecosystem carbon storage and primary production [35]. SMC are also relevant for controlling soilborne diseases and pests in agroecosystems [6,35], although some soil macroinvertebrates are in fact pests for crops. Precipitation regime and aboveground herbivores can regulate SMC through changes induced in shoot/root ratios, plant living biomass and litter. Changes in the plant component may be physiological (alterations in both the production of plant secondary metabolites and foliage nutrient concentration, or increments in root N content)

or in community structure, which result in modifications of the nutritive potential of plant biomass [3]. Consequently, research on SMC regulation, i.e. SMC characteristics and on their ecological determinants (e.g. water availability, land use), is of central importance for understanding ecosystem processes [5,37].

Yet many community and functional ecology issues regarding SMC remain poorly understood. Indeed, the number of descriptive studies on all taxa comprising the SMC is low, and basic ecological characteristics of these communities as well as the response to ecological factors are not well known [14]. To our knowledge, field experiments carried out to date have focused on a limited set of taxa [10]. A few community-level studies have been developed under controlled conditions in micro- and mesocosms [5], showing the marked effects of SMC on ecosystem function.

We present here the results of a field experiment conducted in a semiarid Mediterranean old-field in central Spain. We controlled levels and seasonal occurrence of grazing and soil water to document their effects on SMC taxa and decomposer group structure. Five years after the treatments were established, we sampled the SMC. We asked three questions. First, is macroinvertebrate

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community structure affected by ungulate seasonal grazing? We hypothesized that ungulate grazing may modify the amount, species composition, and species richness of plants and litter input to soil [3,38]; in our study site, plant richness increases more rapidly in grazed than in ungrazed plots [23].

Secondly, we asked to what extent precipitation regime affects the structure of the SMC. Rebollo, Pérez-Camacho, Valencia & Gómez-Sal (2003) found in our study field that artificially increased soil water increases plant standing crop and net primary production. This suggests, from the SMC perspective, that soil macroinvertebrate decomposers can be indirectly influenced by water availability by effects on their food items. Apart from these indirect effects, soil water availability has been linked to the abundance and activities of SMC taxa in semiarid regions [25], and it has been proposed as a major factor in controlling litter decomposition [19,12] and CO_2 efflux from the soil [13,33]. Although the influence of water availability appears to be associated primarily with soil microbes and vegetation productivity [28], it can also be mediated by SMC to some extent when decomposer populations increase under favorable environmental conditions [29]. Furthermore, some macroinvertebrates that are highly sensitive to soil moisture such as earthworms are known to condition nutrient dynamics by affecting soil microbial communities and the processing of organic matter [6,22]. We predicted that greater water availability increases the abundance of decomposers.

The third question we asked is if the effects of grazing and precipitation regime on SMC vary among seasons (autumn and spring). Semiarid Mediterranean continental climate has a marked seasonality, with rains mainly in autumn and spring [2,32]. Some studies in Mediterranean regions have shown that the activity levels and the abundance of soil macroinvertebrate taxa increase in spring and decrease in autumn [29,25]. Hence, to better understand the role of the SMC in the ecosystem and of its regulation, our study has spanned the two growing seasons occurring in the region: autumn and spring. We predicted lesser activity and abundance of SMC in autumn.

2. Materials and methods

2.1. Site description

The study was carried out at the El Encín Experimental Farm (IMIDRA), located in Alcalá de Henares, Madrid, Spain (40°35′ N, 3°25′ W). Climate is semiarid continental Mediterranean, with a mean annual temperature of 13.1 °C and an annual precipitation of 410 mm. The main rainfall periods are autumn and spring. Precipitation is characterized by high year-to-year variation in timing and amount (inter-annual variability) and by a pronounced summer drought (intra-annual variability). The study site is at 565 masl on a flat Quaternary alluvial terrace. The soils have a sand and clay content of 31.8% and 26.4%, respectively, and an average pH of 8.1. The climax vegetation is an *Ulmus minor* Mill. forest, which has long been converted into arable farmland. Plant communities are currently dominated by winter annuals [26].

