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► **To cite this version:**

Jean-François Ponge, Pierre Arpin, Guy Vannier. Collembolan response to experimental perturbations of litter supply in a temperate forest ecosystem. *European Journal of Soil Biology*, 1993, 29 (3-4), pp.141-153. hal-00506014

HAL Id: hal-00506014

<https://hal.science/hal-00506014>

Submitted on 23 Sep 2010

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Collembolan response to experimental perturbations of litter supply in a temperate forest ecosystem

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Abstract

Litter and soil communities of Collembola (Insecta, Apterygota) in a mixed deciduous forest in France were studied for four years after experimental litter removal and doubling. Total abundance was unaffected by these two treatments but substantial changes in species composition occurred at the soil surface. Epigeic groups (Entomobryoidea, Symphypleona) almost disappeared in the no-litter treatment, except for the genus *Sminthurides* whose abundance increased after litter disappearance. Doubling of litter had no significant effect on the Collembola abundance. Relative influences of shifts in habitat structure and food resources are discussed, together with a comparison between macrofaunal and mesofaunal responses to litter manipulations.

Keywords: Collembola, litter supply, soil, food resources, habitat.

Résumé

Réponse des Collemboles à des perturbations expérimentales des apports de litière.

Les peuplements de Collemboles (Insecta, Apterygota) de la litière et du sol d'une forêt feuillue (forêt d'Orléans, France) ont été suivis pendant quatre années au cours d'une expérience de privation et de doublement des apports de litière. L'abondance totale n'a pas été affectée par ces deux traitements mais des changements très nets sont apparus dans la composition spécifique à la surface du sol. Les groupes épigés (Entomobryoidea,

Symphyleona) ont presque disparu dans le traitement sans litière, sauf pour le genre *Sminthurides* dont l'abondance a augmenté après disparition de la litière. Le doublement de litière n'a pas eu d'effet significatif sur l'abondance des Collemboles. L'influence relative des changements intervenant dans l'habitat et les ressources alimentaires sont discutés, et une comparaison est faite entre les réponses respectives de la macrofaune et de la mésofaune aux manipulations de la litière.

Mots-clés: Collemboles, apports de litière, sol, ressources alimentaires, habitat.

INTRODUCTION

The importance of litter supply in the maintenance of soil mesofauna communities within forest ecosystems can be estimated through studies on the effects of clear-cutting and thinning (Huhta *et al.*, 1967; Hill *et al.*, 1975; Betsch *et al.*, 1981; Gers and de Izarra, 1983), fire (Takeda, 1981; Tamm, 1986) or whole tree harvesting (Bird and Chatarpaul, 1986). Results appear to be contradictory, due to local conditions and multiple events accompanying these changes in litter supply (climate, light, vegetation, slash debris, soil disturbance), leading to difficulties when interpreting these results in terms of food availability or habitat disturbance. Experimental studies using perturbation of litter input seem more informative on the role of litter in the maintenance of soil biological activity but they are scarce (Gill, 1969; Arpin *et al.*, 1985; Garay, 1989; Judas, 1990; Betsch, 1991).

An experiment was conducted from 1977 to 1981 to study changes in soil microfauna, mesofauna and microflora following litter deprivation. The site was an oak-hornbeam forest with a calcic mull humus. Most changes were attributed to the disappearance of the herbaceous cover (mainly its root system) but the effects on microfauna and mesofauna were small (Arpin *et al.*, 1985; Betsch, 1991). This was thought to be due to the high carbon content of the A horizon, which was saturated in calcium (chalk-humus assemblages). Some years later another experiment was planned in a site with a higher rate of disappearance of organic matter.

The present experiment was conducted from May 1984 to May 1989 in a temperate oak-beech-hornbeam mixed forest stand with an acid mull humus. Changes in soil animal communities with a normal, double or without any litter input and with or without an herbaceous layer, were followed. Results concerning macrofauna have already been published (David *et al.*, 1991). After litter removal significant decreases (and near extinction) were recorded for earthworms, millipedes, woodlice and saprophagous fly larvae, which are the

major litter-consuming groups, and for centipedes, predatory beetles and fly larvae. Doubling litter input neither increased nor decreased densities of macrofauna. The present paper deals with Collembola, which are one of the major components of mesofauna.

STUDY AREA

The experiment was installed in a mature forest stand (selection thinning within a coppice one century ago). Oak [*Quercus petraea* (Mattus.) Liebl.] is dominant, mixed with beech (*Fagus sylvatica* L.) and hornbeam (*Carpinus betulus* L.). Ground vegetation is sparse, mainly consisting of an herbaceous bramble species (*Rubus schleicheri* Weihe). Soil is an aqualf, with a temporary water table, and humus is of the acid mull type (pH=5.2). A more detailed description of the site has already been published (David *et al.*, 1991).

METHODS

Experimental layout

The experimental area was made of four 6 x 3 m adjacent plots (with and without litter, with and without an herbaceous layer) and another 4 x 4 m plot where litter was added in quantity equivalent to the annual litter fall (about 650 g/m², *see* David *et al.*, 1991). Litter was intercepted on the four adjacent plots by help of 1 x 1 m baskets made of a plastic net of 1 cm mesh size. The baskets were set 50 cm above the ground level and covered the plots permanently. On control plots (with litter, with or without ground vegetation), the litter was supplied by turning over the baskets each fortnight (during the fall). Part of the litter (16 baskets) collected on the treatment plots (without litter, with or without ground vegetation) was immediately spread over the doubling plot. Other basket contents were used for chemical analyses and litter fall estimates (David *et al.*, 1991).

The experiment started on May 1984, but the first date at which a treatment was given to the soil was February 1985, the date after which ground vegetation was fortnightly cut away and the debris exported (until complete death of vegetation on next summer) in two of the four adjacent plots and baskets were installed. Thus the first perturbation of litter supply occurred in the fall of 1985. Doubling was done first at this date.

Each 6 x 3 m plot was divided into 72 squares 50 x 50 cm each, five of them being selected at random two times a year (May and November) and not sampled again thereafter. In the 4 x 4 m plot five samples were

taken at random at the same dates, without any sub-plot design.

Faunal sampling

Mesofauna of the uppermost 10cm (including litter) was collected by forcing a 5 cm diameter steel probe with cutting edge (Vannier and Alpern, 1968). Five samples were taken in each plot each year at two distinct seasons (May and November, total = 11 sampling occasions) from May 1984 to May 1989 in the four adjacent plots and from November 1985 to May 1989 in the 4 x 4m plot (double litter). They were stratified according to depth level: 0–1 cm, 1–3cm, 3–6cm, 6–10cm. The five soil cores collected in the same plot at the same depth were bulked into a composite sample. The problem of the loss of within-plot heterogeneity in the data was debated prior to the experiment but the principle of separating sub-samples was abandoned due to practical reasons.

