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Biocenoses of Collembola in atlantic temperate grass-woodland ecosystems

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Summary. Samples (679) from various forest sites in the atlantic temperate region (lowlands in the northern half of France) have been studied. Their Collembolan species composition (145 species, with only 43 rare species) was analysed by Benzecri's correspondence analysis, a multivariate method. Five groups of species, each associated with a given habitat, were determined: above the ground surface a distinction is evident between light species (open sites), hygrophilic species (moist forest sites) and corticolous species (dry forest sites); edaphic species may be divided into acidophilic species (mor, moder and acid mull humus) and neutroacidocline species (earthworm mull). A depth gradient may be traced from edaphic to atmobiotic species in both forest and open sites. As a conclusion, it is apparent that vegetation in itself does not directly influence Collembola but may effect them indirectly through humus formation.

Key words: Collembola, biocenoses, correspondence analysis, spatial heterogeneity, soil acidity

Introduction

Synecology of soil animals develops with a noticeable delay as compared to plant synecology. As a consequence soil animal communities were not included up to now in the study of vegetation dynamics (Miles 1979; Oldeman 1990). The prominent role of soil fauna in the process of humus formation has been proved, both experimentally and by observing humus profiles (Müller 1889; Romell 1932; Jacot 1940; Kubiëna 1955; Bal 1970; Rusek 1975; Bal 1982; Rusek 1985), but our knowledge of the overall effect of environmental changes on soil animal

communities is very poor. Thus it is impossible for the present time to predict shifts in humus type when vegetation or climate are changing. Collembola are common inhabitants of soil, ground vegetation and tree trunks. Water surfaces are also colonized, especially when vegetation is present. Collembolan communities have been analysed by numerous authors (Gisin 1943; Cassagnau 1961; Nosek 1967; Dunger 1975; Kaczmarek 1975; Ponge 1980; Hågvar 1982, 1983; Ponge 1983, among others). Results of these studies give evidence of strong relationships of species composition with soil conditions and plant cover. The aim of the present study was to analyse the structure of a composite sample comprising the range of biotopes occupied by Collembola in the atlantic climatic zone. In a previous study (Ponge 1980), Collembolan communities were investigated in the Senart forest near Paris, sampling being conducted throughout this forest and in every kind of environment (water surface, tree trunks and rocks included). It was concluded that species composition is determined by combinations of very simple ecological factors: light, humidity, depth, soil type. Direct reference to vegetation was unnecessary, as long as soil conditions had not been modified by trees and forestry practices. For instance, Collembolan communities were the same under pine and oak when humus was of the moder type. Following a shift in humus type as a result of pine plantation, soil Collembolan communities also changed. Similarly, given the mild climate of the atlantic zone where temperature is rarely a limiting factor for soil animal species, differences between seasons were mainly attributed to changes in humidity. Further studies analysed Collembolan communities of litter and underlying soil in the Orleans forest (France, Loiret) and in the Senart forest (Ponge & Prat 1982 ; Ponge 1983; Arpin et al. 1984 ; Poursin & Ponge 1984; Arpin et al. 1985, 1986; Ponge et al. 1986). All these samples (except those under experimental treatments) were incorporated into an unique Benzecri's analysis of correspondences (Greenacre 1984), also called reciprocal averaging (Hill 1973), as no differences were observed in species composition from different forests belonging to the same atlantic c1imate zone. Results of the present study hold only for the French atlantic climate, but comparison will be made in this paper with results from other countries and many convergences will be highlighted.

Materials and Methods

Investigated sites

The Senart forest is composed of oak [*Quercus petraea* (Mattus.) Liebl. mixed with *Q. robur* L.] with an undergrowth of hornbeam (*Carpinus betulus* L.), lime (*Tilia cordata* Mill.) or birch (*Betula pendula* Roth) according to soil conditions. Pine [*Pinus sylvestris* L., *P. strobus* L., *P. nigra laricio* (Poir.) Maire] and Douglas

fir [*Pseudotsuga menziesii* (Mirb.) Franco] have been planted in some places. Soil is well- or poorly drained depending on the slope (gentle in the south- west, level in other parts) and nature of the parent rock (sandy or clay loam, with or without boulders). More than hundred ponds and acid bogs are present, thus offering a great variety of water conditions, sometimes at a few meters distance. Some open sites enclosed in the Forest area (cultivated fields, meadows, heathlands, glades) were also investigated (Ponge 1980; Ponge 1983). Samples were taken from every biotope, the aim being to embrace the whole range of possible habitats in the same area. Thus, some calcareous soils were sampled even though they are very rare in this Forest. The range of the studied biotopes is presented in Appendix II. The sampling in 1973−1977 was not seasonal as each site was visited only once, except one site where the relationships between seasonality and soil water conditions were verified. A rough measurement of soil pH was attained using field colorimetry. Vegetation and soil condition were described qualitatively. Sampling was made by hand or by mean of a spoon or a shovel. Size of the sample was chosen in order to maximize species richness: thus moss samples were of a small size, whereas samples from other habitats such as, e.g., mineral parts of podzolic soils, were larger. Animals were extracted by the dry funnel method, i.e. the animals escaping from the sample during the process of drying fall in a funnel under which they are collected. Determination was made at the species level under a light microscope after due preparation of the animals. Data used for statistical treatment were number of individuals (including immature instars) of each species in a given sample. Other sites were chosen for comparing soil animal communities under different soil or vegetation types, in the Senart forest (Arpin et al. 1984) and in the Orleans forest (Ponge & Prat 1982; Poursin & Ponge 1984; Arpin et al. 1986). In the Senart forest, comparisons were made between different humus types, according to distance from the tree trunk or changes in the parent rock. Stainless steel cylinders 15 cm ∅ and 10 cm height were forced into the soil, ensuring a constant surface and volume for sampling. Soil analyses were performed (for details see Arpin et al. 1984). In the Orleans Forest, comparisons between deciduous, mixed and coniferous stands were based on core samples taken repeatedly (3 samples each month and in each stand during one year and a half) with a 5 cm ∅ soil probe forced into the soil down to 10 cm depth. Following procedures as above. When experimental treatments were applied to soil communities (litter shortage in the Park of the Laboratory, Brunoy, S. E. of Paris, Arpin et al. 1985; litter shortage and doubling in the Orleans Forest, David et al. 1991), then only controls were used in the present analysis for comparison with natural communities.

Statistical treatment

Data (number of animals of each species in a given sample, whatever its size) were arranged in a matrix of 101 species X 679 samples. Analysis was made with the help of correspondence analysis (Greenacre 1984), a multivariate method based on the chis-quare metric, thus allowing variation in sample size. Arbitrarily, species that were present in less than 5 samples (44 species) were discarded from the analysis, because of a great uncertainty about their association with an environmental factor. Ordination of samples and species was based only on affinities between species distributions (relative abundanccs). Raw data were transformed into class numbers on order to give a lesser advantage to extreme environments with few species and high animal densities. The following scale was used: 0 individual → 0; 1 → 1; 1 to 5 → 2; 6 to 25 → 3; 26 to 125 → 4; > 125 → 5. The water-dwelling species *Podura aquatica* was not included in the analysis but projected as a supplementary item, due to too high densities in some monospecific samples (plants at the water surface). Information was given on the environment as supplementary items. These were not involved in the calculation but projected as if they had been present (Greenacre 1984). Coding for each environmental descriptor was 1 or 0 according to the relevance of this descriptor for a given sample. Thus biotopes are represented by points which are placed among the corresponding samples. Only species (three letters coding) and biotopes (numbers) have been represented. Appendix I and II list the 101 species and the 60 biotopes (descriptors).

