

Colonization patterns of decomposing litter in a maquis ecosystem

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Abstract

The arthropod colonization patterns in the decomposing litter of a *Quercus coccifera* formation in northern Greece was studied by using litter bags of different mesh sizes. No difference was recorded between the two litter bag sets used, with respect to the total dry mass loss, which did not exceed 40 % after two years. Changes in the numbers of arthropods in the upper litter layers parallel the seasonal fluctuations of the abiotic parameters. Temperature was found to control mainly oribatid numbers, while numbers of Collembola and the rest of the arthropods studied are influenced by both litter water content and temperature. Seasonality prevents the establishment of a resident arthropod fauna in the litter bags during the early decomposition stages. Differences in the experimental treatment of litter in the two experiments are also discussed.

Keywords: Litter disappearance, Oribatids, Collembola, macrofauna, community structure, abiotic factors.

Modes de colonisation de la litière en décomposition dans un écosystème de maquis.

Résumé

Les modes de colonisation, par des arthropodes, de la litière en décomposition, dans une formation à *Quercus coccifera* dans le nord de la Grèce, ont été étudiés à l'aide de sacs à litière de différentes dimensions de maille. Aucune différence n'a été observée entre les deux jeux de sacs utilisés, en ce qui concerne la perte de masse sèche totale, qui n'a pas dépassé 40 % après deux ans. L'évolution du nombre d'arthropodes dans les couches supérieures de la litière suit les changements saisonniers des paramètres abiotiques. On a trouvé que le nombre d'oribatides est principalement contrôlé par la température, tandis que celui des Collembola et celui du reste des arthropodes étudiés sont influencés et par la teneur en eau de la litière et par la température. La dépendance de la saison empêche l'établissement d'une faune des arthropodes dans les sacs à litière pendant les premières phases de décomposition. Cet article étudie également les différences de traitement de litière dans les deux expériences.

Mots-clés : Décomposition de la litière, Oribatides, Collembola, structure de la communauté, facteurs abiotiques.

INTRODUCTION

This study is part of a wider project concerning the vegetation, soil fauna and nutrient dynamics in evergreen-sclerophyllous formations. These formations are characteristic of the mediterranean vegetation, making up a considerable proportion of the Greek pasture lands.

Litter colonization by soil fauna as well as its role in the decomposition process have been widely investigated over the last 3 decades either by the use of chemicals (Vossbrinck *et al.*, 1979; Santos and Whitford, 1981; Elkins and Whitford, 1982), or by means of exclusion experiments (Edwards and

Heath, 1963; Anderson, 1975; House and Stinner, 1987). Most relevant studies stress the effect of the abiotic environmental factors on the decomposition phenomena. This effect is either direct, through an initial leaching period (Vossbrinck *et al.*, 1979; Sadaka and Poinot-Balaguer, 1987), or indirect, through the regulation of the activity of fungi and arthropods intervening in the decomposition process (Bell *et al.*, 1978).

Litter colonization studies in evergreen-sclerophyllous formations are not, to our knowledge, available. However, such studies can contribute to the understanding of litter degradation, a vital process especially when it comes to the persistence of the

mediterranean vegetation, occupying nutrient limited soils (Specht and Moll, 1983). Naturally, an exhaustive treatment of such phenomena would be very time consuming. The purpose of the present paper is to describe the colonization patterns in these formations during the early decomposition stages and to explore their relationships with seasonality, a feature of the mediterranean climate, which is considered of great importance with respect to the community structure, activity and population dynamics of the soil fauna (Iatrou and Stamou, 1989b, 1991; Asikidis and Stamou, 1991). Data on litter disappearance are also provided. Arthropod colonization patterns during the final decomposition stages will be presented in subsequent papers.

THE STUDY AREA

The present study took place on a gentle hill at the foot of Mt. Hortiatas, about 20 km north east of Thessaloniki, at an altitude of about 400 m a.s.l. The climate of the study area is considered transient from mediterranean to temperate. Mean annual air temperature and precipitation for the period 1985-1989 was 15.6°C and 449.2 mm respectively.

The topography of the wider study area is smooth. The soil is well formed often reaching 1 m in depth, and belongs to the Chromic Luvisol type, according to FAO classification. The depth of litter and humus layers is 0-3 and 0-10 cm respectively. The humic horizon consists of 10-14 % clay and 50-60 % sand, with organic matter and nitrogen content 8-12 % and 0.12-0.14 % respectively. Soil pH is 6.5 (Karagiannakidou, 1983).

The vegetation is dominated by evergreen-sclerophyllous *Quercus coccifera* shrubs. The growth period is in July. We should also note that prolonged grazing by goats and wood removal have resulted in a patchy environment, with randomly distributed *Q. coccifera* shrubs ranging from 0.3-2.5 m high with a total canopy cover of about 43 % and extensive areas in between, covered by herbaceous vegetation (mainly Graminae species) (Papatheodorou in prep.).