Fauna was extracted with a dry-funnel. Collembolans were sorted under a dissecting binocular microscope, mounted under a cover slide in chloral-lactophenol and identified at the species level under a light microscope at the 400 x magnification. Examination of the gut contents was made on the same specimens. Species were arranged in ecological groups according to their commonest habitat: litter and atmobios for epigeic species, mineral soil for endogeic species.

Data analysis

Total abundances or species abundances were analysed by means of ANOVA (Sokal and Rohlf, 1969), sampling dates being used as blocks and plots as treatments. Five treatments were compared (or only four when necessary):

L– H+ = no litter, vegetation

L–H– = no litter, no vegetation

L+H+ = litter, vegetation

L+H– = litter, no vegetation

L++ = double litter

Data were taken raw or transformed when needed into their natural logarithm [$\log(x + 1)$] in order to ensure variance homogeneity (Sokal and Rohlf, 1969). A Student-Newman-Keuls a posteriori test was used to compare means.

Changes in species composition due to treatments or other influences were analysed by means of correspondence analysis (Greenacre, 1984). Coding of species abundances was as follows:

0 individual coded as 0	
1	1
2 to 3	2
4 to 7	3
8 to 15	4
16 to 31	5
32 to 63	6
64 to 127	7

In this analysis, species being present in less than ten samples and samples with less than ten animals were discarded. Thus the analysis was performed on a table crossing 32 species and 208 samples (3 x 4 x 4 before Nov. 85 + 8 x 5 x 4 thereafter).

Seven indicators were used as additional variates (not involved in the analysis but projected as if they were). They were coded as 1 (if the sample considered belongs to this category) or 0 if not:

0–1 cm depth, normal litter

0–1 cm depth, no litter, before May 1987

0–1 cm depth, no litter after May 1987 included

0–1 cm depth, double litter

1–3 cm depth

3–6 cm depth

6–10 cm depth

Other measurements

Air and soil temperature were measured fortnightly at the end of the morning at different depths with a probe digital thermometer. Measurements were taken on the four adjacent plots from January to May 1989, *i.e.* during the last year of the experiment.

Chemical analyses were performed every year on soil samples taken in May at four different depths, with the same procedure as for mesofauna (composite sample made of five sample units taken in the same sub-plots as for fauna). Soil was air-dried, sieved at 2.0 mm and homogenized. Only carbon content and pH have been reported here. Carbon was analysed using a Carlo Erba 1106 analyser and expressed in mg. g⁻¹ dry soil. Water content was measured on samples taken every year in May and November, by weighing again the soil after drying at 105°C during 24h, and was expressed as percentage dry weight. The pH was determined using a glass electrode in a 2:5 soil: water suspension.

Litter fall was collected as mentioned above and weighed after air-drying. Only total mass of litter will be used below.

RESULTS

Total abundance of Collembola

Total abundance of Collembola did not exhibit any marked trend of disappearance or increase due to treatments (*fig. 1*). Some heterogeneity between the plots appeared in the 0–1 cm as well as in the 1–3 cm strata. The plot L–H+ (without litter, with vegetation) exhibited higher numbers of animals in the upper stratum all along the experimental period, this being only perceptible before May 1986 in the second stratum (litter deprivation was effective since the fall of 1985).

Analysis of variance on total abundance of Collembola, the four strata combined (11 blocks from May 1984 to May 1989 with the four treatments L–H+, L–H–, L+H+, L+H–; 8 blocks from November 1985 to May 1989 with the five treatments L–H+, L–H–, L+H+, L+H–, L++) failed to reveal any significant heterogeneity, but this was not true when the upper stratum was analysed separately ($F= 5.23$, $P=0.005$, mean for L–H+ significantly higher than for the other three treatments). The three other strata, when separately analysed, did not exhibit any significant heterogeneity.

Species composition

Correspondence analysis on the pool of data, without any indication given on the treatments, revealed distinct changes in species composition in the upper stratum, due to litter removal (*fig. 2*). The position of the points corresponding to the L- treatments changed after May 87 in the plane of the two first axes (extracted inertia = 30 %). No change could be referred to the disappearance of ground vegetation (H- treatments). Species composition seemed constant in the second (1–3 cm), third (3–6 cm) and fourth strata (6–10 cm).

Additional items indicated that the first axis was clearly related to vertical distribution, the third (3–6cm) and fourth (6–10 cm) strata being poorly differentiated from each other on the basis of their species composition, with a dominance of endogeic species all belonging to the Poduromorpha (*see table 1*).

The second axis was related to the effects of litter disappearance, these being displayed only in the upper stratum (0–1 cm). A new species composition occurred, from May 1987 until the end of the experiment (May 1989). The upper stratum was characterized by the presence of epigeic species (*see table 1*). The points representing the samples taken in the L-H+ and L-H- plots (without litter) after May 1987 were located on the negative side of axis 2 and somewhat displaced towards deeper levels. The two *Sminthurides* species *S. schoetti* (SSC) and *S. parvulus* (SPA) and, to a lesser extent, the species *Orchesella villosa* (OVI), *Xenylla tullbergi* (XTU) and *Ceratophysella denticulata* (CDE), were associated with these samples without litter on the ground. Thus species composition changed following litter disappearance (the soil was estimated bare from the spring of 1987 on, David *et al.*, 1991). There was a relative increase in endogeic species, compared to epigeic species as a bulk (except the genus *Sminthurides*).

Examination of the population trends exhibited by epigeic species showed distinct patterns (*fig. 3*). *Lepidocyrtus lanuginosus* (LLA) and *Sminthurinus signatus* (SSI), for instance, were only present on plots with litter (L+H-, L+H+, and L++) all over the experimental period. Changes were observed after disappearance of litter in the plots L-H- and L-H+. *Parisotoma notabilis* (PNO) was nearly absent in the experimental plots until November 1987. Then this species became abundant only on the plots with litter (L+H+, L+H-, L++). On the contrary the abundance of *Sminthurides* spp. (*fig. 4*) increased only on the plots without litter (after May 1987, *i.e.* when the ground was bare). When total abundance of Entomobryoidea + Symphypleona (all epigeic species), *Sminthurides* spp. discarded, was plotted (*fig. 4*), then an association between the abundance of these species and the presence of litter seemed to appear. When *Sminthurides* spp. were incorporated in the total abundance of epigeic groups, then this trend was somewhat obscured. Furthermore we may notice that seasonality was clearly

visible on abundance curves (*fig. 3*) of the two species *Lepidocyrtus lanuginosus* (LLA) (Entomobryodea) and *Sminthurinus signatus* (SSI) (Symphypleona), the latter being absent from the samples taken in the fall. The same trend was displayed by the curves for total Entomobryodea + Symphypleona (*fig. 4*).