Nomenclature of life forms

Gisin (1943) classified Collembolan species according to their life in “euedaphon” (soil), “hemiedaphon” (litter or other biotopes more or less bound to litter) or “atmobios” (herbs, mosses, trunks, rocks) and associated some morphological characters to their life habits. Despite the practical usefulness of this rule, some exceptions (such as the presence of a functional furcula in some euedaphic species) are noticeable and a new classification was recently proposed by Rusek (1989). The new classification of life forms takes into account these discrepancies and thus I considered it as more convenient. Collembolan species will be divided into atmobiotic species (sub-divided into macrophytobiotic, microphytobiotic, xylobiotic and neustic species) and edaphobiotic species (sub-divided into epigeic, hemiedaphobiotic and euedaphobiotic species). One of the purposes of this study is to identify some species that could be considered characteristic for a given habitat or group of habitats. By characteristic we mean frequent in this habitat or group of habitats and only in it. This implies that i) the species may be frequently found, ii) that this high frequency holds only for this habitat or group of habitat. This definition is different from what is generally admitted by plant synecologists (rare species are excluded) but fits

better our observations. By frequcncy we mean the ratio number of samples where the species is present/total number of samples of the group of samples to be considered. By dominance (i.e. relative abundance) we mean the ratio number of individuals of the species/total number of Collembola in the considered group of samples.

Results

When projected in the sub-space of the first three axes, the cloud of species and samples displayed a tetrapod shape. Four distinct branches are easily visible in the plane of axes 1 and 2 (Fig. 1) and in the plane of axes 2 and 3 (Fig. 2). Branch A (soil) is subdivided into Aa and Ab by axis 4, which is shown in the plane of axes 1 and 4 (Fig. 3). Following axes segregated groups of samples and species that were not judged reliable, as a result of too few number of points in these groups. Interpretation of the axes may be tentatively done as such, with the help of environmental indicators and position of the well separated branches of the cloud: depth of the sampled habitat for axis l, light (or more exactly open opposed to closed environments) for axis 2, dryness for axis 3, soil acidity (and humus type) for axis 4. Nevertheless it must be stressed that three branches for atmobiotic habitats, B (open habitats), C (moist forest habitats) and D (dry forest habitats) are not juxtaposed to axes 2 and 3 (Fig. 2). Thus interpretation of axes 2 and 3 is far from reliable, although branches B, C and D could be interpreted without any doubt as definite communities.

Soil

Branch A is composed of soil samples and species and the farthest points from the origin belong to the samples from the deepest soil horizons in forest biotopes (A horizon: 6, 14, 29, 23). Soil samples from open environments (49 = forest paths; 54 = cultivated fields and meadows, heathlands, glades) are displaced towards the B branch, without accompanying species (Fig. 1). This indicates that the species composition of soils in open places is modified by the presence of atmobiotic species, together with edaphic species. The latter are the same as in forest soil, except perhaps for *Neotullbergia ramicuspis* (NRA) and *Folsomides parvulus* (FPA) which seem to be slightly loosened from the forest soil group, indicating that they are a little more frequent in open environments. Presence of atmobiotic species is also perceptible in the A horizon of moist environments (32 = forest hydromull and more prominently 36 = forest hydro-moder). Conversely, the presence of edaphic species in some atmobiotic habitats may cause a shift in the position of the corresponding points. An example is furnished

by moss cushions which may be sometimes sampled with adhering soil. This caused the displacement of ground moss samples towards the A horizon in acid mull (9) and hydromull humus (32). Axis 4 subdivided the A branch into a group Ab of acidophilic species (with their corresponding samples) and a group Aa of neutro-acidocline species, pH 5 being approximately the shift point (Fig. 3). Tables 1 and 2 list the most frequent species in each of these two branches. *Mesaphorura macrochaeta* (MMA), although considered acidophilic by its position along the Ab branch is also one of the more frequent species of the neutro-acidocline group. Nevertheless its dominance is strikingly less in the Aa group (4%) as compared to the Ab group (32%). Other dominant species common to the two groups are *Isotomiella minor* (lMl), *Paratullbergia callipygos* (PCA), *Megalothorax minimus* (MMI), *Lepidocyrtus lanuginosus* (LLA), *Parisotoma notabilis* (PNO). *Pongeiella falca europea* (PEU) and *Mesaphorura hygrophila* (MHA), although in a pole position (Fig. 3), are in fact rare species: *P. falca europea* is present in 9 samples, *M. hygrophila* in 6 samples. Thus they are not taken into account, except if further studies establish definitely that they belong to soil neutro-acidocline and soil acidophilic communities, respectively. The species underlined in Tabs. 1 and 2 may be considered as characteristic species, since they are both frequent (present in more than 10% of the samples) and placed in a characteristic position by the analysis (thus exclusive of other habitats). Comparison of Tabs. 1 and 2 with Fig. 3 shows that some species are commonly encountered in soil and despite this strongly characteristic of a given community: this is the case for *Micranurida pygmaea* (MPY) (70% of the samples) in the acidophilic group and *Pseudosinella alba* (PAL) (87%), *Mesaphorura hylophila* (MHY) (66%) and *Kalaphorura burmeisteri* (KBU) (65%) in the neutro-acidocline group. Vicariance of species or genera may be highlighted by this analysis. This is true for *Pseudosinella alba* (PAL) and *Pseudosinella decipiens* (PDE) which are replaced by *Pseudosinella mauli* (PMA) in acid conditions. In the same way, *M. hylophila* (MHY) and *Mesaphorura italica* (MIT) are replaced by *Mesaphorura betschi* (MBE) and *Mesaphorura yosii* (MYO) in acid soils and *Onychiurus jubilarius* (OJU), *Onychiurus pseudogranulosus* (OPS) and *K. burmeisteri* (KBU) by *Protaphorura subuliginata* (PSU). Each of the two groups that have been displayed by the analysis is made of several habitats. I separated organo-mineral habitats according to humus type and forest cover. Thus the Aa branch corresponds to earthworm mull humus form (6), which develops only under oak (and accompanying understory such as hornbeam) in the investigated sites. The Ab branch corresponds to moder humus under pines (29), moder humus under oak (23) and acid mull (14), the last form being developed only under oak. The three corresponding points are placed in this order, pine moder being the most characteristic and oak acid mull the least. It seems that the dominant vegetation (pine or oak) does not influence soil animal communities to a great extent, except when changes in humus type are to be

expected. Oak moder and pine moder have quite similar species composition, even though the nature of the litter layer is different. Hydromorphic humus forms (32, 36) are placed in the corresponding branches, but displaced towards the origin, probably due to the presence of atmobiotic species of the C branch.

Epigeic and atmobiotic habitats

Fig. 1 evidences a gradient from soil to atmobiotic habitats along the D branch. For instance, for pine stands, horizons and layers follow this sequence from the A to the D pole: A horizon (29), H layer (28), F layer (27), L layer (26), ground mosses (25), tree trunks (24). The same is true for oak stands, from moder to earthworm mull humus type. Accordingly, a range of species, from edaphic species (see above) to typical cortical species, is distributed along the same path. It must be noticed that the species composition of tree trunk populations does not differ according to nature of the tree, for instance in moder sites pine trunks (24) have exactly the same position as oak trees (15). Tab. 3 displays the mean species composition of samples belonging to the D branch (Fig. 2). This includes fallen wood (2, 8, 16) and herbs (4, 10, 19), whose populations are somewhat similar to those of tree trunks and rocks, although somewhat intermediary with the litter layer (5, 11, 20, 26). If I except *Xenylla xavieri* (XXA) and *Xenylla schillei* (XSC) which are rare species in the studied samples (both only present in 5 samples), species placed in a charasteristic position by the analysis are also very frequent. This is especially the case for *Orchesella cincta* (OCI) (81 % of the samples) and *Xenylla tullbergi* (XTU) (76%). These two species are also present in the litter layers, but bark pieces and tree mosses and lichens shelter far greater populations than does litter.

Figs. l, 2 and Table 4 indicate species composition of moist sites (C branch). Also in this case a gradient is perceptible from soil (32, 36, 41) to herbs (39, 42), both in habitats and in species. Soil with hydro-mull humus (32) belongs to the A branch, but this is no longer the case for hydro-moder soils (36) and definitely not for gley (41). This could be explained by improper conditions of life for soil animals in gley soils and even in the A horizon under hydro-moder (pseudo-gley). Then these soils are very poor in species and presence of atmobiotic hydrophilic species in mixture with true edaphic drive the samples away from the A pole. Better aerated conditions in hydromull offer micro-habitats for edaphic species, with corresponding position along the A branch. Water surface (45), although not included in this gradient in reality, is in a pole position along the C branch. The same Collembolan species moving at the water surface also climb herbs in moist air (39, 42) or are living in litter on the shore (40). The two most frequent species are also placed in a characteristic position by the

analysis, viz. *Isotomurus palustris* (IPA) (74% of the samples) and *Lepidocyrtus lignorum* (LLI) (54%). *Heterosminthurus insignis* (HIN) and *Xenylla brevisimilis* (XBR) are rare species in the studied sample.

