

Some structural and functional characteristics of a soil nematode community from a Mediterranean grassland

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ABSTRACT. This paper refers to the effects of large-scale seasonal fluctuations as well as experimentally induced small-scale variations of soil temperature and moisture on the structural and functional characteristics of a soil nematode community from a Greek Mediterranean grassland. Two levels of soil temperature, with a mean difference of 1.4° C, and two levels of moisture (2.3% difference in water content) were created. The experiment lasted for a six-month period (from July to December).

All nematode community parameters vary significantly with season, with the exception of the environmental constant (C_{env}), which reflects the intensity of competition. The Maturity Index (MI) is affected only by seasonally fluctuating soil conditions, while the Plant Parasite Index (PPI) is affected only by the small-scale differences in soil temperature and moisture. The high value (1.48) of bacterivorous to fungivorous ratio (B/F) indicates mainly bacterial mediated decomposition, resulting in good soil fertility. The B/F ratio is affected both by large and small-scale changes in soil conditions. Diversity and richness show dependence on seasonal variations as well as on small changes in temperature, while no effect of moisture is recorded. The correlations between nematode community parameters, microflora parameters and soil nitrogen pools show independence of nematode parameters from soil N-pools ($N_{organic}$ and $N_{inorganic}$) and parameters relating to microflora, as well as strong dependence on microbially-bounded nitrogen.

KEY WORDS : climatic change, Mediterranean-type ecosystems, functional groups, community structure

INTRODUCTION

Organic matter transformation and nutrient turnover in terrestrial ecosystems involve a large array of soil organisms (SWIFT et al., 1979). Among them, nematodes play a quite important role in determining soil functioning (EKSCHMITT et al., 2001), since the major part of nutrient interchange in soils is due to the activity of microbial-feeding nematodes (GRIFFITHS et al., 1995). Nematofauna has been the target group of different studies aiming to seek effects associated with changes in organic matter input (ARMENDARIZ & ARPIN, 1996 ; ARMENDARIZ et al., 1996 ; FU et al., 2000 ; AKHTAR, 2000), modified microbial productivity (SOHLENIUS, 1990 ; GRIFFITHS et al., 1994), soil pollution (RUESS et al., 1993 ; KORTHALS et al., 1996) etc. Moreover, community diversity indices together with indices such as the ratio of bacterivorous to fungivorous nematodes (B/F), the plant parasite (PPI) and the maturity (MI) indices, accounting for both quantitative and qualitative ecological aspects of nematode communities (BONGERS, 1990, PORAZINSKA et al., 1999), have been extensively used for bioindication purposes, relating to the degree of human intervention in agricultural systems (FRECKMAN & ETTEMA, 1993), the soil quality (YEATES & VAN DER MEULEN, 1996) and the recovery after perturbation (URZELAI et al., 2000).

In the present work, we used the above mentioned parameters of a nematode community in order to assess the impact of climatic changes on soil dynamics. Indeed,

data regarding the effects of the foreseen global climatic changes on soil ecosystem components, especially at a local scale, are missing (BAKONYI & NAGY, 2000). Our work was carried out in a Mediterranean grassland and constitutes a part of our contribution to an EU-project, entitled «Diversity Effects in Grassland Ecosystems of Europe (DEGREE)» focusing on climatic change effects on soil nematodes, microbial processes and nutrient transformation patterns. The soil microclimate at each European grassland included in this project was experimentally manipulated, according to a common design for all partner countries. The microclimatic changes obtained by temperature and moisture manipulations in our field site, were of a small-scale and could be considered similar to those predicted by some climate change scenarios for the Mediterranean region (OSBORNE & WOODWARD, 2001). The effects of those small-scale microclimatic changes on the structural and functional characteristics of the nematode community were explored and compared to the effects of the seasonal changes of temperature and humidity. These latter climatic changes were considered of a large-scale, since the mediterranean climate exhibits a clear-cut seasonality, characterised by hot-dry summers and mild-wet winters. Furthermore, though a full list of the nematode taxa recorded in our field site has already been given in NAGY & STAMOU (1998), information associating the nematode community characteristics with soil biochemical parameters is missing. Thus, in this paper we also tried to correlate the nematode community param-

ters with parameters relating to soil microflora and nitrogen pools.