The fate of rare species, not taken into account in data analysis, should be nevertheless evoked. For instance, *Isotomurus palustris* appeared only after the fall of 1988 in the plots where litter had disappeared.

Data analysis (ANOVA) revealed that spatial heterogeneity was present at the beginning of the experiment (*table 1*), mainly due to the species (*Lepidocyrtus lanuginosus* (LLA)), which represents by itself about one half of the total abundance of epigeic species. Abundance of this species decreased in the order L-H+, L-H-, L+H+, L+H-, *i.e.* from the left to the right of the field experimental layout. This fact cannot be due to experimental effects, since the treatments were not effective until the fall of 1985. *Sminthurides* also followed this trend, except that this species was more abundant on L-H- than on L-H+. Effects due to treatments were displayed by these analyses (*table 3*), except that the increasing abundance of *Lepidocyrtus lanuginosus* (LLA) on the L+H- plot from May 1987 on might obscure the discontinuity between the other plots with litter (L+H+, L++) and the plots without litter (L-H+, L-H-).

Other data

Examination of the gut contents of the animals that were present in the upper stratum (0–1 cm) of the L+H+, L+H- and L++ plots on May 1989 (*table 4*) indicated that epigeic Collembola did not feed on litter, but rather on mineral (probably including organo-mineral earthworm faeces, given the mull humus type), faecal (holorganic = made of highly transformed plant and fungal material mixed with bacteria, *see* Ponge, 1991) or fungal material.

Soil moisture (*fig. 5*) did not vary greatly between the treatments, except in May 1988 and May 1989 where the plots without litter (L-H+ and L-H-) were drier than the plots with litter, especially in the first top centimeter (water content divided by two in May 1989).

A steady increase in the C content of the < 2 mm fraction of the soil was observed in the first top centimeter of the L++ plot (magnified by two from May 1986 to May 1989), this phenomenon being less pronounced in the underlying stratum (*fig. 6*). The influence of litter deprivation is less perceptible.

The annual litter fall was seemingly constant from May 1985 to May 1989 (*fig. 6*), with a gradual increase from May 1985 to May 1988 followed by a small decrease over the last year.

Temperature seemed to be affected by the lack of litter (*fig. 7*), even at the deeper stratum studied (6–10 cm), although no statistical test could be applied to our data. The soil micro-climate seemed milder under a litter cover, at least during the period without living tree foliage.

Chemical properties (pH was exemplary of all measured parameters) were affected at the 0–1 cm and the 1–3 cm depth levels but not underneath (*fig. 8*).

DISCUSSION

Litter removal

By no means was the L++ treatment (doubling) found associated with any definite change in species composition, nor was the H– treatments (no ground vegetation). The only observed effect was the disappearance of litter-dwelling species following litter deprivation (L– treatments). A similar result was observed for the macrofauna in the same experiment by David *et al.* (1991). We may wonder whether this was due to changes in food resources or to changes in the habitat of litter-dwelling species. The disappearance of earthworms following litter deprivation (David *et al.*, 1991) might be thought to result from the disappearance of their main food resources. In the present study, litter cannot be considered directly as a food resource for most collembolan species (*table 4*). Other food resources might have been affected by litter disappearance, mainly faeces of litter-consuming animals and fungi colonizing dead leaves. But their relationship with litter considered as a food is in this case rather indirect. Although rarely eaten by Collembola, dead leaves might nevertheless be necessary for the reproduction of epigeic species, e.g. *Pseudosinella alba*, a mycophagous species, could not be reared in the absence of leaves, although leaves were not ingested (Sharma and Kevan, 1963). The importance of litter substrates, such as wood debris, for spermatophore deposition (Betsch-Pinot, 1977), may be suggested, too. A similar experiment (Gill, 1969), with: i) three times the normal litter fall; ii) without litter and iii) with dacron replacing litter in equivalent amount, demonstrated that an inert substance, without any nutritional value but simulating the litter habitat, did not decrease densities of microarthropod groups. Thus, in the present experiment, changes in collembolan communities might be attributed to a change in the habitat of epigeic species rather than to a change in food resources.

The increased abundance of the genus *Sminthurides* [two species *S. schoetti* (SSC) and *S. parvulus* (SPA)] following litter disappearance might be discussed, since these two species are favoured in moist places, whether in forest or not (Ponge, 1980, 1993). Some authors consider them as typical of *Sphagnum* bogs (Stach, 1956; Gisin, 1960). This could be compared to the development of a moss cover at the surface of the L-H+ and L-H- plots after complete disappearance of litter in Spring 1987. In a similar experiment (Betsch, 1991), increased densities of *Sphaeridia pumilis* (a species belonging to the same family) were observed, following disappearance of litter.

The appearance of *Isotomurus palustris* from the fall of 1988 on in the plots without a litter layer is noticeable. Changes in water content of the soil (*fig. 6*) cannot be used to explain the appearance of this hygrophilic species (Ponge, 1980, 1993), since the 0–1 cm stratum was even slightly drier in the L-H- and the L-H+ treatment plots, but a dense moss cover might offer moister places for epigeic species than litter could do.

Litter doubling

No change of humus type was registered following litter doubling, although more litter accumulated at the surface of the soil, due to significant decrease of the rate of disappearance of dead leaves (David *et al.*, 1991). No increase or decrease occurred (over the five years of the experiment) in animal densities, which might explain why humus remained of the same type. Leaching of organic carbon was probably insignificant, incorporation of excess carbon being apparent (and constant) in the 1–3 cm stratum only (*fig. 6*). Nevertheless we may wonder what could happen in an experiment of a longer duration.

Stability of the mineral soil

The absence of clear trends in the mineral part of the soil might be explained by the constancy of its organic matter content (*fig. 6*). Some decrease of the C content occurred in the L-H+ and L-H- treatment plots as compared to the control (L+H+ and L+H-) in the 0–1 cm and 1–3 cm strata but this was not shown at lower levels.

Other data were registered at different depth levels such as soil moisture (*fig. 5*), temperature (*fig. 7*), and chemical parameters, such as pH (*fig. 8*). The soil water content was slightly depressed following litter

removal and slightly increased following litter doubling, but this was only evident in the upper stratum (0–1 cm), far less at the 1–3 cm depth and not at all in the underlying soil. This could be attributed to changes in the content in organic matter near the surface.

The milder climate when the litter is present (*fig. 7*), visible in all strata, might be attributed to the protective effect of a stratified layer made of dead leaves, thus reducing the turbulence of the soil atmosphere. This effect, both in cold and in warm periods, has been already observed after mulching a bare soil (Unger, 1978).