MATERIALS AND METHODS

To determine the rate of litter accumulation 10 sieves 20 cm in diameter and 1 mm opening were placed under randomly selected *Q. coccifera* shrubs. The accumulated material was collected every month, dried to constant weight at 60 °C, and weighed.

Measurements of water content and temperature of the organic layers were taken on a weekly basis. Temperature was recorded by means of 5 min-max thermometers, placed in the interphase between litter and humus. Water content was gravimetrically determined.

The colonization and decomposition patterns were examined by means of the litter bag method. Two sets of bags of different mesh size (120 litter bags each) were used. The first set, placed in the field in October 1984, consisted of 10 × 10 cm nylon mesh bags with 1 mm opening (fine mesh bags). The second, placed in the field in September 1987, consisted of 18 × 18 cm bags with 7 mm opening (coarse mesh bags). In both cases, freshly fallen litter was collected, air dried and enclosed in the bags (5 ± 0.2 g in the fine and 16 ± 0.3 g in the coarse mesh bags) together with three 1 cm² pieces of plastic grid (0.1 mm opening) for a rough determination of hyphae development (Garay, 1980). The water content of litter was estimated by oven-drying (60 °C) five randomly selected air-dried samples to constant weight.

After weighing, both sets of bags were placed in the L-layer of randomly selected *Q. coccifera* shrubs with their upper surface exposed in the air, so that the contained litter would constitute a unique layer with the freshly fallen one. The fine mesh bags were set in 12 blocks of 10 bags and the coarse mesh bags in 24 blocks of 5. We should mention here that these experiments were actually designed to start simultaneously in autumn 1984, but the coarse mesh bags were contaminated by throughfall, which influences both decomposition and colonization processes and puts severe limitations on the interpretation of the results (Bolger, 1985). Therefore, this experiment was repeated in autumn 1987 using a plastic grid tent of 1 mm opening, which was placed over the bags at a distance of 0.5-1 cm to avoid litter contamination. From each litterbag set, five randomly selected replicates were retrieved from the field at monthly intervals and placed in a Berlese-Tullgren apparatus for the extraction of soil fauna. The animals were collected in vials containing a 3:1 solution of 70 % alcohol and glycerin. They were counted and identified under a stereo-microscope. Then, the litter samples were oven dried at 60 °C to constant weight and weighed.

Data on colonizers' densities are presented as arithmetic means. In order to minimize the effect of random population density variations, mainly caused by space heterogeneity and extraction method inefficiency, census data were smoothed by using the filter $Y_t = X_t/m$, where X is the raw data, $m=3$ and t is time (Stamou and Sgardelis, 1989).

RESULTS

Litterfall - Temperature - Water content

Litterfall in *Q. coccifera* (fig. 1) is a continuous process that peaks in the summer. Autocorrelation Analysis (Chatfield, 1975) showed that the phenomenon displays annual periodicity ($P < 0.05$).

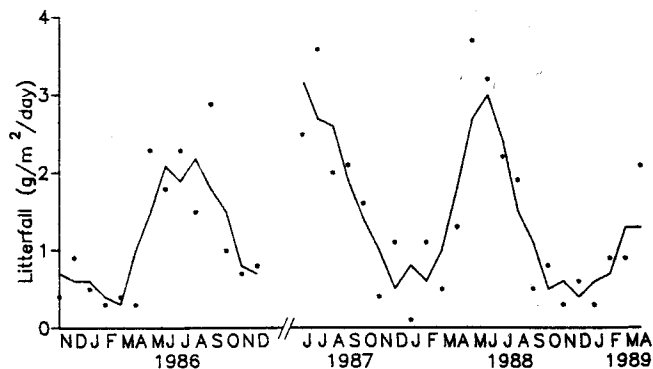


Figure 1. - Mean monthly litterfall in *Q. coccifera* (solid line: smoothed data).

Temperature and water content of the *Q. coccifera* litter layers exhibited marked fluctuations during the periods studied. Mean monthly temperature varied between 2.5 and 26.5 °C, mean minimum between -1.5 and 15 °C and mean maximum between 6.0 and 39.5 °C (fig. 2). Litter water content varied from 8 to 64 % (fig. 3).

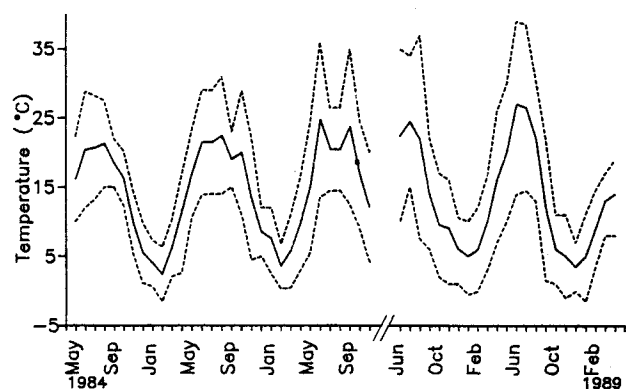


Figure 2. - Changes in mean monthly temperature in the organic layers of the *Q. coccifera* shrubs (dashed lines: mean minimum and maximum temperature).