The B branch may be studied by help of Fig. 1 and 2 and Table 5. Fig. 1 shows that species in an intermediary position between herbs (52) and soil (54) are lacking. This is because litter, that offers an intermediary layer between soil and vegetation, is absent. Soil surface (53), which is in an intermediary position between edaphic and atmobiotic habitats, is occupied both by atmobiotic and hemiedaphic species, but not by typical epigeic species that are quite absent. The case of glades is somewhat more complicated. Species composition seems to be influenced by the presence of trees and their associated atmobiotic forest species and accordingly the position of environmental descriptors is modified. See the position of tree trunks along forest paths (46). On Fig. 2 this environment belongs to the D branch (tree trunks and rocks), but the point is displaced towards the B branch. On Fig. 1 this point seems to fall within the C branch, which is an artifact. Moreover, in glades, the rise of the water level due to absence of absorption by tree roots (and following transpiration) makes these sites moister than the rest of the forest. Consequently, hydrophilic species are present in openings, making the species composition somewhat puzzling. See for instance the position of herbs in clearings (50) on Fig. 1, 2: it may not be decided whether this environment belongs to the B or the C branch, which is the reflect of its complicated species composition.

Discussion

The most extensive studies on Collembolan communities, i.e. those including a wide range of biotopes, are the works of Gisin (1943), Cassagnau (1961), Nosek (1967) and Szeptycki (1967). The former three scientists studied mountain sites with great ecological diversity, elevation having a marked influence both on vegetation and on soil biocenoses. Gisin (1943) recognized the influence of macroclimatic factors (elevation and exposure) together with microclimatic influence (humidity), soil acidity and human influence (N enrichment). Cassagnau (1961) and Nosek (1967) did not recognized the direct influence of soil chemistry on soil communities but postulated instead that the vegetation determines the living habits of soil animals, except in some extreme cases with poorly developed vegetation. For Cassagnau (1961), soil chemistry acted only upon necrophilous populations. Nosek (1967) described distinct plant communities according to the nature of the parent rock (limestone opposed to granite and gneiss) and found accordingly distinct soil animal communities but he never tried to separate vegetational influence from direct soil influence (for instance in sampling rare habitats where

vegetation and soil are conflicting, like in the present study). Both Gisin (1943), Cassagnau (1961) and Nosek (1967) divided their composite sample into distinct units, so called “synusies” , each being characterized by a typical species composition, and assessed them by numerical methods. In addition, Gisin (1943) recognized the sensitivity of some Collembolan species to particular environmental factors and classified the species into ecological categories: xerophilous, hydrophilous, acidophilous, etc. Szeptycki (1967) ordinated the samples and species by mean of their relationship to known plant associations. Gisin (1943) and Szeptycki (1967) recognized the influence of soil acidity upon Collembolan communities, but attributed this effect to the influence of coniferous vegetation.

Among numerous studies that were conducted on Collembolan communities, but in a narrower range of environments, those of Hågvar (1982, 1983) and Hågvar & Abrahamsen (1984) deserve a special attention . They selected 15 sites belonging to 7 forest types (spruce and pine stands) at two different elevations and classified the species according to their affinities with plant communities and ecological factors such as soil chemistry. Their study, although limited in time and space, may be considered as a reference work, because of the extent of the thorough calculations that were made on the data matrix. Other recent studies have used multivariate analysis as a tool for delineating communities but unfortunately only on a small number of sites (Arbea & Jordana 1985; Pozo 1986; Mateos 1988). In the present discussion I will analyse results in the light of existing knowledge on Collembolan communities and tentatively trace the way in which these animals are sensitive to environmental influences.

Vertical distribution (A to B, C *and D branches)*

Axis 1 was interpreted as corresponding to a depth gradient from the mineral soil horizon through humus and litter layers to the atmobiotic habitats (herbs and trees). This influence must be considered as prominent, at least in lowland sites. Gisin (1943) recognized that the influence of depth was complicated, and included temperature, light and humidity. Nature of the food and behavioural adaptations of the species could also be added to these niche components. Despite the complicated nature of the depth gradient, the present results agree well with other papers dealing with the influence of depth (Gisin 1943; Szeptycki 1967; Bödvarsson 1973; Kaczmarek 1975; Hågvar 1983; Gerdsmeier & Greven 1987; Pichard et al. 1989). Nevertheless it must be stressed that Gisin (1943) related vertical distribution to morphological characters, especially the development of legs, eyes, furcula and pigment, which were reduced or absent in edaphic species and well-developed in atmobiotic species. This is

not always the case, as was discussed recently by Rusek (1989), where the terms were newly defined and applied to ecological analysis.

The problem which arises concerning the present results as compared to literature is that distinct communities were not registered according to the type of plant cover. André (1983) stated that no c1ear relationships could be found between Collembolan corticolous species and a given epiphyte or tree cover, this was not the case when co-occurring oribatid mites were analysed separately (André 1984) or added to the same analysis (André 1985). Site influence (independent of ecological factors) was prominent, which led André (1984) to consider distinct forests as isolated islands. He interpreted the lack of specificity of Collembola towards bark cover as the result of the absence of true corticolous communities in Collembola. This can be compared with the results of Bauer (1979) and Bowden et al. (1976) who demonstrated that Collembola climb from litter to tree trunks in some seasons and thus that there are no permanent trunk populations. The problem is now shifted towards the litter: does litter type influence Collembola? The present results show that pine stands and oak stands had similar litter-dwelling populations: on Fig. 1, 3 see the position of points 26 (litter L layer on moder humus under pines) and 20 (same biotope under oaks). Gisin (1943) did not note links betwen the nature of the litter and species composition. Cassagnau (1961), Szeptycki (1967), Nosek (1967) and Kaczmarek (1973) did not separate forest populations according to depth, thus their work cannot be used for comparison. Hågvar (1982, 1983) separated each 3 cm in soil cores and studied vertical distribution but unfortunately comparison between soil types were made on whole soil samples. Pozo (1986) analysed a composite sample where depth and vegetation both varied and also used correspondence analysis. He registered differences in species composition in the litter, but examination of his graphs shows that these variations were mainly due to humidity and light, and not to vegetation. Mateos (1988) compared different soil types under the same dominant vegetation (*Quercus ilex*) and found differences in litter populations. As he used correspondence analysis too, some information can be gained from examination of his data. It is probable that the two stands that differ in their litter Collembolan communities have distinct features, apart from soil chemistry. In one stand litter seems inhabited by typical corticolous (or "tree-c1imbing") species: *Xenylla* spp. And *Entomobrya nivalis*, epigeic species being prevalent in the other stand. Probably the first stand has a moss cover that confers to its litter the character of an atmobiotic habitat, with corresponding dry-tolerant species. Thus in this case site differences could be assigned to differences in aeration of the litter, i.e. to the depth gradient. The question remains open, but it is clear that in my samples no difference in litter, herbs and tree trunks communities could be attributed to vegetation. This is not unexpected, as Collembola living on the ground surface mainly feed on algae, pollen grains and fungi, and not directly on

leaf or bark litter (Anderson & Healey 1972; Ponge & Charpentié 1981; Kilbertus & Vannier 1981; Verhoff et al. 1988; Ponge 1991).

