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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.

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