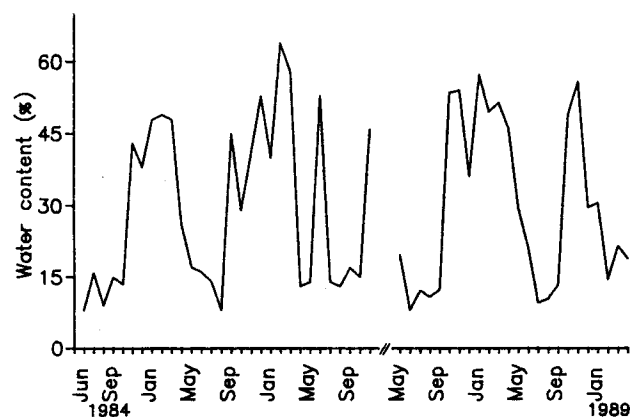


Figure 3. - Changes in mean monthly water content of the *Q. coccifera* litter.

Decomposition

In figure 4 changes in the remaining plant material in the fine (A) and in the coarse (B) mesh litter bags are depicted. The total dry mass loss after two years was 36 and 38 % for the fine and coarse mesh bags respectively. Nevertheless, in the fine mesh bags decomposition displays a plateau from February to May of the first experimental year, while in the coarse mesh bags the decline in the remaining material is continuous. A t-paired test showed that differences in decomposition rates between the two litter bag sets during the first year were statistically significant ($P < 0.05$). On the contrary, no statistically significant differences were recorded during either the second year, or the total experimental period.

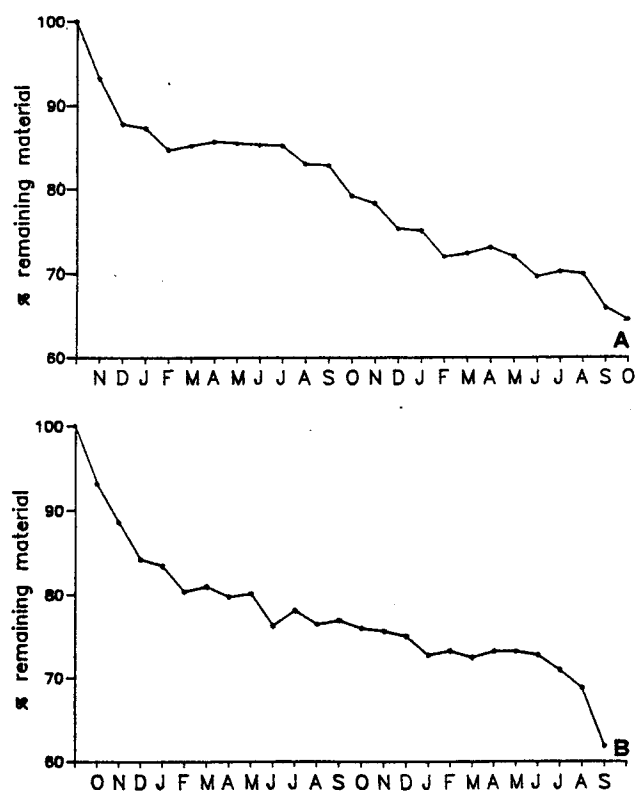


Figure 4. - Changes in the remaining material in the fine (A) and in the coarse (B) mesh bags.

Colonization of the litter bags

Data on mean annual and overall population densities of the various taxa and hyphae colonizing the two litter-bag sets are included in table 1. In the coarse mesh bags the mean number of Collembola, oribatids and hyphae did not differ significantly between the two years of the experiment. In contrast, in the fine mesh bags the mean number of oribatids and hyphae exhibit a statistically significant increase in the second year (t-test, $P < 0.05$), whereas the increase of

Table 1. – Mean annual and overall density of the colonizers recorded in the fine and coarse decomposition bags.