The decrease in pH near the surface (*fig. 8*) following litter deprivation (about half an unit) is probably due to the development of a dense moss cover once the ground was bare, but no change in species composition could be attributed to this phenomenon.

The importance of litter for soil Collembolan communities

What could be inferred from these data about the role of annual litter input in the organization of soil Collembolan communities? The stability of the carbon content and other chemical properties of the organo-mineral part of the soil may be compared to the stability of endogeic Collembolan populations. It seems probable that a great part of each annual litter fall rapidly disappears through microbial mineralization and that another part may be considered as recalcitrant to any biological processing (Seastedt, 1984). Most endogeic organisms (animal and microbial) must thus feed on a carbon compartment the sources of which are primarily leachates and roots. In the present experiment these resources were seemingly unaffected by perturbations of litter supply. Climate conditions (depicted by temperature) were affected by litter deprivation, but this could not be considered as dramatic for most endogeic species, given the mild climate of the countries under atlantic influence (Vannier, 1972, 1973).

The absence of definite changes following litter doubling seemed more difficult to interpret, as already emphasized for macrofauna by David *et al.* (1991). We cannot discard the hypothesis of opposite trends (increase in food resources counterbalanced by a decrease in habitat quality) that could lead to an apparent steady state in animal densities, but this seems highly questionable on the basis of the changes we observed in species composition. Rather we prefer to invoke the absence of dramatic changes in habitat features compared to the control, at least at the present state of our experiment, and for the animal group we studied. The fact that no

increase in density (even at the species level) was observed all along the four years of litter doubling implies that food resources were not the limiting factor for litter-dwelling species in this humus type.

If we compare the results of the present experiment with those we obtained in a rendzina soil (Arpin *et al.*, 1985) it may be seen that more changes were obtained on Collembolan populations in this soil type. Most dramatic changes were observed at the 6–10 cm level, with a strong decrease (near disappearance) in total Collembola. This effect disappeared once ground vegetation resumed after an accidental tree-fall gap (deciding the end of the experiment). In this case the luxuriant ground vegetation had rapidly disappeared following litter deprivation. Our interpretation was that the root system of herbs was the main source of food for endogeic animals.

Now we may question in turn the importance of litter for Collembolan populations. It seems that two distinct categories of species are differently affected by litter disappearance. Epigeic species undergo strong changes in their species composition, the reason being probably the lack of a suitable habitat. Endogeic species seems more recalcitrant to this treatment, except when other kind of resources are secondarily affected, such as root systems.

Acknowledgements

The authors are greatly indebted to Pr D.C. Coleman (Athens, Georgia) for helpful comments and revising of the English language.

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Legends of figures

Figure 1. – Densities of total Collembola from 1984 to 1989 at four depth levels. First litter intercept and cutting-away of ground vegetation: February 1985. First doubling of litter: September 1985. L–: without litter. L+: normal litter fall. L++: double litter fall. H–: without ground vegetation. H+: with ground vegetation.

Figure 2. – Correspondence analysis crossing 208 samples and 32 Collembolan species. Species present in less than 10 samples excluded. Samples with less than 10 animals excluded. (1) L+: upper stratum (0–1 cm), normal litter. (1) L++: upper stratum, double litter. (1) L– (1): upper stratum, no litter, from May 84 to Nov. 86. (1) L– (2): upper stratum, no litter, from May 87 to May 89. (2): 2nd stratum (1–3 cm). (3): 3rd stratum (3–6 cm). (4): 4th stratum (6–10 cm). For species codes (3 letters) *see table 1*.

Figure 3. – Densities of three epigeic species of Collembola with decreasing abundance following litter deprivation.

Figure 4. – Densities of the genus *Sminthurides* (two species confounded), of total epigeic groups (Entomobryoidea and Symphypleona) with or without *Sminthurides*.

Figure 5. – Soil moisture at the first two investigated depth levels, in percentage of dry soil weight.

Figure 6. – Carbon content (mg.g^{-1} dry soil sieved to 2 mm) at the first two investigated depth levels. Total litter fall over the four years 1985 to 1988 (histogram).

Figure 7. – Temperature measured in the air (50 cm above the ground surface) and at four different depth levels, from January to May 1989, on the four adjacent plots (symbols as in other figures).

Figure 8. – pH values at the first two investigated depth levels.

Table 1. – List of Collembolan species used as active items in correspondence analysis.

		Epigeic	Endogeic
ASE	<i>Arrhopalites sericus</i> (Gisin, 1947)	*	
CDE	<i>Ceratophysella denticulata</i> (Bagnall, 1941)	*	
CMA	<i>Caprainea marginata</i> (Schott, 1893)	*	
DFU	<i>Dicyrtoma fusca</i> (Lucas, 1842)	*	
DMI	<i>Dicyrtomina minuta</i> (Fabricius, 1783)	*	
EMU	<i>Entomobrya muscorum</i> (Nicolet, 1841)	*	
FQU	<i>Folsomia quadrioculata</i> (Tullberg, 1871)	*	
FTR	<i>Friesea truncata</i> (Cassagnau, 1958)		*
IMI	<i>Isotomiella minor</i> (Schiffner, 1896)		*
LLA	<i>Lepidocyrtus lanuginosus</i> (Gmelin, 1788)	*	
LLU	<i>Lepidocyrtus lignorum</i> (Fabricius, 1781)	*	
MHY	<i>Mesaphorura hylophila</i> (Rusek, 1982)		*
MJA	<i>Mesaphorura jarmilae</i> (Rusek, 1982)		*
MKR	<i>Mesaphorura krausbaueri</i> (Börner, 1901)		*
MMA	<i>Mesaphorura macrochaeta</i> (Rusek, 1976)		*
MMI	<i>Megalothorax minimus</i> (Willem, 1900)	*	
MPY	<i>Micranurida pygmaea</i> (Börner, 1901)		*
OCI	<i>Orchesella cincta</i> (Linné, 1758)	*	
OVI	<i>Orchesella villosa</i> (Geoffroy, 1764)	*	
PCA	<i>Paratullbergia callipygos</i> (Börner, 1902)		*
PMA	<i>Pseudosinella maui</i> (Stomp, 1972)	*	
PMI	<i>Proisotoma minima</i> (Absolon, 1901)		*
PNO	<i>Parisotoma notabilis</i> (Schäffer, 1896)	*	
SAU	<i>Sminthurinus aureus</i> (Lubbock, 1862)	*	
SDE	<i>Stenaphorura denisi</i> (Bagnall, 1935)		*
SPA	<i>Sminthurides parvulus</i> (Krausbauer, 1898)	*	
SPU	<i>Sphaeridia pumilis</i> (Krausbauer, 1898)	*	
SSC	<i>Sminthurides schoetti</i> (Axelson, 1903)	*	
SSI	<i>Sminthurinus signatus</i> (Krausbauer, 1898)	*	
WME	<i>Wankeliella mediochaeta</i> (Rusek, 1975)		*
XGR	<i>Xenylla grisea</i> (Axelson, 1900)	*	
XTU	<i>Xenylla tullbergi</i> (Börner, 1903)	*	

Table 2. – Analysis of variance. Before any effect of experimental perturbations. One factor with four treatments (L–H+, L–H–, L+H+, L+H–). Means belonging to the same homogeneous group (a posteriori Student-Newman-Keuls test when null hypothesis has been rejected) are indicated by a common letter. Significance: N.S. = insignificant; * = significant at the 0.05 level.