2.2. Experimental design and layout

A 0.5 ha old-field was set aside from cultivation in 1991. The experiment was established in September 1997 and consists of 18, 11.5 m × 14 m fenced rectangular plots, each separated from adjacent plots by a 2 m walkway. The plots were arranged into two blocks, each receiving nine randomly distributed treatments as factorial combinations of three sheep grazing treatments and three irrigation regime treatments (surrogate of precipitation). Sheep grazing treatments comprised 4 and 5 sheep per plot for a week in

late November (autumn grazing treatment) and between late April and early May (spring grazing treatment), respectively, because of the greater plant biomass in spring. These treatments correspond to mean stocking rates of 4 and 5 sheep ha^{-1} year^{-1}, respectively [23]. The control grazing treatment was non-grazing. The autumn-and-spring irrigation treatment ensured water availability at the most critical periods for germination and plant growth, respectively, reducing inter-annual precipitation variability. The all-year irrigation treatment also mitigated the effects of summer drought, reducing inter- and intra-annual precipitation variability. The time and amount of extra water added by irrigation depended largely on the precipitation of each year. The control irrigation treatment was non irrigation (natural levels of precipitation). Irrigation treatments were applied with sprinklers that ensured a homogeneous distribution; soil moisture was maintained at >20% by volume within the top 16 cm during the irrigation periods. Soil moisture was monitored using the Time Domain Reflectometry technique. Mean water addition to soil (irrigation + precipitation) per year recorded in the all-year and autumn-and-spring irrigation plots was 878 mm and 525 mm, respectively, during the last five years. Mean water per year collected in non-irrigated plots was 445 mm during the same period, therefore the all-year and autumn-and-spring irrigation represented a surplus of 97.3% and 18% of the yearly precipitation, respectively.

2.3. Sampling

Sampling was carried out in October 2002 and in March—April 2003, i.e. five years after the grazing and irrigation treatments were established. Both sampling periods took place just before the grazing treatments occurred, the first coincided with the period in which the winter annual plants germinate (autumn), and the second with the plant growing season (spring). Samples comprised 72 soil monoliths (four randomly located soil monoliths per plot) together with the aboveground vegetation. Each soil monolith had a surface area of 30 cm × 30 cm and a depth of 30 cm, and was collected using metal blades [1], and at a distance at least 1.5 m apart from the plot border to avoid edge effects. All soil macroinvertebrates greater than 2 mm long were manually collected (excluding macroinvertebrates in the litter layer) on site by sieving the soil through a 2 mm sieve and preserved in a solution of ethanol—formalin (3:1) [20]. Aboveground plant parts were also collected, and dead plant material (litter) was analyzed separately. No attempt to separate litter was made in autumn, as it was not possible to differentiate it from decaying but apparently still alive plant parts. In both sampling periods, visual estimations of percentage cover of aerial plant species were also made in each plot in nine fixed quadrants of 50 cm × 50 cm. Plant species richness (R) was obtained from these nine quadrats. Macroinvertebrate specimens were identified to class, order or family, and the number of individuals of each taxon in each plot was recorded. All plant material was dried prior to weighing.

2.4. Data analysis

The unit of analysis was the plot in order to avoid pseudoreplication. This means that data corresponding to subsamples taken in each plot (i.e. fauna and plant biomass data obtained from four soil monoliths, and plant species richness data obtained from nine fixed quadrats) were pooled before the analyses, rendering a total of 18 analysis units. This gave us six replicates for testing direct effects (grazing and irrigation regimes) and two replicates for analysing the grazing by irrigation interaction [27,24]. The abundance data of each macroinvertebrate taxon were analyzed with repeated-measures ANOVA using SPSS 11.5.1; the two seasons were

considered subjects (repeated-measures). Grazing and irrigation treatments were included as fixed factors (between-subjects). LSD multiple comparison tests were used to test for significant differences between means. With the exception of Diplopoda and Isopoda, data for all taxa met the assumptions required for repeated-measures ANOVA and were not transformed. Large numbers of zero values in the Diplopoda and Isopoda groups made transformations ineffective, so we adopted a compromise solution. We applied repeated-measures ANOVA on untransformed data and compared the results with those provided by Kruskal–Wallis nonparametric tests. Results from both analyses were similar and only those given by the repeated-measures ANOVA are presented. Litter data obtained in spring were analyzed with two-way ANOVA, with grazing and irrigation as main factors. Plant species richness and litter data were log10 transformed before analysis to attain normality and homogeneity of variances.

3. Results

3.1. Soil macroinvertebrate fauna

Twice as many macroinvertebrates were collected in spring as in autumn (1371 and 656, respectively), although the same 13 supraspecific taxa were found in both seasons (Table 1). Decomposers constituted most of the individuals collected both seasons (505 and 1248 in autumn and spring, respectively), mostly due to large numbers of Oligochaeta.