Colonizers	Coarse mesh bags			Fine mesh bags		
	Mean density (ind.m ⁻²)			Mean density (ind.m ⁻²)		
	1st yr	2nd yr	overall	1st yr	2nd yr	overall
Hyphae ($\times 10^8$)	4.50	4.59	4.55	1.33	20.69	11.01
Collembola	4206	4184	4195	5721	8371	7046
Oribatids	1672	2804	2238	1120	3849	2484
Psocoptera	108.3	126.5	117.4			
Insect larvae	79.5	74.7	77.1			
Thysanoptera	30.7	66.5	48.6			
Araneae	27.7	28.3	28.0			
Coleoptera	7.7	41.0	24.3			
Protura	28.0	13.4	20.7			
Polyxenida	20.7	19.4	20.0			
Pseudoscorpions	11.8	5.8	8.8			
Glomerida	12.1	2.4	7.3			
Isopoda	6.7	7.5	7.1			

collembolan numbers in the second year hardly fails to be significant. Moreover, during the first year the only statistically significant difference recorded between the two litter-bag sets was the higher number of hyphae developed in the coarse mesh bags ($P < 0.05$). During the second year the number of the three above-mentioned colonizers in the fine mesh bags was significantly higher than that in the coarse mesh bags ($P < 0.05$). As far as the densities of the other meso- and macrofaunal taxa are concerned, no statistically significant differences were recorded between the two years of the experiment.

Mean monthly density fluctuations of Collembola, oribatids and hyphae, recorded in the two experiments, are depicted in *figure 5* (a-g). Since the densities of the rest of the arthropod groups are more or less of the same order of magnitude (from 10 to 100 ind.m⁻²), they will be treated as one group from now on. In general, the numbers of the colonizers change

markedly in time. In the case of the coarse mesh bags, the numbers of colonizers respond to the seasonality of the mediterranean climate, increasing during the favourable periods of the year (mainly Autumn and Spring). In the fine mesh bags, seasonality is less visible, while numbers of oribatids and hyphae display a notable increase during the second year of the experiment. In these bags, the linear trend in both numbers of oribatids and hyphae can be described by the equations $Y = 72.3 + 211.6X$ ($P < 0.01$) and $Y = -141.5 + 40.8X$ ($P < 0.01$), respectively (Y = mean monthly density, X = time).

In order to determine relationships between the numbers of colonizers, recorded in both litter-bag sets, and seasonally fluctuating environmental parameters, Canonical Correlation Analysis was used (Gauch and Wentworth, 1976). The sets of biotic parameters, i.e. mean monthly numbers of hyphae (detrended), oribatids (detrended) and Collembola in the fine mesh bags, as well as those of hyphae, oribatids, Collembola and the other arthropods in the coarse mesh bags, were linearly combined with the set of abiotic variables, i.e. mean monthly litter water content and temperature (*table 2*). In the case of oribatids and hyphae in the fine mesh bags, linear trend removal was considered necessary in order to reveal any possible seasonal fluctuations in their numbers, probably masked by the linear increase during the second year. From the two canonical functions obtained in the case of the fine mesh bags, only the first reaches the level of statistical significance ($P < 0.01$). This is characterized by the combined correlation of oribatid and to a lesser extent of collembolan numbers, with changes in soil temperature. In data sets from the coarse mesh bags, the first canonical function is highly significant ($P < 0.01$) and the second one is significant ($P < 0.05$). The first is determined by a combined correlation of the numbers of arthropods (oribatids excluded) and hyphae with litter water content, the second by the

Table 2. – Canonical Correlation between numbers of colonizers and abiotic variables in the two litter-bag sets.

Fine mesh bags			Coarse mesh bags		
Function	Canonical functions Eigenvalue	P	Function	Canonical functions Eigenvalue	P
1	0.6163	0.0013	1	0.7078	0.0010
2	0.1316	0.2440	2	0.4331	0.0415
Coefficients for canonical variables			Coefficients for canonical variables		
Hyphae $\times 10^{-8}$	0.1967		Hyphae $\times 10^{-8}$	-0.5069	-0.3928
Oribatids (Log)	1.0901		Oribatids (Log)	-0.0363	-1.4711
Collembola (Log)	-0.6690		Collembola (Log)	-0.4711	1.3467
			Other arthropods (Log)	-0.5801	-0.5219
Coefficients for canonical variables			Coefficients for canonical variables		
Water content	-0.0966		Water content	-0.9838	0.6960
Temperature	-1.0598		Temperature	0.0285	1.2048

P: significance level.