Animal group	Dates	F value	P value	Significance	Means			
					L–H+	L–H–	L+H+	L+H–
<i>Lepidocyrtus lanuginosus</i>	May 84 to Nov 86	3.51	0.041	*	37.3a	24.3ab	22.7ab	19.7b
<i>Sminthurinus signatus</i>	May 84 to May 87	3.09	0.053	N.S.	9.9	3.6	1.3	4.9
<i>Parisotoma notabilis</i>	May 84 to May 86	0.22	0.882	N.S.	1.6	2.0	1.0	1.8
<i>Sminthurides</i>	May 84 to Nov 86	3.68	0.036	*	3.3ab	5.5a	1.5ab	1.3b
Ent.+Symph. (without <i>Smin.</i>)	May 84 to Nov 86	4.00	0.028	*	69.0a	45.2b	41.0b	37.3b
Ent.+Symph. (total)	May 84 to Nov 86	4.53	0.019	*	72.3a	51.3ab	42.3b	38.3b

Table 3. – Analysis of variance. After visible effects of experimental perturbations. One factor with five treatments (L–H+, L–H–, L+H+, L+H–, L++). Means belonging to the same homogeneous group (a posteriori Student-Newman-Keuls test when null hypothesis has been rejected) are indicated by a common letter. Significance: N.S. = insignificant; * = significant at the 0.05 level, *** = significant at the 0.001 level.

Animal group	Dates	F value	P value	Significance	Means				
					L–H+	L–H–	L+H+	L+H–	L++
<i>Lepidocyrtus lanuginosus</i>	May 87 to May 89	9.60	0.0004	***	7.6b	5.2b	25.6b	63.2a	25.2b
<i>Sminthurinus signatus</i>	Nov 87 to May 89	4.75	0.016	*	0.5ab	0.0b	2.5ab	5.8a	6.3a
<i>Parisotoma notabilis</i>	Nov 86 to May 89	8.20	0.0005	***	2.5b	1.2b	9.7a	15.3a	6.3a
<i>Sminthurides</i>	May 87 to May 89	21.0	0.0000	***	26.6a	20.4a	2.0b	0.5b	0.2b
Ent.+Symph. (without <i>Smin.</i>)	May 87 to May 89	10.9	0.0002	***	18.0b	12.4b	42.0b	86.4a	48.4b
Ent.+Symph. (total)	May 87 to May 89	10.0	0.0003	***	44.8b	33.2b	44.0b	88.0a	48.4b

Table 4. – Gut contents of most abundant Collembolan species (May 1989, 0–1 cm, L+H+, L+H– and L++ plots), expressed as percentage of frequency of the different food categories (number of animals with a given category in their intestine divided by total number of animals). Animals with empty guts were not accounted for.

Species	Number	Algae	Pollen	Plant tissues	Fungi	Faeces	Mineral	Cuticles
Epigeic species								
<i>Lepidocyrtus lanuginosus</i>	45	2.2	0	1.1	60.0	25.6	11.1	0
<i>Folsomia quadrioculata</i>	35	0	1.4	0	2.9	35.7	60	0
<i>Sminthurinus signatus</i>	12	12.5	8.3	0	4.2	33.3	33.3	8.3
<i>Orchesella cincta</i>	9	0	5.6	0	0	55.6	38.9	0
<i>Parisotoma notabilis</i>	9	0	0	0	11.1	33.3	55.6	0
<i>Megalothorax minimus</i>	9	0	0	0	0	22.2	77.8	0
Endogeic species								
<i>Isotomiella minor</i>	20	0	0	0	0	7.5	92.5	0