MATERIAL AND METHODS

Site description

The research site lies at an altitude of 210-215m, 55km south-east of Thessaloniki (40° 20' N latitude, 23° 12' E longitude), and has a south-easterly orientation. It lies on a limestone block of Kimmeridgian-Portlandian age, surrounded by Miocene-Pliocene deposits. The soil is shallow, discontinuous and generally not more than 10 cm deep. The profiles are classified as lithic leptosols (FAO) with a gravely and stony clay-loam texture. Soil particles bigger than 2 mm represent 69.46% of fresh weight of soil. Soil organic carbon varies from 4.01 to 5.32% and total amount of organic matter from 6.89 to 9.18% dry matter of soil. The pH (H₂O) and pH (KCL) is 7.7 and 6.6 respectively.

According to previous data (DIAMANTOPOULOS et al., 1996), the climate of the region is characterized as Mediterranean with small amounts of rainfall during the hot summer months. The dry period lasts from mid June to mid October. Mean annual air temperature and precipitation is 16.03° C and 435.53 mm, respectively.

Experimental design and sampling

The experiment lasted for a six-month period, from July to December, during which soil microclimate was manipulated in 12 adjacent field plots (1x1m), covered by the grasses *Stipa bromoides* (L) Dorf., *Aegilops geniculata* (Roth.), *Aegilops triuncialis* (L.), *Avena sterilis* (L.), *Brachypodium distachyum* (L.) Beauv., *Bromus tectorum* (L.) and *Dactylis glomerata* (L.) among others (DALAKA 2001). In order to modify soil temperature conditions, we used vertical windshields and horizontal transparent greenhouse roofs (cutting off also precipitation). Soil water content was manipulated by weekly irrigation. The experimental set-up of the whole DEGREE project, common for all partner countries, aimed at obtaining different combinations of soil temperature and water content in the field plots, and superimposing them on the local seasonal variations of these climatic variables. A detailed description of DEGREE's experimental design is given in EKSCHMITT et al. (1999) as well as in BAKONYI & NAGY (2000).

The within plots microclimatic conditions were quantified by measuring soil temperature and soil water content on a monthly basis for the 6-month experimental period. Temperature was measured by min-max thermometers placed 5 cm below surface and left in the field plots for the whole month, while soil water content at each plot was determined by drying 5g of soil at 104° C for 24h and estimating evaporation loss.

Finally, the experimental manipulations of microclimate resulted in a full factorial scheme of two temperature (warm, cold) x two moisture (wet, dry) levels. Each treatment, i.e. each temperature x moisture combination comprised three plots. Average temperature for the whole sampling period was 23.6° C and 25° C in cold and warm plots respectively. A t-paired test showed that this differ-

ence (1.4° C on average) was statistically significant ($p < 0.05$). Regarding moisture levels, the average difference between dry and wet plots was 2.3% d.w., and this difference was highly significant ($p < 0.01$). Thus, although the experimental modifications of moisture and temperature were of small scale, they were not masked by the seasonal variations of those variables, which were of a larger scale.

Soil sampling was conducted on a monthly basis for the 6-month experimental period. On each sampling occasion, three random soil cores were taken from the top 8 cm of soil of each field plot with a steel cylinder (7 cm diameter). The three cores from each plot were unified in one composite sample, packed in polythene bags, transported to the laboratory and stored at 4° C for further analyses. The composite samples taken from plots of each treatment were grouped as replicates. In total, 12 composite samples (3 replicate plots x 4 treatments) were taken each month.

Nematode analyses

A portion of 100g fresh weight was separated from the composite soil sample from each plot for the purposes of nematode extraction. Nematodes were isolated using Cobb's sieving and decanting method (S'JACOB & VAN BEZOOIJEN 1984). Nematode extraction through a double layer of cotton wool filters lasted for two days. After total numbers of specimens were counted, nematodes were fixed in 4% formalin. Expert assistance was offered by the Hungarian partners of DEGREE for the identification of nematodes to genus level and their classification to feeding types following YEATES et al. (1993). The group of plant-feeders was separated into epidermal and root-air feeding nematodes and plant parasites.