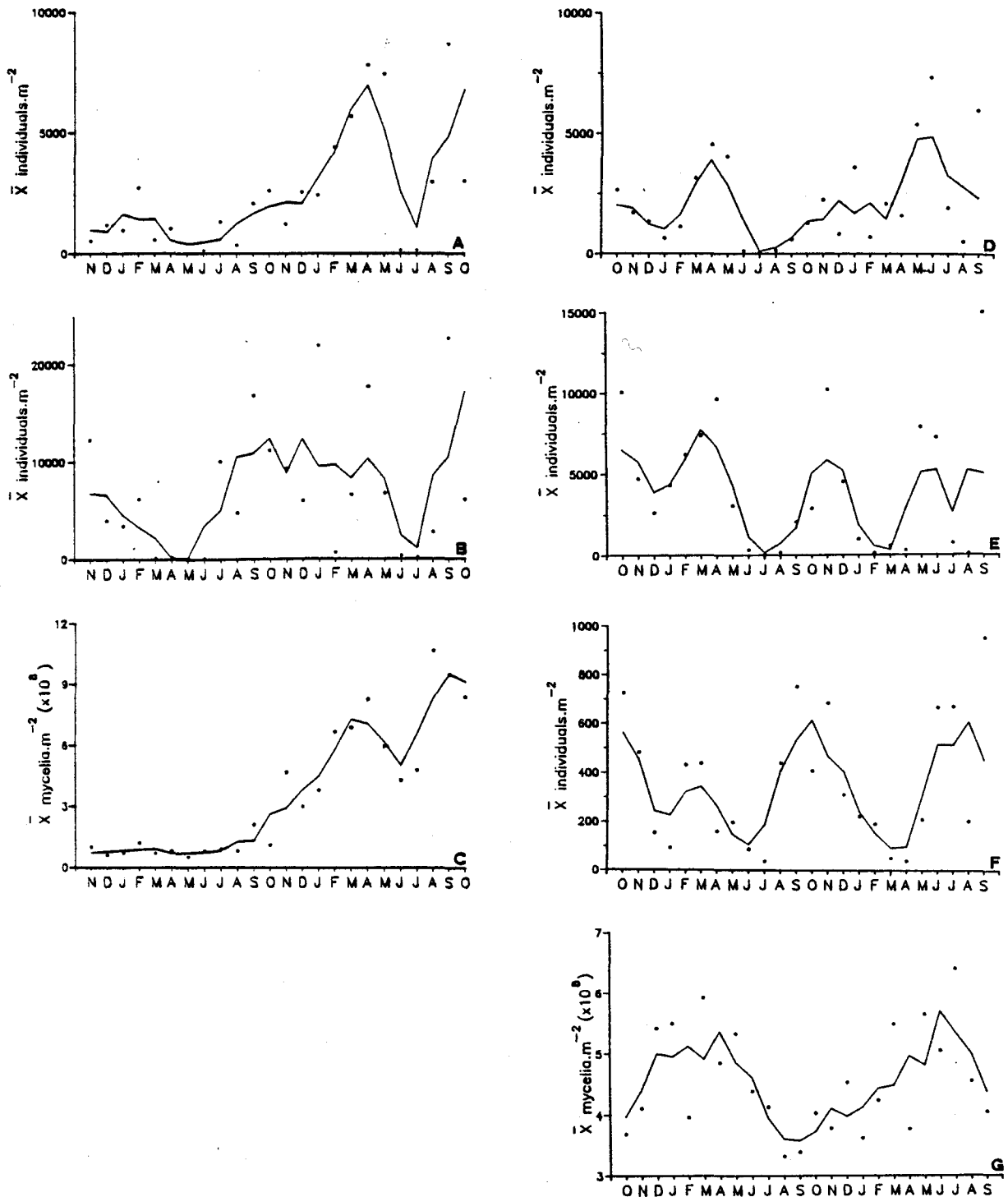


Figure 5. – Monthly changes in the number of colonizers recorded in the litter bags. A, B, C: Oribatids, Collembola and hyphae in the fine mesh bags, D, E, F, G: Oribatids, Collembola, other arthropods and hyphae in the coarse mesh bags. (solid line: smoothed data).

combined correlation of oribatids and Collembola with temperature.

In order to throw more light on the relationships, which emerged from Canonical Correlation analysis, Cross-Correlation analysis was used (Chatfield, 1975).

As shown in *table 3*, in most of the above mentioned cases, cross-correlations reach the levels of statistical significance with a maximum time-lag of one month. This fact shows that changes in the numbers of colonizers parallel the seasonal temperature and water

Table 3. – Estimated Cross-Correlations between biotic and abiotic variables in the two litter bag sets.

Variables	Time lag (months)	Maximum correlation coefficient	P
A. Oribatids-Temperature	0	-0.64	0.01
Collembola-Temperature	3	0.63	0.01
B. Hyphae-Water content	1	0.57	0.05
Collembola-Water content	0	0.81	0.01
Other arthropods-Water content	1	0.51	0.05
Oribatids-Temperature	0	-0.68	0.01
Collembola-Temperature	1	-0.56	0.05

A: fine mesh bags, B: coarse mesh bags, P: significance level.