Contrast between open (B branch) and forest sites (C *and D branches)*

References to this phenomenon are numerous and comparisons can be made between results presented here and those of other authors. Gisin (1943) described two distinct "synusies" in open sites, an hemi-edaphic group, with *Brachystomella parvula, Isotoma viridis* and *Lepidocyrtus cyaneus* as characteristic species, and an atmobiotic group with *Sminthurus viridis* Linné 1758, *Bourletiella* spp. and *Entomobrya nivalis.* If we consider that *Sminthurus nigromaculatus* was confused with S. *viridis* until the work of Gisin (1957), and *Entomobrya multifasciata* with *E. nivalis* until Gisin (1947), there is a strong analogy between these two ecological groups and my "B branch". Gisin's (1943) distinction between "hemi-edaphon" and "atmobios" for grasslands is rather unreliable since animals move frequently from the base to the top of herb culms. Cassagnau (1961) indicates, among others, that *Brachystomella parvula* has preferences towards grasslands versus woodlands. Other species noted by him are absent from my sample, except *Isotomurus palustris,* which I consider as typical of moist environments (see further). Nosek (1967) considered *Entomobrya lanuginosa* as a constant species of the *Folsomia alpina* synusy, characteristic for the initial stages of vegetation at the alpine level. Szeptycki (1967) indicates, among others, *Entomobrya multifasciata* as typical for dry open environments, and *Brachystomella parvula, Isotoma viridis, Isotomurus palustris* and two *Lepidocyrtus* species absent from my sample as typical for moist open environments. No distinction could be made between moist and dry open environments in my data, except for bogs and sunny ponds which are dominated by hydrophilic species, *Isotomurus palustris* being one of them (see the discriminating power of multivariate analysis, when separating light from water species, as on Fig. 2). In fact dryness is not a commonly encountered feature in the region here studied, thus it is quite normal that most of the present open species falls into Szeptycki's (1967) "photophilous euryhygric" group. In the work of Kaczmarek (1973) some species are typical or preferential inhabitants of meadows as compared to woodland and these (*Entomobrya multifasciata*, *Lepidocyrtus cyaneus* and *Isotoma viridis*) are present in the "B branch". *Isotoma olivacea* Tullberg 1871, whose true identification is probably *Isotoma tigrina* [see Fjellberg (1979) for revision of the *tigrina* group] and which belongs to the "B branch", was also noted by this author as a light species. Reference to two of the present light species, namely *Entomobrya lanuginosa* and *Brachystomella parvula,* is found in Dunger (1975) as typical for the first stages of natural successions leading to the

establishment of forests on coal mine spoils. Gers & Izarra (1983) and Pozo (1986) noted *Brachystomella parvula, Isotoma viridis, Lepidocyrtus cyaneus* and *Sminthurinus elegans* as meadow species. Thus 1 consider that all but one species belonging to the "B branch" in my analysis [the exception being *Sminthurides assimilis,* which is considered as a rare species by Gisin (1960)] are found in the literature as typical for open environments. Do these species have a common adaptation to the constantly changing environmental conditions of open sites? Trophic reasons cannot be discarded, but data on the specificity of Collembolan species towards food resources are rather conflicting (MacMillan 1976; Marshall 1978; Ponge & Charpentié 1981; Kilbertus & Vannier 1981; Saur & Ponge 1988), and thus nothing can be said definitely about the selection of species by food resources. Ecophysiology might be more adequate for explaining the specific influence of open habitats, especially if we consider that only atmobiotic species are concerned. Betsch & Vannier (1977) compared the juvenile and adult stages of two species belonging to related genera, the one, *Allacma fusca* (AFU) being a forest species, and the other, *Sminthurus viridis,* a meadow species. Both adult stages were able to support dryness several days long, but the first juvenile stage of *A. fusca* was unable to stay alive more than a few hours, contrary to one day for S. *viridis.* Thus a physiologically minor difference in the life history of these species may explain an ecological segregation between forest and meadow species. This is not the case for *Isotoma viridis* (IVI), which has been proved to be very sensitive to desiccation by Joosse (1970). Perhaps in this species, and in the case of other light species of the "photophilous euryhydric" group of Szeptycki (1967), attraction to light might simply be the driving force. My own observations (unpublished data) showed that some springtail species such as *Entomobrya multifasciata* (EMA), one of the "B branch species", is easily trapped with a light apparatus inside houses.

Contrast between moist (C *branch) and dry forest sites (D branch)*

Gisin (1943) distinguished well-defined communities in soil, litter and atmobios according to their water requirements. I do not agree with him regarding the soil, but we have similar results in the other two habitats. In the "mesophile hemiedaphon", Gisin placed *Sphaeridia pumilis* (SPU) (called by him *Sminthurides pumilis), Sminthurides schoetti* (SSC), *Isotomurus palustris* (IPA), *Orchesella villosa* (OVI), that belong to the "C branch", and he placed in the "xerophile hemi-edaphon" *Vertagopus arboreus* (VAR) (called by him *Isotoma arborea), Entomobrya nivalis* (ENI), *Orchesella cincta* (OCI), *Xenylla tullbergi* (XTU), *Pseudosisotoma sensibilis* (PSE) (called by him *Isotoma sensibilis),* that belong to the "D branch", Cassagnau (1961) considered

the following species belonging to the "C branch" as hygrophilous: *Podura aquatica* (PAQ), *Sminthurides malmgreni*, *Isotomurus palustris.* Szeptycki (1967) did not separate dry and moist habitats in forests but considered *Tomocerus minor* (TMI) as abundant near springs and ponds and *Sminthurides malmgreni* (SMA) and *Podura aquatica* (PAQ) as aquatic species. The most complete work on hygro- and hydrophilic species is the paper by Pichard et al. (1989), whose sampling area partly includes our sites (Senart forest). They found *Podura aquatica* (PAQ) and *Sminthurides malmgreni* (SMA) on water surfaces. In the vicinity of ponds they found *Lepidocyrtus lignorum* (LLI), *Sphaeridia pumilis* (SPU), *Isotomurus palustris* (IPA), *Tomocerus minor* (TMI), *Heterosminthurus insignis* (HIN), *Protaphorura lata* (PLA) (= *Onychiurus latus* in their paper), *Sminthurides schoetti* (SSC), *Orchesella villosa* (OVI), *Ceratophysella denticulata* (CDE), *Arrhopalites caecus* (ACA), *Folsomia quadrioculata* (FQU), i.e. all of my "C branch" species, except *Xenylla brevisimilis* (XBR). The case of *Folsomia quadrioculata* is somewhat particular and needs to be discussed. In Pichard et al. (1989) this species was abundant only around Senart forest ponds and was replaced by *Folsomia nana* Gisin 1957 *(F. manolachei* in the present paper), a closely related species, in the other investigated site. I consider that precise identification of this group of species needs additional work. Although distinctly separated by morphological characters (Deharveng 1982; Wetton 1987) no clear physiological behaviour or environmental differences are able to explain why populations of these two species are so sharply segregated in the field. Concerning the hydrophilic status of *F. quadrioculata,* I observed that these animals were able to live within a water pellicle, their cuticle being rapidly wettened when placed on a drop of water. This was impossible with *F. manolachei* even when forced with a brush. The reason is probably anatomical differences in the tegument and seta furnishing (Deharveng 1982; Wetton 1987). The problem is that *F. quadrioculata* occurs both in water-saturated litter (on pond shores or at the bottom of intermittent drains) and in well aerated litter in common forest stands. Do these populations belong to the same species? The question remains open.

Contrast between neutro-alkaline (Aa branch) and acid (Ab branch) soils

Differences between softwood and hardwood species were often attributed to vegetational influences (Cassagnau 1961; Szeptycki 1967; Bödvarsson 1973) but since the work of Gisin (1943) it has been established that humus type is a decisive factor in the establishment of soil Collembola communities. Other works showed that changes in soil conditions under the same tree species supported changes in species composition (Hågvar 1982; Hågvar & Abrahamsen 1984; Mateos 1988) and our own research presents evidence that the way in which litter is