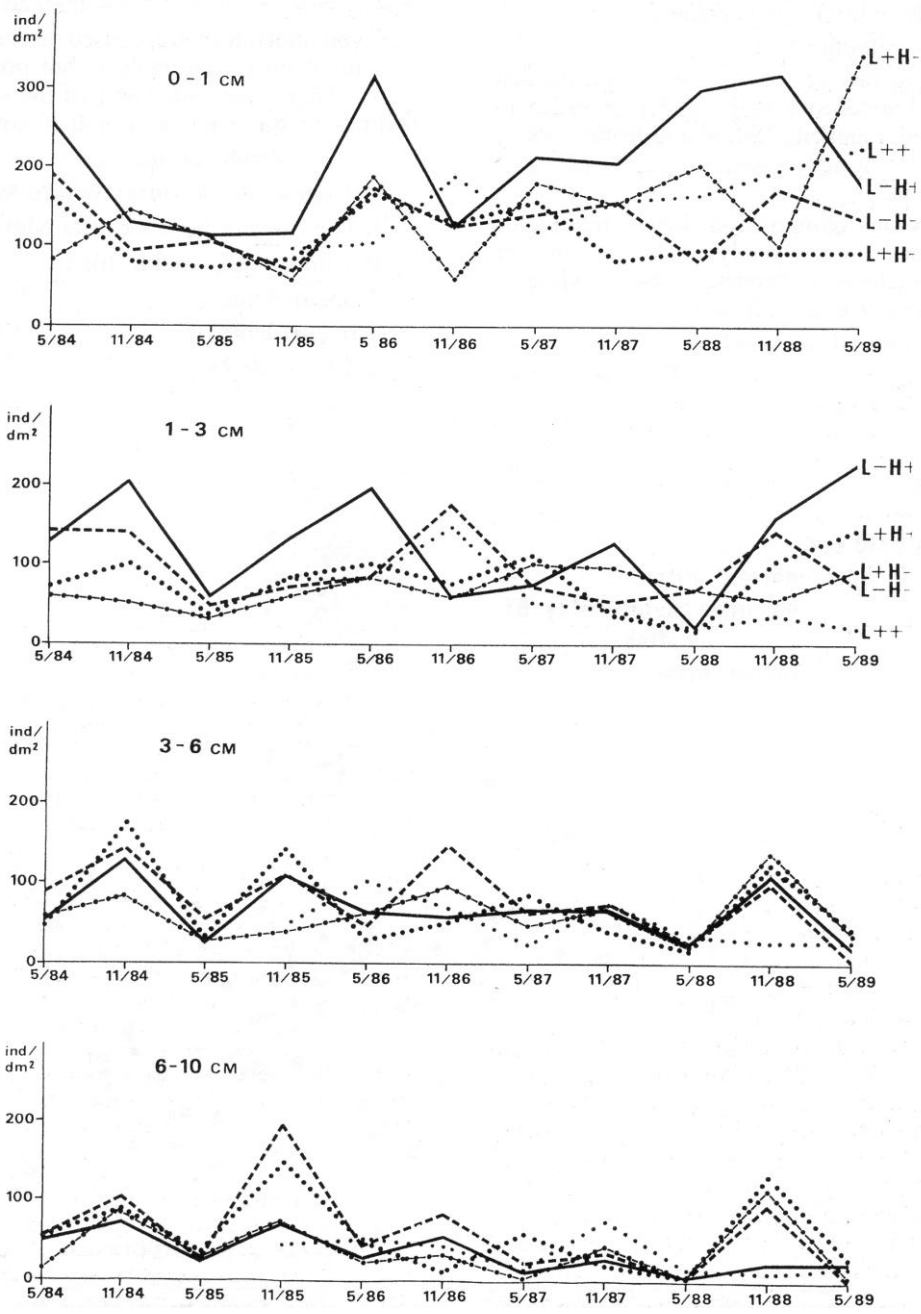


Fig. 1

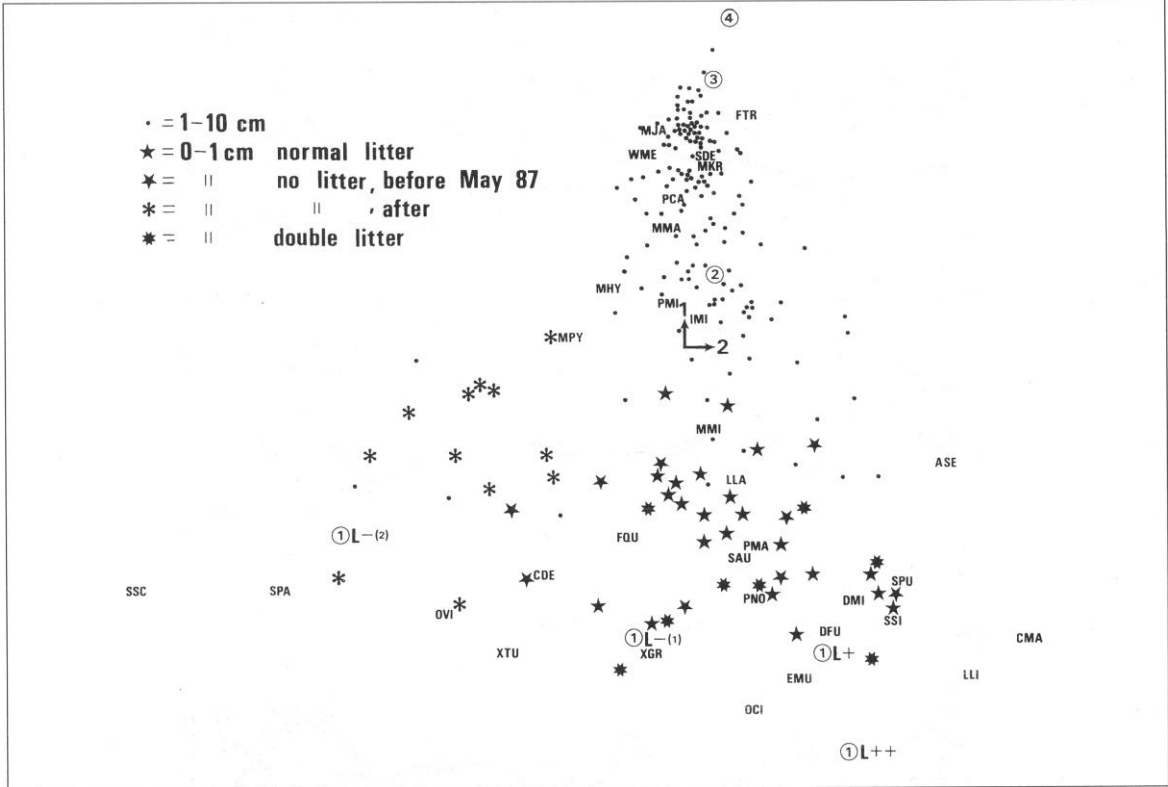


Fig. 2

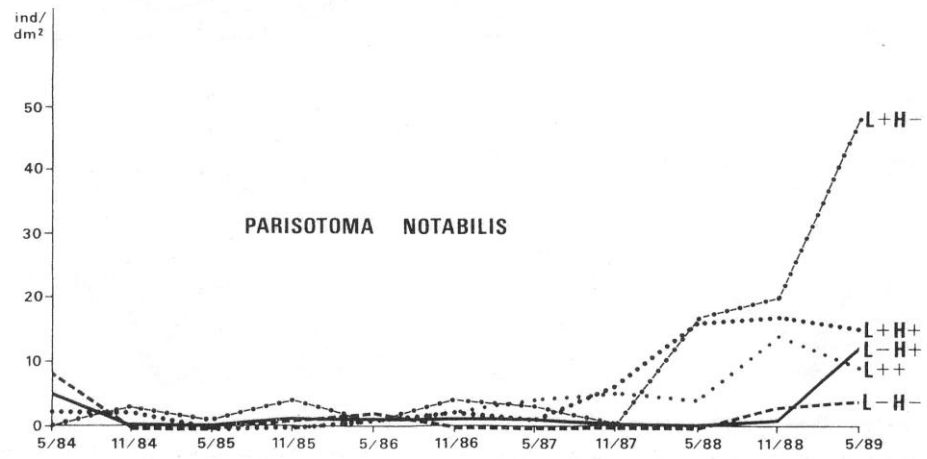
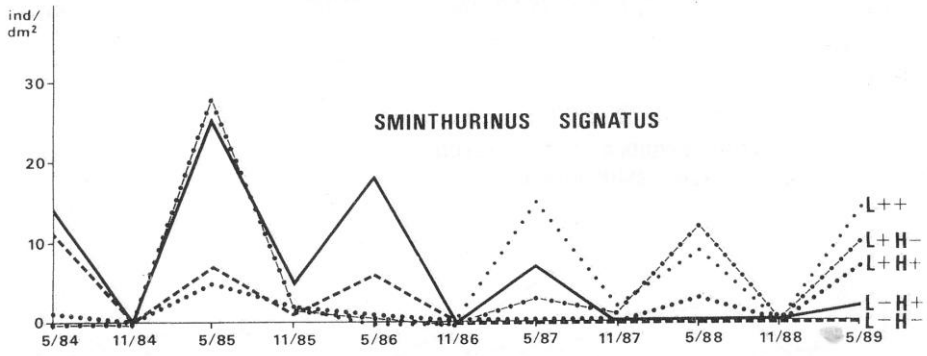
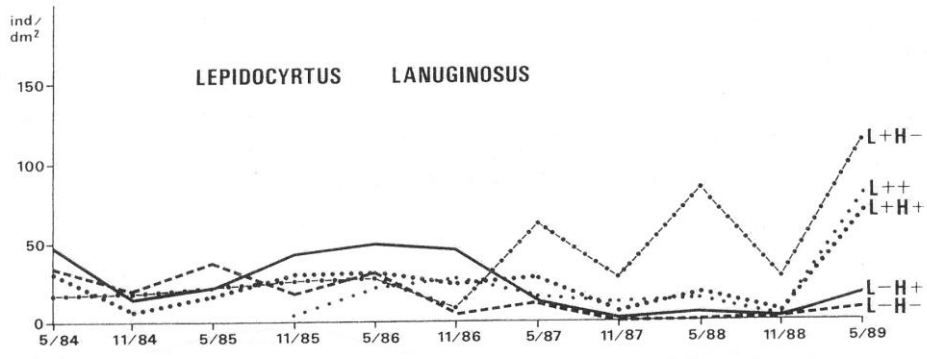