Maturity Index (MI) and Plant Parasite Index (PPI) were calculated according to BONGERS (1990), while diversity (Shannon-Weaver index) together with evenness and richness were calculated according to PIELOU (1975). The assessment of genera biomass was based on average body dimensions and was calculated via the formula of ANDRASSY (1984). For the assessment of nematode activity, a model developed by EKSCHMITT et al. (1999) was used. For the construction of the model, data concerning abundance of nematode genera and body dimensions were used. Activity was expressed as released carbon mass per hour and g dry mass soil.

The environmental constant (C_{env}), which reflects the intensity of competition, was estimated from the rank/abundance plots, as proposed by MAY (1975) and MOTOMURA (1932). In a geometric series, the abundance of genera ranked from most to least abundant is:

$$n_i = N C_{env} (1 - C_{env})^{i-1} [1 - (1 - C_{env})^s]^{-1}$$

where n_i = nb. of individuals in the i th genus, N = total nb. of individuals, s = total nb. of genera and C_{env} = environmental constant.

Biochemical analyses

Ergosterol was used as an index of active fungal biomass. It was estimated from 5 g fresh mass soil by means of quantitative HPLC analysis after ethanol extraction (DJAJAKIRANA et al., 1996). For the determination of soil

microbial-C the fumigation-incubation method of JENKINSON & POWLSON (1976), with the modifications recommended by ROSS (1990) for grassland soils, was used. N-microbial was measured by the method of BROOKES et al. (1985). Soil respiration was measured by absorption in alkali (1 N KOH) followed by titration with 0.1 N HCL after incubation for three days at 10° C (ISEMEYER 1952). Bacterial substrate utilization, which reflects the functional diversity of the bacterial community, was estimated in Gram-negative plates by a modified BIOLOG method (VAHJEN et al., 1995). Inorganic-N (NO₃⁻ and NH₄⁺) was determined by distillation, while organic-N was assessed by the Kjeldahl method (ALLEN, 1974).

RESULTS

In total 39 nematode genera with an overall mean density of about 16 ind.g⁻¹ were sampled during the six-month period. In Table 1 mean values of different nematode community parameters are presented. Parameters related to phenology and activity exhibited the higher var-

iation (from 55 to 69%), whereas the opposite held for parameters related to diversity.

TABLE 1

Overall mean values of some structural and functional characteristics of the nematode community as well as some indices relating to life history strategies. Values for 95% confidence limits, minimum, maximum and estimates for the coefficient of variation are also given

| Variable | Mean | Min. | Max. | CV% |
|--|------------|-------|-------|-------|
| Abundance (ind./g d.w.) | 16.00±2.08 | 3.01 | 53.50 | 55.23 |
| Richness (nb. genera) | 21.26±0.70 | 16.00 | 27.00 | 14.11 |
| Diversity | 2.56±0.04 | 2.21 | 2.97 | 7.03 |
| Evenness | 83.93±0.92 | 75.41 | 92.93 | 4.64 |
| C _{env} | 0.21±0.01 | 0.09 | 0.59 | 33.00 |
| Biomass (µg f. w./g d.w.) | 12.18±1.83 | 2.77 | 41.49 | 63.79 |
| Activity (ng CO ₂ -C/g d.w.* h) | 4.57±0.74 | 0.75 | 17.09 | 68.92 |
| B/F | 1.48±0.18 | 0.18 | 3.69 | 53.89 |
| MI | 2.33±0.05 | 2.00 | 2.92 | 7.72 |
| PPI | 2.47±0.04 | 2.11 | 2.94 | 6.88 |

TABLE 2

Percentage contribution of the different nematode functional groups to abundance, richness, biomass, activity, MI and PPI.