decomposed is more important than the nature of the litter (Ponge 1980; Ponge & Prat 1982; Poursin & Ponge 1982; Ponge 1983; Poursin & Ponge 1984; Arpin et al. 1984; Arpin et al. 1986; Ponge et al. 1986). If we compare the results of the present study to those in the literature, there are many similarities. Gisin (1943) quoted *Willemia anophthalma* (WAN), *Friesea mirabilis* (FMI) (all belonging to my Ab branch) as acidophilic species and *Onychiurus pseudogranulosus* (OPS) (called at this date O. *granulosus*), *Folsomides parvulus* (FPA) (all belonging to my Aa branch) as neutro-alkalinophilic species. Incomplete taxonomy at the time of Gisin's (1943) study makes comparisons invalid for most species. Haybach (1959) quoted *Lipothrix lubbocki* (LLU), *Friesea mirabilis* (FMI), *Micranurida pygmaea* (MPY), *Willemia anophthalma* (WAN) (Ab branch) as inhabitants of acid soils with pH 3 to 5 (from podzol to brown leached soil) and *Lepidocyrtus curvicollis* (LCU), *Kalaphorura burmeisteri* (KBU), *Dicyrtomina minuta* (DMI), *Onychiurus pseudogranulosus* (OPS) (Aa branch) as inhabitants of other soils (pH more than 5). Cassagnau (1961) did not accept that soil acidity had any influence upon Collembola populations but associated *Ceratophysella armata* (CAR) and *Willemia anophthalma* (WAN) (Ab branch) to coniferous stands with raw humus (dysmoder). Szeptycki (1967) noted *Willemia anophthalma* (WAN) (Ab branch) as characteristic for coniferous forests. Hågvar & Abrahamsen (1984) made numerous calculations between densities of Collembola populations and environmental parameters and found that three species, namely *Micranurida pygmaea* (MPY), *Willemia anophthalma* (WAN) and *Mesaphorura yosii* (MYO) (Ab branch), were acidophilic. This was confirmed by acidification experiments (see further). Segregation between acidophilic and neutro-alkalinophilic species was showed by Ponge (1980,1983) and influence of vegetation on humus type was postulated as a decisive factor in the establishment of soil Collembola communities (Ponge & Prat 1982; Poursin & Ponge 1984; Arpin et al. 1984, 1986; Ponge et al. 1986). Dunger (1986) questioned Hågvar's and our findings concerning the ecology of *Mesaphorura yosii* since he found it in the more basic substrates along a pollution gradient. I nevertheless question his results, since he studied a site where human influence (toxic emissions from a factory chimney) was probably not negligible. It would have been necessary to sample unpolluted areas with similar substrates before negating the influence of soil chemistry.

The present results support the hypothesis that soil springtails are not directly influenced by vegetation (for example through plant remains as food) but rather depend on soil chemistry. Let us examine how this contention may be supported by both literature and my own results. I found that pH 5 is a threshold for species composition, i.e. below this value some species are present that are replaced by others at higher pH's, the other (few) species being tolerant to both acid and neutro-alkaline conditions. I recognize that pH does not reflect the entire soil

chemistry (Jenny 1961), but it is usually found that pH 5 could be taken as a threshold in herbaceous vegetation and Collembolan communities changes. It must be remembered that this value is the threshold under which aluminium is free in soil and most organic acids have their main acidic activity (Bruckert & Rouiller 1979). Acidity may influence the animals both directly and indirectly. Food resources may be affected via the balance between bacteria and fungi, fungi being favoured at lower pH's (Davey & Danielson 1968; Collins et al. 1978). In the case of Collembolan communities, I did not find any shift in the part played by fungal feeding species from acidic to neutro-alkaline soils. Mycetophagous species are present in my Aa branch [*Pseudosinella alba* (PAL), *Pseudosinella decipiens* (PDE), *Willemia buddenbrocki* (WBU)] as well as in the Ab branch [*Willemia intermedia* (WIN), *Willemia anophthalma* (WAN), *Pseudosinella mauli* (PMA)], and one of these species proved to feed indifferently on any fungal strain that was present in its environment (Ponge & Charpentié 1981). On the contrary experimental results give evidence that acidity directly influenced some Collembolan species. Mertens (1975) measured the movement of *Orchesella villosa* (OVI) when placed on an agar substrate adjusted to different pH levels. He observed that the animals moved as pH differed from an optimum value of about 6.5 where they stay motionless. Huston (1978) presented evidence that pH acted upon survival time and fecundity of *Folsomia candida* (FCA) populations. Jaeger & Eisenbeis (1984) measured absorption of water by *Pogonognathellus flavescens* (PFL) at different pH's of the offered solution and observed a continuous trend, with a sharp decrease from pH 5 to pH 2. During acidification experiments in the field or in greenhouses, changes in species composition were observed (Hågvar & Abrahamsen 1980; Abrahamsen et al. 1980; Hågvar 1984). Three acidophilic species, namely *Mesaphorura yosii* (MYO), *Micranurida pygmaea* (MPY) and *Willemia anophthalma* (WAN), proved to be favoured by addition of sulphuric acid to a near neutral substrate (pH 6) and disfavoured by liming for the former two species. Competition was hypothesized as a key factor, since monocultures gave results that conflicted with full faunal cultures (Hågvar 1990).

Seasonal changes

No mention was made of changes in species composition that could be attributed to seasonal influences. It can be seen on Fig. 1, 2, 3, that identifying points for the four seasons (57, 58, 59, 60) are placed near the origin by the analysis. This means that no axis has a good correlation with seasonality. This does not imply a lack of seasonal trends in Collembolan communities and this discrepancy with other studies (Ponge 1973; Bödvarsson 1973; Prat & Massoud 1981; Gers & Izarra 1983; Wolters 1983; Rusek 1984; Gerdsmeier & Greven 1987) is only apparent.

Collembola in temperate forest ecosystems may move towards more favourable environments in cold or dry seasons, either downwards or to other places on the ground floor. Prat & Massoud (1982) proved that *Vertagopus cinereus* (Nicolet 1841) that was living in the moss layer in winter and early spring migrated into the soil during summer. Climbing behaviour of epigeic Collembola proved to be correlated with rainfall (Bowden et al. 1976; Bauer 1979) and this may explain seasonal variations in trunk populations. Hygrophilic species such as *Tomocerus minor* (TMI) may be more aggregated in summer than in other seasons, due to concentrations in moister places (Verhoff & van Selm 1983). My conclusion is that in the investigated site, like in other temperate countries, no disappearance of species takes place during the year, just that changes occur in the place where animals are living. This could not be true under harder climates such as in mountains, but Cassagnau (1961) and Gers & Izarra (1983) gave indirect evidence of species movement that followed changes in the snow coyer. I registered in the same place (on the bank of a little stream in forest) changes in species composition from July to October 1974, "dry litter" species such as *Lepidocyrtus lanuginosus* (LLA) and *Sminthurinus signatus* (SSI) being respectively replaced by "moist litter" species such as *Lepidocyrtus lignorum* (LLI) and *Sminthurinus aureus.* Thus the bulk of variation due to seasonality is in fact included in other environmental factors, humidity and depth being prominent.

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References

Abrahamsen, G., Hovland, J., Hågvar, S. (1980) Effects of artificial acid rain and liming on soil organisms and the decomposition of organic matter. In: Hutchinson, T.C., Havas, M. (eds) Effects of acid precipitation on terrestrial ecosystems. Plenum Publishing Corporation, 341−362.

Anderson, J.M., Healey, I.N. (1972) Seasonal and inter-specific variation in major components of the gut contents of some wood land Collembola. Journal of Animal Ecology **41**, 359−368.

André, H.M. (1983) Notes on the ecology of corticolous epiphyte dwellers. II. Collembola. Pedobiologia **25**, 271−278.

André, H.M. (1984) Notes on the ecology of corticolous epiphyte dwellers. III. Oribatida. Acarologia **25**, 385−395.

André, H.M. (1985) Associations between corticolous microarthopod communities and epiphytic cover on bark. Holarctic Ecology **8**, 113−119.

Arbea, J.I., Jordana, R. (1985) Estudio ecologico de la colembofauna de los suelos del macizo de Quinto Real (Pirineos Occidentales) y descripcion de dos especies nuevas: *Anurida flagellata* sp. n. y *Onychiurus subedinensis* sp. n. (Insecta, Collembola). Boletin de la Estacion Central de Ecologia **14**, 57−80.

Arpin, P., David, J.F., Guittonneau, G.G., Kilbertus, G., Ponge, J.F., Vannier, G. (1986) Influence du peuplement forestier sur la faune et la microflore du sol et des humus. I. Description des stations et étude de la faune du sol. Revue d'Ecologie et Biologie du Sol **23**, 89−118.

Arpin, P., Kilbertus, G., Ponge, J.F., Vannier, G., Verdier, B. (1985) Réactions des populations animales et microbiennes du sol à la privation des apports annuels de litière: exemple d'une rendzine forestière. Bulletin d 'Ecologie **16,** 95−115.

Arpin, P., Ponge, J.F, Dabin, B., Mori, A. (1984) Utilisation des nématodes Mononchida et des collemboles pour caractériser des phénomènes pédobiologiques. Revue d 'Ecologie et Biologie du Sol **21**, 243−268.