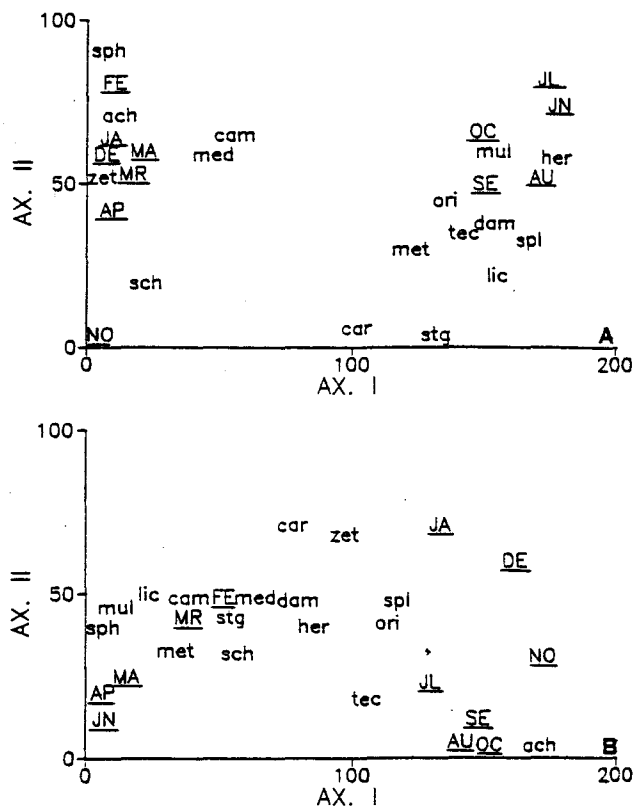
content fluctuations in the litter bags, their numerical response being almost immediate.

Detrended Correspondence Analysis (Hill and Gauch, 1980) was used in order to examine whether the changes in the specific composition of the fauna colonizing the litter bags were seasonal or successional, i.e. linked to the litter degradation process. The detrending procedure followed was the one proposed by Hill (1979). The parameters of the analysis are given in table 4. In the case of oribatids (fine mesh bags) (*fig. 6a-b*), it is obvious that in the first experimental year the changes in the composition of their community are seasonal rather than successional. Fundamental changes in the community composition occur during the transition from the wet to the dry period, which are discriminated along the first axis. As regards the second axis, the first month of the experiment (November) is ordinated separately, occupying its lower endpoint. During the second sampling year, the community composition changes evenly from November, occupying the right endpoint of the first axis, to June, occupying the left one and then again from June to October. Most species are ordinated towards the middle of the plain, indicating an even temporal distribution the year round. Minor changes can be observed along the second axis. Colder months are ordinated closer to the upper endpoint,

Table 4. – Parameters of the D.C.A. applied to monthly samples of oribatids (fine mesh bags), Collembola and the rest arthropod taxa (coarse mesh bags).

		% total variation		Axis length (in Standard Deviations)	
		AX.I	AX.II	AX.I	AX.II
Oribatids	1	86.79	7.55	1.78	0.78
	2	90.67	7.77	1.72	0.67
Collembola	1	74.47	17.02	2.17	1.66
	2	68.89	20.00	1.68	1.37
Other arthropods	1,2	74.68	15.79	1.89	1.06

1: first sampling year, 2: second sampling year, 1,2: whole experimental period.

**Figure 6.** – Ordination of monthly samples and oribatid species recorded in the fine mesh bags on the plane of the two first axes of the D.C.A. A: November 1984–October 1985, B: November 1985–October 1986.

sph: *Sphaerochthonius splendidus* (Berlese), med: *Medioppia obsolleta* (Paoli), sch: *Scheloribates latipes* (Koch), her: *Hermaniella granulata* (Nicolet), tec: *Tectocephus velatus* (Michael), ach: *Achipteria oudemansi* (Van der Hammen), zet: *Zetorchestes micronychus* (Berlese), cam: *Camisia horrida* (Hermann), stg: *Steganacarus pulcherimus* (Berlese), spl: *Scheloribates pallidulus* (Koch), lic: *Licnodamaeus pulcherimus* (Paoli), met: *Metabelba pulverulenta* (Koch), dam: *Damaeus sp.*, mul: *Multioppia sp.*, ori: *Oribatula sp.*, car: *Carabodes sp.*

warmer ones closer to the lower endpoint of this axis.

As regards the community structure of the collembolan community in the coarse mesh bags (*fig. 7a-b*), this is also conditioned by seasonality during the first year, since dry months are clearly discriminated from the wet ones, along the first axis. Here again, the phase of the first invasion (October–November) differentiates with respect to the second axis. In the second year, the pattern of community changes is not very clear and no axis can be related to a specific abiotic factor. As is the case with oribatids, most species are evenly distributed the year round, being ordinated in the centre of the plane. We should note that the euedaphic species *O. meridiatus*, *M. bipartita* and *C. bipunctatus*, which hardly appeared during the first year, now increase their densities.