| Variables | Bacterivorous | Fungivorous | Root feeders | Plant Parasites | Predators | Omnivorous |
|--|---------------|-------------|--------------|-----------------|-----------|------------|
| Abundance (ind./g d.w.) | 31.36 | 27.37 | 17.35 | 16.52 | 0.56 | 6.87 |
| Richness (nb. genera) | 32.07 | 21.67 | 9.39 | 20.44 | 2.55 | 13.87 |
| Biomass (µg f.w/gd.w.) | 18.95 | 12.06 | 2.22 | 5.82 | 1.10 | 59.82 |
| Activity (ngCO ₂ -C/g d.w. * h) | 27.00 | 17.69 | 4.73 | 9.20 | 1.05 | 40.32 |
| MI | 41.40 | 37.75 | | | 1.25 | 19.55 |
| PPI | | | 41.63 | 58.19 | | |

TABLE 3

Statistically significant effects of seasonal large-scale fluctuation and experimentally created small-scale variation in soil temperature and moisture conditions on nematode community parameters.

| Variables | Season | Moisture | Temperature | Interactive effect |
|--|--------|----------|-------------|--------------------|
| Abundance (ind./g d.w.) | 0.01 | | | 0.00 |
| Biomass (µg f.w./g d.w.) | 0.05 | 0.01 | 0.01 | 0.01 |
| Diversity | 0.05 | | 0.00 | |
| Richness (nb. genera) | 0.01 | | 0.05 | |
| Activity (ngCO ₂ -C/g d.w. * h) | 0.01 | | | 0.05 |
| C _{env} | | 0.05 | 0.00 | 0.05 |
| MI | 0.00 | | | |
| PPI | | 0.00 | | 0.00 |
| B/F | 0.05 | | | 0.00 |

In Table 2, the percentage contribution of the different feeding groups to nematode biomass, activity, richness, density, MI and PPI is displayed. Omnivorous nematodes contributed most to biomass and activity, whereas their contribution to MI value was quite important. Among the remaining groups, bacterivorous and fungivorous nematodes contributed more to total density and richness followed by plant-parasite and root-hair feeders. Finally, predacious nematodes had the lowest contribution to all community parameters.

In order to explore the effect of the large-scale seasonal changes of soil temperature and moisture as well as the

small-scale effect of our experimental manipulations on the nematode community, we analysed data from the whole sampling period by a Two-way ANOVA. The experimental temperature and moisture levels were the grouping variables, while the month of sampling, which accounts for the effect of seasonality, was the blocking one. The seasonal effect was significant for all parameters except C_{env} and PPI (Table 3). Higher values for nematode abundance, biomass and activity occurred in September in dry-cold samples (Fig. 1). The ratio B/F displayed a significant temporal pattern and was significantly affected by small-scale differences in soil temperature and moisture (Table 3, Fig. 2). Bacterivorous

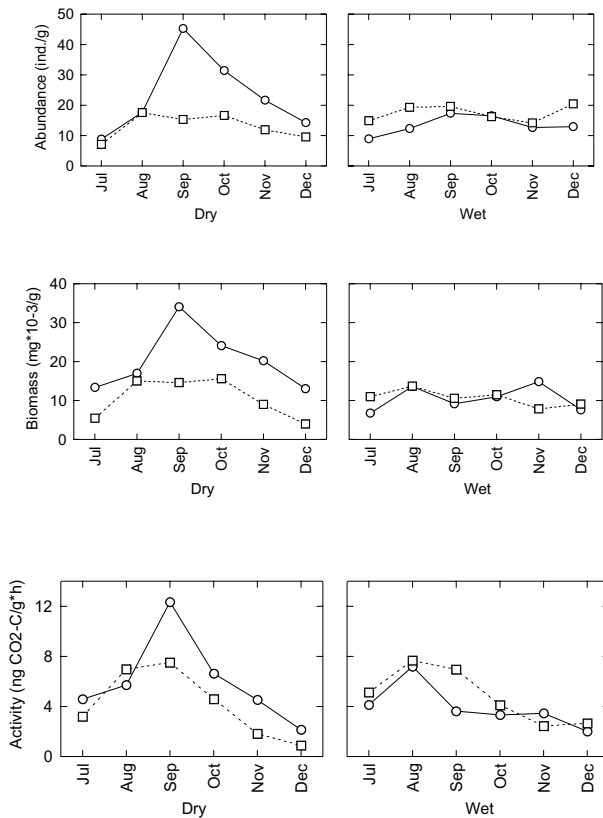


Fig. 1. – Abundance, biomass and activity of nematodes in relation to time and moisture conditions. Circles and squares correspond to cold and warm samples respectively.