Repeated-measures ANOVA showed significant responses of several decomposer taxa to season and irrigation. Oligochaeta and Diplopoda were more abundant in spring, and in the irrigated plots of both autumn-and-spring and all-year irrigation treatments (Table 2). Isopoda were more abundant in all-year irrigated plots only. A significant interaction between season and irrigation for Oligochaeta indicated that reducing inter- and intra-annual precipitation variability had a positive effect on the abundance of this taxon in spring but not in autumn (Fig. 1). Grazing treatments did not cause any significant effect.

3.2. Vegetation

A total of 85 plant species were present in the plots, 68 annuals (57 forbs and 11 grasses) and 17 perennials (13 forbs and 4 grasses).

Table 1

Mean density (individuals m^{-2}, ±1SD in brackets, $n = 18$) of soil macroinvertebrate taxa in the two sampled seasons. Data are given according to taxa and decomposer group.

	Autumn 2002	Spring 2003
Coleoptera		
Tenebrionidae	1.7 (2.3)	2.6 (4.7)
Elateridae	2.00 (3.7)	1.1 (1.8)
Chrysomelidae	0	0.69 (1.5)
Curculionidae	1.4 (2.5)	2.2 (5.0)
Melolonthidae	1.2 (2.1)	0.13 (0.62)
Staphylinidae	8.2 (6.3)	1.7 (2.5)
Carabidae	0.15 (0.65)	3.2 (3.6)
Orthoptera		
Grillidae	0.30 (0.9)	0.13 (0.6)
Chilopoda	5.8 (4.8)	7.2 (5.7)
Decomposers	68.70 (42.4)	189.96 (86.6)
Oligochaeta	48.30 (29.5)	166.51 (70.7)
Diplopoda	2.62 (4.9)	12.34 (14.7)
Isopoda	8.95 (15.8)	10.80 (15.6)
Diptera larvae	8.79 (29.7)	0.30 (0.89)

Table 2

Mean values for the abundance (individuals per plot) of the three out of 13 soil macroinvertebrate taxa that were affected by season and irrigation. Significant interactions between these variables for Oligochaeta can be seen in Fig. 1. For each taxa, different letters in the mean of Grazing (G) and Irrigation (I) treatments indicate significant differences with the LSD test ($P < 0.05$). Significant p-values in bold.

Taxa	Source of variance	Mean	df	Mean square	F value	P value
Oligochaeta	Season (S)		1	16298.78	91.14	**0.000**
	Autumn	17.40 b				
	Spring	60.00 a				
	Grazing (G)		2	111.58	0.568	0.58
	None	40.75				
	Autumn (AU)	40.08				
	Spring (SP)	35.16				
	Irrigation (I)		2	2776.083	14.13	**0.002**
	None	21.25 b				
	AU-and-SP	49.33 a				
	All-year	45.41 a				
	S × G		2	253.86	1.42	0.29
	S × I		2	839.69	4.69	**0.04**
	S × G × I		4	174.65	0.97	0.46
	G × I		4	225.54	1.14	0.39
Diplopoda	Season		1	110.25	9.38	**0.014**
	Autumn	0.94 b				
	Spring	4.40 a				
	Grazing		2	6.19	0.60	0.56
	None	1.91				
	Autumn	3.33				
	Spring	2.83				
	Irrigation		2	63.44	6.15	**0.02**
	None	0.08 b				
	AU-and-SP	3.60 a				
	All-year	4.41 a				
	S × G		2	25.58	2.17	0.16
	S × I		2	37.00	3.15	0.09
	S × G × I		4	9.33	0.79	0.55
	G × I		4	7.27	0.70	0.60
Isopoda[a]	Season		1	0.092	1.57	0.24
	Autumn	3.22				
	Spring	3.89				
	Grazing		2	0.069	2.55	0.13
	None	5.58				
	Autumn	3.66				
	Spring	1.42				
	Irrigation		2	0.861	31.83	**0.000**
	None	0.16 b				
	AU-and-SP	1.70 b				
	All-year	8.83 a				
	S × G		2	0.063	1.07	0.38
	S × I		2	0.034	0.58	0.57
	S × G × I		4	0.13	2.26	0.14
	G × I		4	0.067	2.48	0.11