Bal, L. (1970) Morphological investigation in two moder-humus profiles and the role of the soil fauna in their genesis. Geoderma **4,** 5−36.

Bal, L. (1982) Zoological ripening of soils. Pudoc, Wageningen.

Bauer, T. (1979) Die Feuchtigkeit als steuernder Faktor für das Kletterverhalten von Collembolen. Pedobiologia **19**, 165-175.

Betsch, J.M. Vannier, G. (1977) Caractérisation des deux phases juvéniles *d'Allacma fusca* (Collembola, Symphypleona) par leur morphologie et leur écophysiologie. Zeitschrift für Zoologische Systematik und Evolutionsforschung 15, 124−141.

Bödvarsson, H. (1973) Contributions to the knowledge of Swedish forest Collembola, with notes on seasonal

variation and alimentary habits. Royal College of Forestry, Stockholm, Institute of Forest Zoology, Research Notes 13.

Bowden, J., Haines, I.H., Mercer, D. (1976) Climbing Collembola. Pedobiologia **16**, 298-312.

Bruckert, S., Rouiller, J. (1979) Mécanismes de régulation du pH des sols. In: Bonneau, M., Souchier, B. (eds) Pédologie. Vol. 2. Constituants et propriétés du sol. Masson, Paris, 354−365.

Cassagnau, P. (1961) Ecologie du sol dans les Pyrénées centrales. Les biocénoses des Collemboles. Hermann, Paris.

Collins, V.G., D'Sylva, B.T., Latter, P.M. (1978) Microbial populations in peat. In: Heal, O.W., Perkins, D.F. (eds) Ecological studies, Vol. 27. Springer Verlag, Berlin, 94−112.

Davey, C.B., Danielson, R.M. (1968) Soil chemical factors and biological activity. Phytopathology 58, 900−908.

David, J.F., Ponge, J.F., Arpin, P., Vannier, G. (1991) Reactions of the macrofauna of a forest mull to experimental perturbations of litter supply. Oikos **61,** 316−326.

Deharveng, L. (1982) A propos des *Folsomia* du groupe *quadrioculata* Tullberg, 1871. Revue d'Ecologie et Biologie du Sol **19**, 613-627.

Dunger, W (1975) On the delimitation of soil microarthropod coenoses in time and space. In: Vanek, J. (ed) Progress in soil zoology, Proceedings of the 5th International Colloquium on Soil Zoology, Prague, Czechoslovakia, 17/IX−22/IX 1973. Academia, Prague, 43−49.

Dunger, W. (1986) Observations on the ecological behaviour of some species of the *Tullbergia krausbaueri* group. In: Dallai, R. (ed) 2nd International Seminar on Apterygota, Siena, Italy, 4/IX−6/IX 1986, 111−115.

Fjellberg, A. (1979) Revision of the European species in the *Isotoma olivacea-group* (Collembola: Isotomidae). Entomologica Scandinavica **10**, 91−108.

Gerdsmeier, J., Greven, H. (1987) Zur Kenntnis der Collembolenfauna des Eggegebirges. Abhandlungen aus dem Westfalischen Museum für Naturkunde **49**, 1−49.

Gers, C., de Izarra, D.C. (1983) Rupture de l'équilibre biocénotique des populations de collemboles à la station

de ski de Calmazeille-Formiguères (Pyrénées Orientales). Bulletin de la Société d'Histoire Naturelle de Toulouse **119**, 63−69.

Gisin, H. (1943) Ökologie und Lebensgemeinschaften der Collembolen im schweizerischen Exkursionsgebiet Basels. Revue Suisse de Zoologie **50**, 131−224.

Gisin, H. (1947) Le groupe *Entomobrya nivalis* (Collembola) avec quelques remarques sur la systématique, la biocénotique et l'évolution des espèces jointives. Mitteilungen der Schweizerischen Entomologischen Gesellschaft **20,** 541−550.

Gisin, H. (1957) Sur la faune européenne des collemboles. I. Revue Suisse de Zoologie **64**, 475−496.

Gisin, H. (1960) Collembolenfauna Europas. Museum d'Histoire Naturelle, Geneva.

Greenacre, M.J. (1984) Theory and applications of correspondence analysis. Academic Press, London.

Hågvar, S. (1982) Collembola in Norwegian coniferous forest soils. I. Relations to plant communities and soil fertility. Pedobiologia **24,** 255−296.

Hågvar, S. (1983) Collembola in Norwegian coniferous forest soils. II. Vertical distribution. Pedobiologia **25**, 383−401.

Hågvar, S. (1984) Effects of liming and artificial acid rain on Collembola and Protura in coniferous forest. Pedobiologia **27**, 341−354.

Hågvar, S. (1990) Reactions to soil acidification in microarthropods: is competition a key factor? Biology and Fertility of Soils **9**, 178−181.

Hågvar, S., Abrahamsen, G. (1980) Colonisation by Enchytraeidae, Collembola and Acari in sterile soil samples with adjusted pH levels. Oikos **34**, 245−258.

Hågvar, S., Abrahamsen, G. (1984) Collembola in Norwegian coniferous forest soils. III. Relations to soil chemistry. Pedobiologia **27**, 331−339.

Haybach, G. (1959) Über die Collembolenfauna verschiedener Waldböden. Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien **98/99**, 31−51.

Hill, M.O. (1973) Reciprocal averaging: an eigenvector method of ordination. Journal of Ecology **61**, 237−249.

Hutson, B.R. (1978) Influence of pH, temperature and salinit y on the fecundity and longevity of four species of Collembola. Pedobiologia **18**, 163−179.

Jacot, A.P. (1940) The fauna of the soil. The Quaterly Review of Biology **15**, 28−58.

Jaeger, G., Eisenbeis, G. (1984) pH-dependent absorption of solutions by the ventral tube of *Tomocerus flavescens* (Tullberg, 1871) (Insecta, Collembola). Revue d'Ecologie et Biologie du Sol **21**, 519−531.

Jenny, H. (1961) Reflections on the soil acidity merry-go-round. Soil Science Society of America Proceedings **25**, 428−432.

Joosse, E.N.G. (1970) The formation and biological significance of aggregation in the distribution of Collembola. Netherlands Journal of Zoology **20**, 299−314.

Kaczmarek, M. (1973) Collembola in the biotopes of the Kampinos National Park distinguished according to the natural succession. Pedobiologia **13**, 257−272.

Kaczmarek, M. (1975) An analysis of Collembola communities in different pine forest environments. Ekologia Polska **23**, 265−293.

Kilbertus, G., Vannier, G. (1981) Relations microflore-microfaune dans la grotte de Sainte-Catherine (Pyrénées ariégeoises). II. Le régime alimentaire de *Tomocerus minor* (Lubbock) et *Tomocerus problematicus* Cassagnau (Insectes Collemboles). Revue d'Ecologie et Biologie du Sol **18**, 319−338.

Kubiëna, W. L. (1955) Animal activity in soil as a decisive factor in establishment of humus forms. In: Kevan, D.K. McE. (ed) Soil zoology, Proceedings of the University of Nottingham Second Easter School in Agricultural Science, 1955. Butterworths Scientific Publications, London, 73−82 + 2 inlet plates.

MacMillan, J.H. (1976) Laboratory observations on the food preference of *Onychiurus armatus* (Tullb.) Gisin (Collembola, family Onychiuridae). Revue d'Ecologie et Biologie du Sol **13**, 353−364.

Marshall, V.G. (1978) Gut content analysis of the Collembolan *Bourletiella hortensis* (Fitch) from a forest nursery. Revue d'Ecologie et Biologie du Sol **15**, 243−250.

Mateos, E. (1988) Ecología de los colémbolos (Collembola, Insecta) edáficos del encinar montano del Montseny (Barcelona). Miscellania Zoologica **12**, 97−107.

Mertens, J. (1975) L'influence du facteur pH sur le comportement de *Orchesella villosa* (Geoffroy, 1764) (Collembola, Insecta). Annales de la Société Royale de Zoologie de Belgique **105**, 45−52.

Miles, J. (1979) Vegetation dynamics. Chapman and Hall, London.