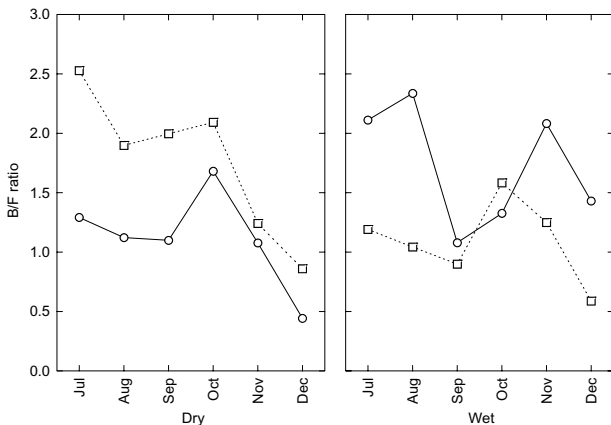


Fig. 2. – Ratio bacterivorous to fungivorous nematodes in dry and wet samples plotted against time. Circles and squares correspond to cold and warm samples respectively.

nematodes dominated over fungivorous during almost the whole sampling period especially in dry-warm and in wet-cold samples. Values of C_{env} were controlled by small-scale changes in temperature and moisture. Higher C_{env} values were recorded in wet than in dry and in warm than in cold samples (Table 3, Fig. 3). For PPI, the independent effect of small-scale changes in moisture as well as the interactive effect of temperature x moisture were highly significant (Table 3, Fig. 4). Higher PPI values were recorded in wet than in dry and in dry-warm than in dry-cold samples. MI was the only parameter that exhib-

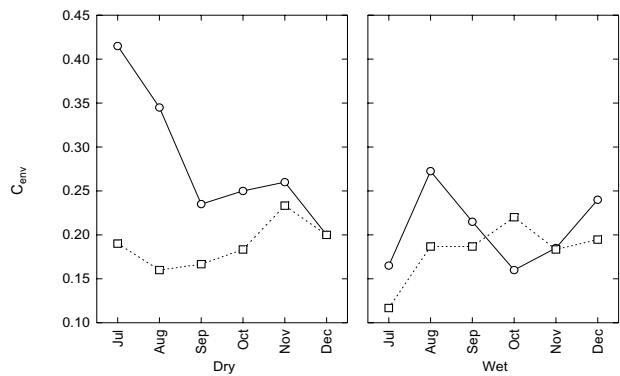


Fig. 3. – Estimates of the environmental constant in dry and wet samples plotted against time. Circles and squares correspond to cold and warm samples respectively.

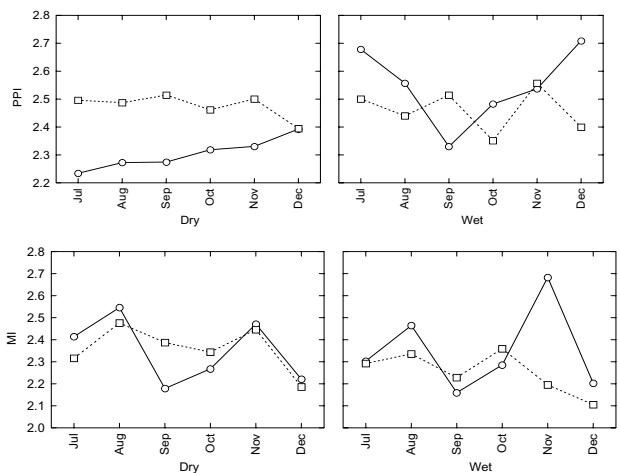


Fig. 4. – PPI and MI values in dry and wet samples plotted against time. Circles and squares correspond to cold and warm samples respectively.

ited only seasonal fluctuations with higher values in August and November (Table 3, Fig. 4). For richness and diversity, beyond the seasonal effect, the independent effect of small-scale differences in temperature was also significant. Higher values occurred in the middle of the sampling period in warm samples (Table 3, Fig. 5).