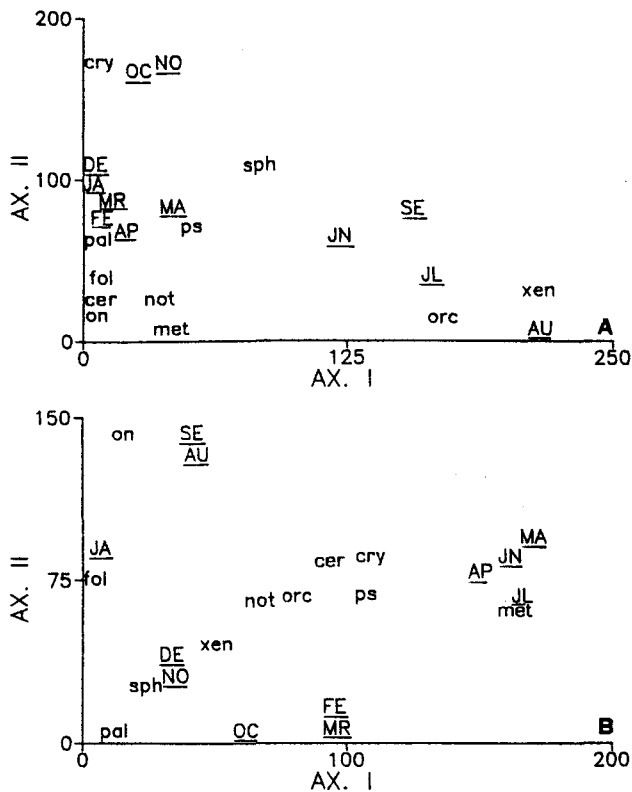


Figure 7. – Ordination of monthly samples and Collembola species recorded in the coarse mesh bags on the plane of the two first axes of the D.C.A. A: October 1987-September 1988, B: October 1988-September 1989.

sph: *Sphaeridia pumilis* (Krausbauer), cry: *Cryptopygus bipunctatus* (Axelson), not: *Parisotoma notabilis* (Schaffer), pal: *Isotomurus palustris* (Muller), fol: *Folsomia quadrioculata* (Tullberg), ps: *Pseudosinella albida* (Stach), orc: *Orchesella irregularilineata* (Stach), xen: *Xenylla sp.*, cer: *Ceratophysella engadinensis* (Gisin), on: *Onychiurus meridatus* (Gisin), met: *Metaphorura bipartita* (Handschin).

As far as the rest of the arthropod species are concerned, monthly samples of both experimental years are ordinated along the first axis of the D.C.A. (fig. 8). Samples taken during the wet period of the first year are placed at the right end of the axis, while those taken during the dry period occupy the left end. Most monthly samples of the second year occupy the centre of the axis, representing intermediate humidity conditions. Thus, the seasonal effect of the first year on the community structure exceeds the seasonal effect during the second year as well as the interannual one.

DISCUSSION

Our results show that the litter degradation process in the study area is quite slow. The dry mass loss recorded in both fine and coarse mesh bag sets did not exceed 40% after 2 years. Similar results are reported for other evergreen-sclerophyllous formations (Schlesinger and Hasey, 1981; Vardavakis,

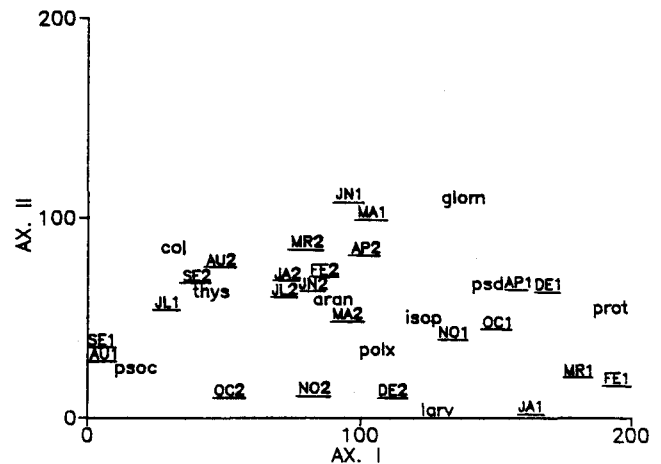


Figure 8. – Ordination of monthly samples of the two experimental years and arthropod taxa recorded in the coarse mesh bags on the plane of the two first axes of the D.C.A.

glom: Glomerida, prot: Protura, psd: Pseudoscorpions, isop: Isopoda, polx: Polyxenida, larv: Insect larvae, aran: Araneae, thys: Thysanoptera, col: Coleoptera, psoc: Psocoptera.