Fig. 3

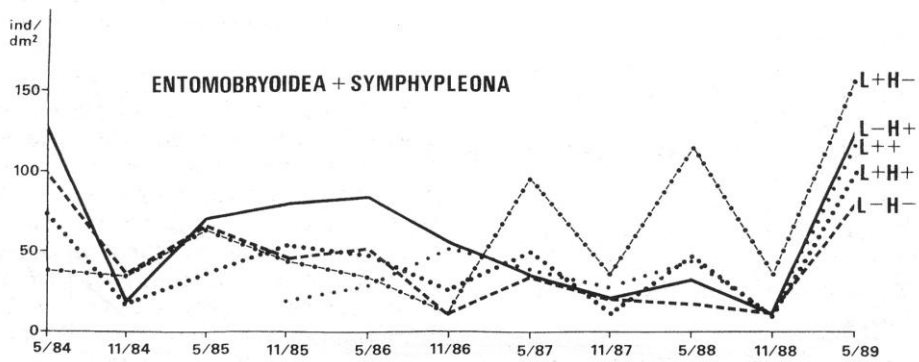
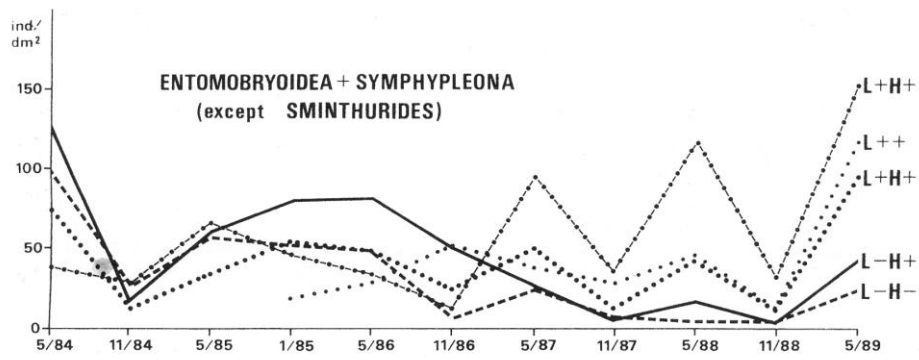
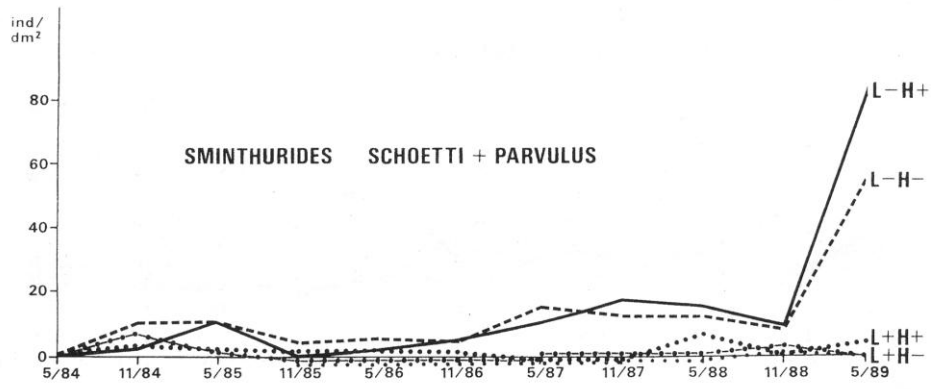