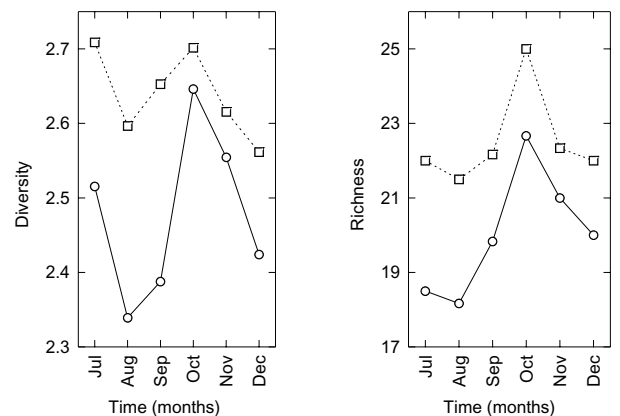


Fig. 5. – Shannon diversity and Richness plotted against time. Circles and squares correspond to cold and warm samples respectively.

No correlation between nematode community parameters and parameters associated with soil nitrogen pools was revealed (Table 4). Among microbial community

parameters, only N-microbial was correlated positively with nematode abundance, richness, biomass and activity.

TABLE 4

Correlation of nematode community parameters with parameters relating to soil microflora and nitrogen pools. Only significant values are figured.

| Variables | CO ₂ (mgC/g d.w. * h) | Biolog (Ext.650/g d.w.) | C-mic (mgC/g d.w.) | N-mic (mgN/g d.w.) | Ergoster. (µg/g d.w.) | N-NO ₃ (mgN/g d.w.) | N-NH ₄ (mgN/g d.w.) | N-org (mgN/g d.w.) |
|--|-------------------------------------|----------------------------|-----------------------|-----------------------|--------------------------|-----------------------------------|-----------------------------------|-----------------------|
| Abundance (ind./g d.w.) | | | 0.34 | 0.50 | | | | |
| Richness (nb. genera) | | -0.24 | | 0.31 | | | | |
| Diversity | | | | | | | | |
| MI | | | | | -0.26 | | | |
| PPI | | | | | | | | |
| Biomass (µg f.w./g d.w.) | | | | 0.45 | | | | |
| Activity (ngCO ₂ -C/g d.w. * h) | 0.37 | | | 0.33 | | | | |
| C _{env} | | | | | | | | |

DISCUSSION

The number of nematode genera recorded in the mediterranean grassland of our study is comparable with that of other European grasslands (COOK et al., 1992 ; FRECKMAN & ETTEMA, 1993 ; HANEL, 1996 ; BONGERS, 1998 ; BONGERS et al., 1998 ; NAGY, 1998), while nematode density is much lower than that recorded in Hungarian and Germany grasslands subject to similar experimental treatments (NAGY 1998, BONGERS et al., 1998). MI is lower and PPI is similar to those recorded in a Spanish Mediterranean grassland (URZELAI et al., 2000), while they are lower than those recorded in Australian and New Zealand soils (YEATES, 1996 ; YEATES & VAN DER MEULEN, 1996). Concerning diversity, its value is comparable to data reported by FRECKMAN & ETTEMA (1993) ; YEATES (1996) and URZELAI et al. (2000).

The composition of nematode community is typical of a dry mediterranean soil. As in Spanish mediterranean grasslands (URZELAI et al., 2000), predators represented a small proportion of the community. Bacterivorus and fungivorus nematodes had a good contribution to overall density, a feature commonly shared by nematode communities from dry soils (GRIFFITHS et al., 1995). Contrary to coniferous forests where this ratio is much lower than unit (DE GOEDE et al., 1993), the mean value of the B/F ratio in our site showed bacterial predominance, probably reflecting good soil fertility (POPOVICI & CIOBANU, 2000). Omnivorous feeders made a good contribution to biomass, activity and MI. Obviously, it is due to weighty persisters with high metabolic rate.