[a] Mean square values correspond to transformed variable ($\log_{10} (x + 1)$), mean values are not transformed.
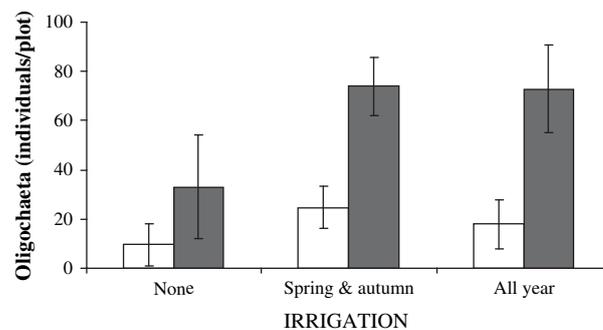
Fig. 1. Interaction between season and irrigation treatments for abundance of Oligochaeta. Autumn and spring samples are indicated by white and black columns, respectively. Vertical bars are standard errors of means.

Annual plant species were the most variable component of the plant community throughout the year, as indicated by their cover (12% in autumn *vs.* 64% in spring). On the other hand, perennials exhibited similar cover in both seasons (23% in autumn *vs.* 27% in spring). Repeated-measures ANOVA on estimates of plant richness showed direct effects of irrigation regime and season, with higher plant species richness in plots irrigated all year ($R_{\text{non irrigation}} = 13.18$; $R_{\text{autumn-and-spring irrigation}} = 13.54$; $R_{\text{all-year irrigation}} = 20.88$; $F = 5.16$, $P = 0.032$), and also in spring ($R_{\text{autumn}} = 8.14$; $R_{\text{spring}} = 29.55$; $F = 485.32$, $P < 0.0001$). The interaction between these two factors indicated that the positive effects of adding water all year increase plant richness in autumn ($F = 17.97$, $P < 0.001$). No effects of grazing were found for plant species richness.

No effects on above plant biomass were found for irrigation, but more biomass was recorded in spring than in autumn (698.97 g m^{-2} vs. 90.36 g m^{-2}, respectively; $F = 180.18$, $P < 0.0001$, repeated-measures ANOVA). An interaction between season and grazing indicated that the increase of plant biomass in spring was greater for ungrazed plots ($F = 13.36$, $P = 0.001$). The separation of dead plant material performed in spring allowed to expand this result. Litter increased 29% in non-grazed plots, and 38% in all-year irrigated plots ($F = 3.97$, $P < 0.045$ and $F = 4.349$, $P = 0.036$).

4. Discussion

Our first result is that seasonal grazing did not have any detectable effect on the SMC after five years, despite the fact that it did affect several vegetation characteristics. Specifically, both total aboveground plant biomass and litter increased in non-grazed plots in spring [cf. 17,27], which could have affected soil macroinvertebrates due to the extra amounts of food occurring in these circumstances. Several studies carried out in other climatic conditions found that the abundance and/or activity of decomposers increased with the amount or quality of the dead plant material [e.g. 15,34,36,40]. Even so, decomposers (the most abundant trophic group in our SMC: 77% and 91% of specimens in autumn and spring, respectively) did not respond to the grazing-induced differences of plant material availability we observed in spring, which can be interpreted as reflecting that food was not limiting soil macroinvertebrate fauna in our study site [21]. Additionally, our data also allow us to reject the hypothesis that grazing indirectly determines SMC characteristics through effects caused on plant richness, particularly because grazing did not cause any significant change in plant richness or in SMC characteristics. Nevertheless, it should be noted that this study was carried out only five years after the treatments commenced; Pérez-Camacho (2004) observed that albeit sheep grazing does not significantly affect plant species richness in this early successional plant community, the trends of vegetation during these five years indicate that plant richness is increasing more rapidly in grazed than in ungrazed plots. Therefore, we cannot discount the possibility that grazing indirectly determines SMC characteristics through effects caused on plant richness in later stages of secondary succession.