Fig. 4

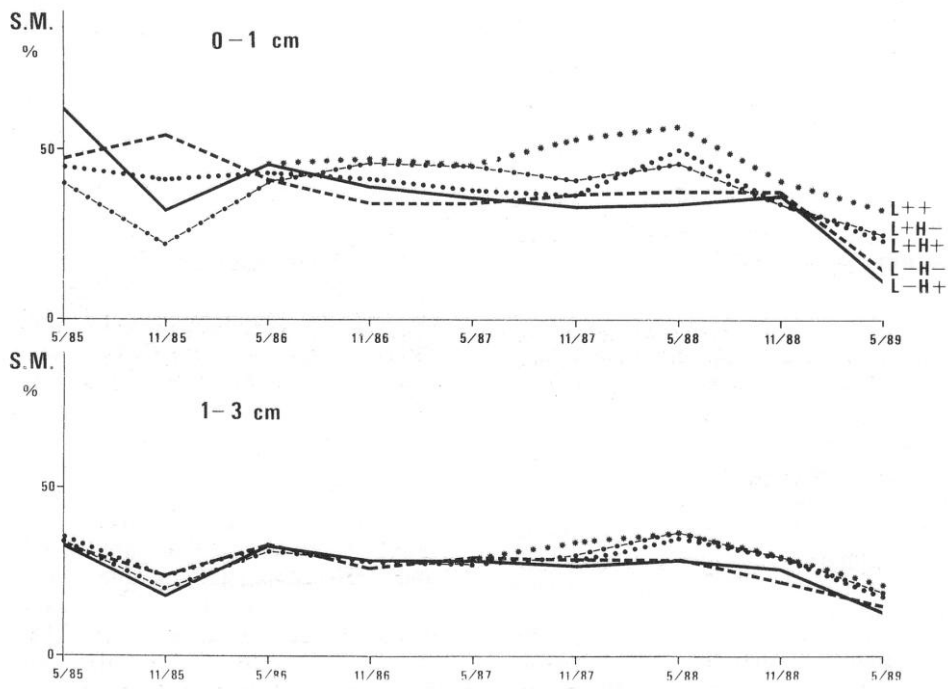


Fig. 5

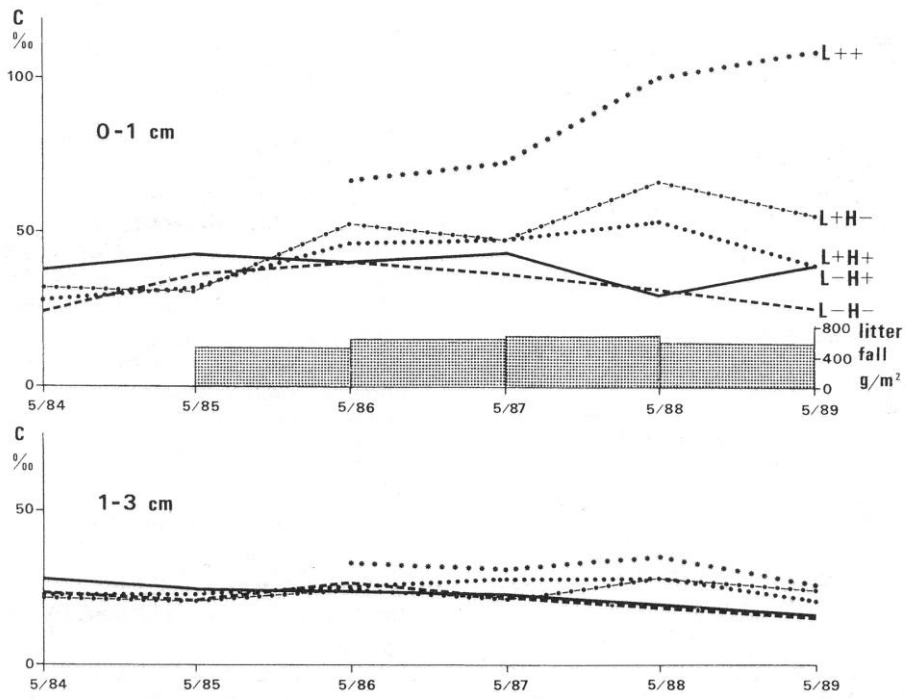


Fig. 6

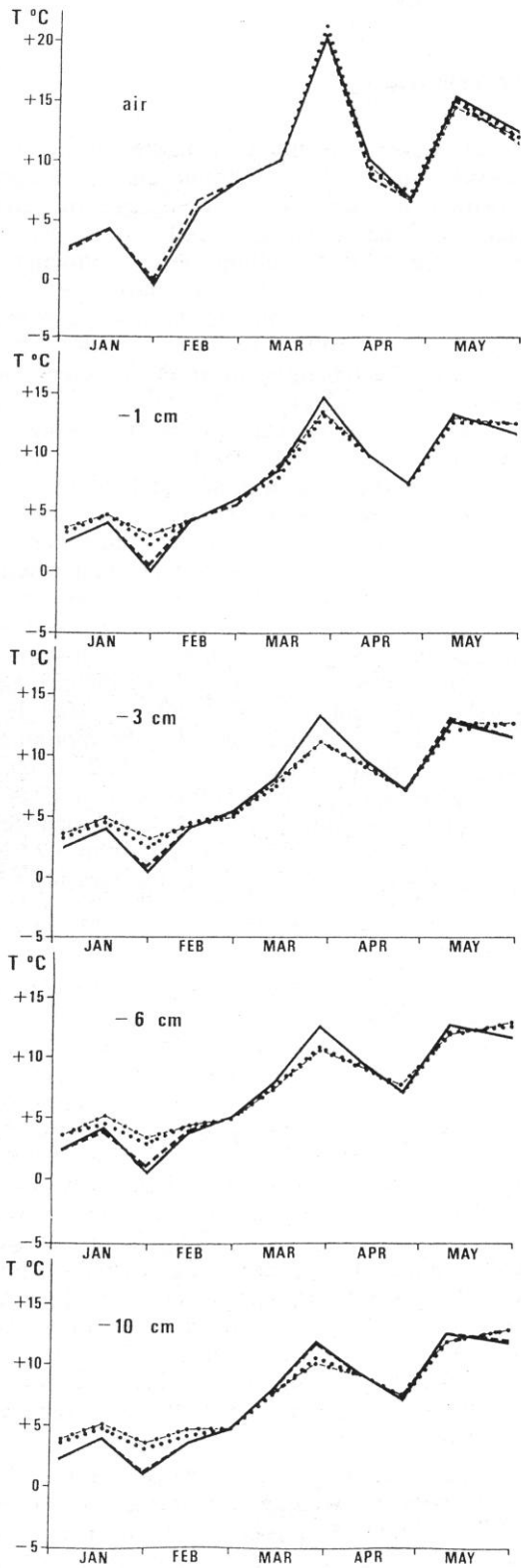


Fig. 7

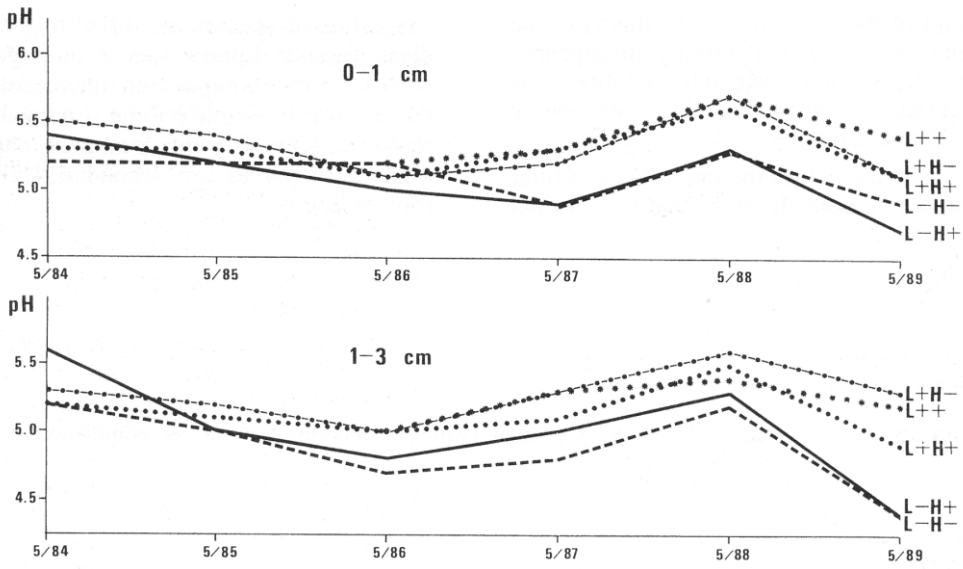


Fig. 8