Concerning the effects of seasonality, most nematode indices exhibited temporal fluctuations. This is in agreement with data referring to Netherlands grasslands (VERSCHOOR et al., 2001). However, as with data from a semi-arid zone in West-Africa (PATE et al., 2000), crucial parameters regarding the structure of the nematode community remained rather invariable in time. Indeed, our results showed temporal constancy of C_{env} and slight temporal variations of MI (in the range 2.20-2.47). Following PORAZINSKA et al. (1999) and BONGERS & FERRIS (1999) we can infer that presumably, large seasonal variations of soil temperature and moisture do not stimulate microbial

activity and consequently no changes either in dominance or in the ratio persisters/opportunists occur.

The effect of the experimentally created small-scale changes in soil temperature and moisture was variable. Moisture manipulations proved inadequate to induce significant changes in MI. This is opposite to suggestions of PORAZINSKA et al. (1998) for positive correlation between nematode MI and irrigation levels. By contrast, C_{env} was significantly affected by such differences. Thus, this parameter proved efficient for indicating effects of small-scale microclimatic changes, analogous to those of climate change scenarios. Microclimatic manipulations significantly affected most other parameters. The temperature effect on nematode community appeared much more pronounced in dry than in wet plots. In dry-cold samples higher values of nematode abundance, biomass and respiration were recorded accompanied by low C_{env} values. Interpreted in terms of competition, these latter values indicate non-effective exploitation of resources. Taking into account that under these conditions PPI values are lower, it is inferred that increased phenological and activity parameters in dry-cold samples result from increased abundance of all nematode groups except persister plant feeding nematodes. Finally, concerning diversity, it is remarkable that beside temporal variation, diversity components are sensitive also to small-scale changes in temperature, a fact that was also reported by BAKONYI & NAGY (2000) for Hungarian soil nematodes. PATE et al. (2000) argued that changes in diversity parameters might reflect changes in ecological resilience related to the quality of soil conditions. Thus, we may infer that in our study site most favorable temperature conditions for resilience occurred in the middle of the sampling period in warm plots.

Small-scale changes in temperature and moisture also influenced the ratio B/F and consequently the outcome of the decomposition processes (WASILEWSKA, 1979 ; HENDRIX et al., 1986). Bacterial feeders dominated over fungal feeders in samples from dry-warm and wet-cold plots. Following PORAZINSKA et al. (1999) the dominance of bacterial feeders might be related to the quick turnover of the available organic matter in these samples. Moreover, changing soil conditions result in a switch to a fungal pathway probably accompanied by slow rate of decompo-

sition. In dry-warm samples higher PPI values were also recorded. Changes in PPI relate to changes in the soil nutritional status following modifications in the dynamics of vegetation (BONGERS *et al.*, 1997). The higher PPI values in dry-warm samples compared to dry-cold ones could be probably attributed to the development of more diverse or more favorable, in terms of nutrients, ground vegetation (VERSCHOOR *et al.*, 2001).

Analysing DEGREE's data from a geographical-climatic cross-gradient (from Greece to Sweden), EKSCHMITT *et al.* (2001) reported significant correlation between nematode abundance, biomass, activity and soil nitrogen pools. This is not the case with data from the Mediterranean grassland of our study. Furthermore, EKSCHMITT *et al.* (2001) reported richness as the only nematode parameter that was correlated with soil microflora parameters. Again, this fact is not supported by our results. By contrast, this paper shows a remarkable correlation between N-microbial and the majority of the nematofauna parameters such as biomass, density, activity and richness. Moreover, it shows no effect of the microflora characteristics (biolog, ergosterol) on nematode community. Non correlation between microbivorous nematodes and microflora is often recorded (WARDLE *et al.* 1995) and it is generally attributed to non-linear trophic interactions (ETTEMA *et al.* 1999). According to ANDERSSON (1995), linear trophic synchronization follows environmental disturbances. If this holds true, we may infer that the experimentally induced changes in soil temperature and moisture conditions cannot be considered serious disturbance for the Mediterranean grassland. Besides, previous studies (STAMOU 1998) showed limited significance of much more pronounced disturbances, such as fire and overgrazing on the structure and functioning of soil biota in Mediterranean areas.

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