Müller, P.E. (1889) Recherches sur les formes naturelles de l'humus et leur influence sur la végétation et le sol. Annales de la Science Agronomique Francaise et Etrangère **6**, 85−423.

Nosek, J. (1967) The investigation on the Apterygotan fauna of the Low Tatras. Acta Universitatis Carolinae. Biologica **5/6**, 349−528.

Oldeman, R.A.A. (1990) Forests: elements of silvology. Springer Verlag.

Pichard, S., Massoud, Z., Elkaim, B. (1989) Ecologie des peuplements de collemboles de quelques mares et de leurs abords en région parisienne. Revue d'Ecologie et Biologie du Sol **26**, 451−472.

Ponge, J.F. (1973) Application de l'analyse factorielle des correspondances à l'étude des variations annuelles dans les populations de microarthropodes. Bulletin d'Ecologie **4**, 319−327.

Ponge, J.F. (1980) Les biocénoses des collemboles de la forêt de Sénart. In: Pesson, P. (ed) Actualités d'écologie forestière. Gauthier-Villars, Paris, 151−176.

Ponge, J.F. (1983) Les collemboles, indicateurs du type d'humus en milieu forestier. Résultats obtenus au sud de Paris. Acta Oecologica, Oecologia Generalis **4**, 359−374.

Ponge, J.F. (1991) Food resources and diets of soil animals in a small area of Scots pine litter. Geoderma **49**, 33−62.

Ponge, J.F., Charpentié, M.J. (1981) Etude des relations microflore-microfaune: expériences sur *Pseudosinella alba* (Packard), collembole mycophage. Revue d'Ecologie et Biologie du Sol **18**, 291−303.

Ponge, J.F., Prat, B. (1982) Les Collemboles, indicateurs du mode d'humification dans les peuplements résineux, feuillus et mélangés: résultats obtenus en forêt d'Orléans: Revue d'Ecologie et Biologie du Sol **19**, 237−250.

Ponge, J.F., Vannier, G., Arpin, P., David, J.F. (1986) Caractérisation des humus et des litières par la faune du sol. Intérêt sylvicole. Revue Forestière Française **38**, 509−516.

Poursin, J.M., Ponge, J.F. (1982) Comparaison de trois types de peuplements forestiers (feuillu, mixte, résineux) à l'aide de la mésofaune du sol (Collemboles et Oribates). Comptes-Rendus des Séances Hebdomadaires de l'Académie des Sciences de Paris **294**, 1021−1024.

Poursin, J.M., Ponge, J.F. (1984) Etude des peuplements de microarthropodes (Insectes Collemboles et Acariens Orbates). Pedobiologia **26**, 403−414.

Pozo, J. (1986) Ecological factors affecting Collembola populations. Ordination of communities. Revue d'Ecologie et Biologie du Sol **23**, 299−311.

Pozo, J., Selga, D. , Simon, J.C. (1986) Studies on the Collembolan populations of several plant communities of the Basque Country (Spain). Revue d'Ecologie et Biologie du Sol **23**, 215−232.

Prat, B., Massoud, Z. (1981) Etude de la communauté des Collemboles dans un sol forestier. II. Evolution du peuplement. Revue d'Ecologie et Biologie du Sol **18,** 59−76.

Prat, B., Massoud, Z. (1982) Etude de la communauté des Collemboles dans un sol forestier. III. Phénologie des espèces. Revue d'Ecologie et Biologie du Sol **19**, 403−410.

Romell, L.G. (1982) Mull and duff as biotic equilibria. Soil Science **34**, 161−188.

Rusek, J. (1975) Die bodenbildende Funktion von Collembolen und Acarina. Pedobiologia **15,** 299-308.

Rusek, J. (1984) Zur Bodenfauna in drei Typen von Überschwemmungswiesen in Süd-Mähren. Rozpravy Ceskoslovenske Akademie Ved, Rada Matematickych a Prirodnich Ved **94,** 1−26 + 8 inlet plates.

Rusek, J. (1985). Soil microstructures. Contributions on specific soil organisms. Quaestiones Entomologicae **21**, 497−514.

Rusek, J. (1989) Ecology of Collembola. In: Dallai, R. (ed) 3rd International Seminar on Apterygota, 21/VIII−26/VIII 1989, Siena, Italy. University of Siena, 271−281.

Saur, E., Ponge, J.F. (1988) Alimentary studies on the Collembolan *Paratullbergia callipygos* using transmission electron microscopy. Pedobiologia **31**, 355−379.

Stainer, J.E.R., Kevan, D.K.McE. (1973) A preliminary study of the biology of *Entomobryoides purpurascens* (Packard, 1873) (Collembola: Entomobryidae). Entomological News **84**, 217−224.

Szeptycki, A. (1967) Fauna of the springtails (Collembola) of the Ojców National Park in Poland. Acta Zoologica Cracoviensia **12**, 219−280 + 6 inlet plates.

Verhoef, H.A. , Prast, J.E., Verweij, R.A. (1988) Relative importance of fungi and algae in the diet and nitrogen nutrition of *Orchesella cincta* (L.) and *Tomocerus minor* (Lubbock) (Collembola). Functional Ecology **2**, 195−201.

Verhoef, H.A., van Selm, A.J. (1983) Distribution and population dynamics of Collembola in relation to soil moisture. Holarctic Ecology **6**, 387−394.

Wetton, M.N. (1987) Morphological variation in British *Folsomia quadrioculata* Tullberg (Collembola: Isotomidae): a multivariate study. Systematic Entomology **12**, 257−270.

Wolters, V. (1983) Ökologische Untersuchungen an Collembolen eines Buchenwaldes auf Kalk. Pedobiologia **25**, 73−85.

Legends of figures

Fig. 1. Correspondence analysis. Projection in the plane of the axes 1 and 2

Fig. 2. Correspondence analysis. Projection in the plane of the axes 2 and 3

Fig. 3. Correspondence analysis. Projection in the plane of the axes 1 and 4

Table 1. Collembolan species in soil (neutro-acidocline conditions). List of more frequent species of Aa branch

Species	Frequence (%)	Abundance (%)
Characteristic species		
Pseudosinella alba	87	6
Mesaphorura hylophila	66	2
Kalaphorura burmeisteri	65	3
Folsomia penicula	41	2
Stenaphorura denisi	39	1
Heteromurus nitidus	36	1
Mesaphorura italica	34	1
Onychiurus jubilarius	32	1
Micranurida sensillata	32	<0.5
Onychiurus pseudogranulosus	24	2
Monobella grassei	19	<0.5
Wankeliella pongei	17	<0.5
Pseudosinella decipiens	17	<0.5
Megalothorax incertus	15	<0.5
Tomocerus botanicus	14	<0.5
Pseudachorutes subcrassus	13	<0.5
Accompanying species		
Isotomiella minor	96	28
Paratullbergia callipygos	85	3
Megalothorax minimus	80	4
Folsomia manolachei	78	15
Lepidocyrtus lanuginosus	76	6
Mesaphorura macrochaeta	69	4
Friesea truncata	66	6
Parisotoma notabilis	64	5
Mesaphorura krausbaueri	40	1
Sminthurinus aureus	25	1
Heteromurus major	22	1
Dicyrtoma fusca	15	<0.5
Orchesella cincta	14	<0.5
Dicyrtomina minuta	14	<0.5
Orchesella villosa	10	<0.5

Nota: Dominance (relative abundance) and frequence have been rounded to the nearest percent unit.
Number of samples = 143

Table 2. Collembolan species in soi1 (acid conditions). List of more frequent species of Aa branch

Species	Frequence (%)	Abundance (%)
Characteristic species		
Mesaphorura macrochaeta	94	32
Micranurida pygmaea	70	6
Mesaphorura betschi	51	3
Protaphorura subuliginata	35	3
Pseudosinella mauli	29	3
Willemia anophthalma	17	2
Willemia intermedia	17	<0.5
Proisotoma minima	14	<0.5
Mesaphorura yosii	14	<0.5
Accompanying species		
Isotomiella minor	90	26
Paratullbergia callipygos	48	7
Parisotoma notabilis	35	4
Megalothorax minimus	35	3
Lepidocyrtus lanuginosus	32	3
Sminthurinus signatus	22	2
Vertagopus arboreus	17	1
Folsomia quadrioculata	14	1