A second result is that three of the four decomposer taxa (Isopoda, Oligochaeta and Diplopoda) increased their abundance in irrigated plots which might be due to direct and/or indirect effects of water availability. In the case of Isopods, they were more abundant in the all-year irrigated plots, where there was also more litter mass, at least in spring; when we were able to quantify litter. However, considering that litter was also higher in ungrazed plots, and that there were no observable effects of grazing on SMC characteristics (see above), it seems unlikely that litter was a major determinant of these effects. Another

possibility is that this response of isopods was associated with variations in plant richness across the plots, given that a larger variety of plants increases the likelihood of having species that produce high quality food. The plots exhibiting higher isopod abundance (i.e. the all-year irrigated plots) have also been reported to have higher plant richness, both during the study period and in earlier years (as documented by Rebollo, Pérez-Camacho, Valencia, Gómez-Sal, 2003). Additionally, a given plant species may produce a litter with a higher quality when supplied abundantly with water. Another plausible explanation for the effects of soil water on Isopods is that they were direct and not mediated by vegetation. As for Oligochaetes and Diplopods, both increased their abundance in the treatments with all-year and autumn-and-spring irrigation. However, since there were not parallel increases of litter and plant species richness in the autumn-and-spring irrigated plots, it seems clearer that the effects of water on both groups were mainly direct in this case.

Overall, the observed effects of irrigation on decomposers point to precipitation regime as a key determinant of the abundance of these groups [25,29]. As soil macroinvertebrates depend on water availability from a physiological point of view, a more stable environment in terms of humidity could increase decomposer survival and reproduction rates [11,9]. Less variable humidity could maintain the microbial biomass on the litter, a potentially limiting factor for Oligochaeta [30]. The three groups of decomposers responding to irrigation are hygrophilous and relatively long-lived. Isopods (with branquial respiration and low capacity to migrate vertically into the soil) were only abundant in all-year irrigated plots; i.e. when inter- and intra-annual precipitation variability was reduced. These crustaceans, due to their respiration system, have a low capacity to regulate body humidity, which might be related with the observation that they were only abundant when irrigation eliminated summer drought and high soil moisture was kept through the year. This suggests that the direct water effects were crucial in this taxon. However, oligochaetes (with cutaneous respiration and high capacity to migrate vertically into the soil) and diplopods (with tracheal respiration and with a lower digging capacity than oligochaetes), increased in both autumn-and-spring irrigated plots and in all-year irrigated plots. Thus, both groups increased when inter-annual precipitation variability was reduced and high soil moisture in spring and autumn was assured. All in all, our data suggest that inter- and intra-annual variability in precipitation is a key environmental condition for the decomposer soil fauna in Mediterranean ecosystems, with each group responding differently to this factor depending on its respiration system and capacity to migrate vertically into the soil.

A third set of results shows the reaction of the system to seasonal variation. The response of the SMC consists in an increase in the abundance of two decomposer taxa (Oligochaeta and Diplopoda) in spring. Similar increments of decomposer density during benign seasons have been reported by Dangerfield (1997) [8] and Sharon, Degani, & Warburg (2001) [31]. As expected in the markedly seasonal continental Mediterranean climate, plant species richness and total aboveground plant biomass increased in spring. We interpret that seasonal variation of soil fauna and vegetation could be either functionally linked or represent parallel responses to the more favorable environmental conditions prevailing in spring. We think that the catch of oligochaetes and diplopods decreased in autumn due to vertical migration into the soil (deeper than 30 cm from the soil surface), probably caused by the increase of temperature during summer–autumn or by an endogenous rhythm. Peterson, Hendrix, Haydu, Graham & Quideau (2001) found that earthworms became active when precipitation provided adequate soil moisture in a southern California chaparral community. In our study, the low number of these groups (Oligochaetes

and Diplopods) in autumn was independent of the occurrence of the summer drought. Contrarily, Romanya, Casals, Cortina, Bottner, Couteaux & Vallejo, (2000) reported that the CO_2 efflux from the soil of a semiarid Mediterranean forest increased after irrigation in summer, and argued that this increment was attributable to the high activity of earthworms. The increased abundance in spring was not significant in oligochaeta in none irrigated plots. However, Fig. 1 shows a difference in oligochaetes abundance between autumn and spring. Further research is necessary to asses whether such difference between irrigation treatments has a biological explanation. By contrast with oligochaetes and diplopods, the low digging capacity of the isopods allowed us to detect its abundance in the two seasons with the sampling method used in this study.

We conclude that soil macroinvertebrates, in particular de-composers, react to the reduction of the inter-annual variability of autumn and spring precipitations (Oligochaeta and Diplopoda) and to the elimination of summer drought (Isopoda). This is an important observation when considering predicted intensification of aridity in the Mediterranean basin during warm seasons [39,18], and the implication of SMC in ecosystem processes such as carbon storage and primary production. Our study pinpoints the urgency for further research on SMC regulation.

Acknowledgments

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