1988, among others). A review of the relevant literature showed that, generally, decomposition rates in the above-mentioned formations are much lower than those reported for deciduous forests, pine forests or phryganic ecosystems (Stamou, 1981; Reddy, 1981; Fouseki and Margaris, 1981, among others), complying with those reported for more-or-less extreme environments, such as tundras and semiarid systems (Douce and Crossley, 1982; Elkins and Whitford, 1982). Indeed, the strong seasonality may to an extent justify the use of the term "extreme" when referring to environments such as the study area. The wide temperature fluctuations within a range of over 40°C, as well as the abrupt transition from dry to wet seasons and vice versa, constitute inhibiting factors for the activity of soil animals on the upper litter layers, reducing in this way their contribution to the decomposition process. Furthermore, low decomposition rates may also be attributed to the structural and chemical characteristics of the *Q. coccifera* leaves. The leaves of sclerophyllous shrubs have a lower concentration of mineral elements, such as nitrogen and phosphorus and a high concentration of polyphenolic and lignin compounds (Handley, 1954 in Read and Mitchell, 1983), factors inhibiting the feeding activity of the saphrophages (Satchell, 1974).

Over the two-year study period, differences in the mesh size of the litter bags did not seem to play any significant role in the total disappearance of litter. Similar results are reported by other authors (Anderson, 1975; House and Stinner, 1987), but for a shorter time period. This fact implies that the role of macrofauna becomes apparent in later decomposition stages. Indeed, the main mechanism of litter fragmentation in the study area is a population of the diplopod *Glomeris balcanica* mainly confined

in deeper litter and humus layers (Iatrou and Stamou, 1991), while earthworms, julids and isopods, which are known to have a considerable effect on litter degradation (Wallwork, 1976) are either absent or few (Iatrou and Stamou, 1989a).

Nevertheless the experimental treatment of litter seems to affect our results, to an extent, especially during the first year of the experiment. During the second, due to litter accumulation, the bags of both sets are gradually covered by a new L-layer, providing a more moderate environment for the settlement of populations (Takeda, 1987). We believe that this is the main reason for the differences in the structure of the arthropod communities between the two experimental years, as shown by D.C.A. As regards the first year of the experiment, it is possible that the tent over the coarse mesh bags may, to an extent, substitute the new L-layer of the second year, thus smoothing the field conditions. This is the reason why no differences either in colonizers' densities or in the decomposition rate are recorded between the two years, in this set of litter bags. On the contrary, the fine mesh bags, during the first year, are exposed and, thus, more subject to the influence of temperature fluctuations than the coarse mesh bags. Therefore, the smoothing effect of the new L-layer of the second year is more pronounced in this set of litter bags, resulting in the increase of colonizers' densities. Litter water content, as shown by Canonical Correlation Analysis, does not seem, in this case, to control the fluctuations in numbers of colonizers, because the small mesh size creates an environment with more constant humidity conditions, than in the coarse mesh bags (Curry, 1969; House and Stinner, 1987).

Despite the differences between the two experiments, changes in the colonizers densities in both litter bag sets exhibited notable similarities throughout the experimental period. This is in accordance with the predictability of the mediterranean climate. Indeed, soil arthropods in our study area are characterized by interannual stability, annual periodicity and rapid changes in their population size just before or after the adverse summer period (Stamou *et al.*, 1993). Thus, the parallel changes of arthropod numbers and abiotic parameters, revealed by Canonical and Cross Correlation Analysis, are due to the synchronization of the arthropods' life-cycles with their seasonally varying environment.

As regards the structure of the arthropod communities, DCA revealed differences between the two sampling years, suggesting that there is no establishment of a resident arthropod fauna in the litter bags at least until the second year of the experiment. In all cases, community structure is determined by seasonality during the first year, and three phases in the microarthropod colonization process can be distinguished; the phase of the initial invasion in the litter bags, the second phase, where favourable conditions allow the upward migrations of the populations and their activity until the end of spring, and the third phase, coinciding with the adverse period of drought, arresting the life-cycle development and activity of the arthropods (Stamou *et al.*, 1993; Iatrou and Stamou, 1989b, 1991). During the second year, although community changes are still induced by seasonality, the distinction of these three phases is no longer evident; after the populations' recovery from the summer drought, the gradually changing habitat properties permit the establishment of a more resident fauna in the litter bags, compared with that of the first year, and more-or-less stable distribution patterns are revealed. In the case of Collembola, the appearance of some new species, mainly dwelling in deeper litter and humus layers, characterize the composition of their community.

However, the problem concerning the intervention of these microarthropods in the early decomposition stages remains open. Although most microarthropod species found in mediterranean type ecosystems are cosmopolitan, displaying wide tolerance to environmental gradients (Sgardelis *et al.*, 1981; Asikidis and Stamou, 1991), most of them are food specialists, mainly feeding on lichens (Stamou and Asikidis, 1992; Argyropoulou, unpubl.). This material is an essential constituent of litter in the study area. Indeed, grazing in the study area results in an increase of the development of lichenoflora on the aerial plant parts (Papatheodorou in prep.). Our point is that a partitioning of the litter decomposition process might be possible. During the first year, the nutrient limited system is enriched with nutrients from lichen decomposition, while during later years the smoothing of the effect of the environmental constraints ensures enrichment with nutrients from evenly decomposing plant materials.

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