Nota: Dominance (relative abundance) and frequence have been rounded to the nearest percent unit.
Number of samples = 69

Table 3. Collembolan species in forest habitats (tree, trunks, rocks, herbs). List of more frequent species of D branch

Species	Frequence (%)	Abundance (%)
Characteristic species		
Orchesella cincta	81	14
Xenylla tullbergi	76	50
Vertagopus arboreus	38	3
Entomobrya albocincta	30	1
Pseudisotoma sensibilis	24	17
Entomobrya nivalis	14	1
Accompanying species		
Lepidocyrtus lanuginosus	49	2
Folsomia manolachei	22	3
Parisotoma notabilis	22	2
Pseudachorutes parvulus	22	2
Heteromurus major	22	1
Neanura muscorum	19	<0.5
Micranurida pygmaea	16	1
Lepidocyrtus curvicollis	14	<0.5
Sminthurinus signatus	14	<0.5
Lepidocyrtus lignorum	14	<0.5
Tomocerus minor	11	<0.5
Xenylla grisea	11	<0.5
Orchesella villosa	11	<0.5

Nota: Dominance (relative abundance) and frequence have been rounded to the nearest percent unit.
Number of samples = 37

Table 4. Collembolan species at the water surface and in moist habitats (herbs and litter). List of more frequent species of C branch

Species	Frequence (%)	Abundance (%)
Characteristic species		
Isotomurus palustris	74	16
Lepidocyrtus lignorum	54	11
Sminthurides malmgreni	47	8
Folsomia quadrioculata	46	16
Protaphorura lata	39	10
Tomocerus minor	33	2
Sminthurides schoetti	27	2
Podura aquatica	13	10
Heterosminthurus insignis	13	1
Ceratophysella denticulata	10	<0.5
Accompanying species		
Friesea truncata	36	4
Orchesella villosa	26	2
Isotomiella minor	24	3
Micranurida pygmaea	24	2
Sphaeridia pumilis	21	1
Lepidocyrtus cyaneus	20	4
Smithurinus aureus	16	2
Neanura muscorum	16	1
Folsomia manolachei	10	5

Nota: Dominance (relative abundance) and frequence have been rounded to the nearest percent unit.
Number of samples = 70

Table 5. Collembolan species in open sites (herbs and soil surface). List of more frequent species of B branch

Species	Frequence (%)	Abundance (%)
Characteristic species		
Lepidocyrtus cyaneus	71	20
Sminthurinus elegans	58	2
Brachystomella parvula	54	21
Entomobrya lanuginosa	50	1
Sminthurides assimilis	42	2
Isotoma viridis	33	1
Bourletiella viridescens	25	<0.5
Entomobrya multifasciata	21	2
Sminthurus nigromaculatus	13	<0.5
Accompanying species		
Parisotoma notabilis	50	4
Isotomurus palustris	38	3
Sphaeridia pumilis	33	7
Mesaphorura krausbaueri	29	1
Pseudosinella alba	17	1
Lepidocyrtus lanuginosus	17	<0.5
Sminthurides schoetti	17	<0.5
Mesaphorura macrochaeta	13	<0.5

Nota: Dominance and frequence have been rounded to the nearest percent unit.
Number of samples = 24

Appendix 1: List of Collembolan species used as active items + PAQ as a supplementary item

ACA	*Arrhopalites caecus* (Tullberg, 1871)
AFU	*Allacma fusca* (Linné, 1758)
AGA	*Allacma gallica* (Carl, 1899)
APR	*Arrhopalites principalis* Stach, 1945
APY	*Arrhopalites pygmaeus* (Wankel, 1860)
ASE	*Arrhopalites sericus* Gisin, 1947
BPA	*Brachystomella parvula* (Schäffer, 1896)
BVI	*Bourletiella viridescens* Stach, 1920
CAL	*Cyphoderus albinus* Nicolet, 1841
CAR	*Ceratophysella armata* (Nicolet, 1841)
CDE	*Ceratophysella denticulata* (Bagnall, 1941)
CMA	*Caprainea marginata* (Schott, 1893)
DFL	*Deuterosminthurus flavus* (Gisin, 1946)
DFU	*Dicyrtoma fusca* (Lucas, 1842)
DMI	*Dicyrtomina minuta* (Fabricius, 1783)
EAL	*Entomobrya albocincta* (Templeton, 1835)
ELA	*Entomobrya lanuginosa* (Nicolet, 1841)
EMA	*Entomobrya multifasciata* (Tullberg, 1871)
EMU	*Entomobtya muscorum* (Nicolet, 1841)
ENI	*Entomobrya nivalis* (Linné, 1758)
FCA	*Folsomia candida* (Willem, 1902)
FCL	*Friesea claviseta* Axelson, 1900
FMA	*Folsomia manolachei* Bagnall, 1939
FMI	*Friesea mirabilis* (Tullberg, 1871)
FPA	*Folsomides parvulus* Stach, 1922
FPE	*Folsomia penicula* Bagnall, 1939
FQU	*Folsomia quadrioculata* (Tullberg, 1871)
FTR	*Friesea truncata* Cassagnau, 1958
GFL	*Gisinianus flammeolus* (Gisin, 1957)
HIN	*Heterosminthurus insignis* (Reuter, 1876)
HMA	*Heteromurus major* (Moniez, 1889)
HNI	*Heteromurus nitidus* (Templeton, 1835)
IMI	*Isotomiella minor* (Schäffer, 1896)
IPA	*Isotomurus palustris* (Müller, 1776)
ITI	*Isotoma tigrina* (Nicolet, 1841)
IVI	*Isotoma viridis* Bourlet, 1839
KBU	*Kalaphorura burmeisteri* (Lubbock, 1873)
LCU	*Lepidocyrtus curvicollis* Bourlet, 1839
LCY	*Lepidocyrtus cyaneus* Tullberg, 1871
LLA	*Lepidocyrtus lanuginosus* (Gmelin, 1788)
LLI	*Lepidocyrtus lignorum* (Fabricius, 1781)
LLU	*Lipothrix lubbocki* (Tullberg, 1872)
LVI	*Lepidocyrtus violaceus* Lubbock, 1873
MBE	*Mesaphorura betschi* Rusek, 1979
MGR	*Monobella grassei* (Denis, 1923)
MHA	*Mesaphorura hygrophila* (Rusek, 1971)
MHY	*Mesaphorura hylophila* Rusek, 1982
MIN	*Megalothorax incertus* (Börner, 1903)
MIT	*Mesaphorura italica* (Rusek, 1971)
MJA	*Mesaphorura jarmilae* Rusek, 1982
MKR	*Mesaphorura krausbaueri* Börner, 1901
MMA	*Mesaphorura macrochaela* Rusek, 1976
MMI	*Megalothorax minimus* (Willem, 1900)
MMS	*Mesaphorura massoudi* Rusek, 1979
MPY	*Micranurida pygmaea* Börner, 1901
MSA	*Micranurida sensillata* (Gisin, 1953)
MYO	*Mesaphorura yosii* (Rusek, 1967)
NMU	*Neanura muscorum* (Templeton, 1835)
NRA	*Neotullbergia ramicuspis* (Gisin, 1953)
OCI	*Orchesella cincta* (Linné, 1758)
OJU	*Onychiurus jubilarius* Gisin, 1957
OLA	*Odontella lamellifera* (Axelson , 1903)
OPS	*Onychiurus pseudogranulosus* Gisin, 1951
OVI	*Orchesella villosa* (Geoffroy, 1764)
PAL	*Pseudosinella alba* (Packard, 1873)
PAQ	*Podura aqualica* Linné, 1758
PAS	*Pseudachorutella asigillata* (Borner, 1901)
PCA	*Paratullbergia callipygos* (Börner, 1902)
POE	*Pseudosinella decipiens* Denis, 1924
PEU	*Pongeiella falca europea* Rusek, 1991
PFL	*Pogonognathellus flavescens* (Tullberg, 1871)
PLA	*Protaphorura lata* (Gisin, 1956)
PLO	*Pogonognathellus longicornis* (Müller, 1776)
PMA	*Pseudosinella mauli* Stomp, 1972
PMI	*Proisotoma minima* (Absolon, 1901)
PMU	*Proisotoma minuta* (Tullberg, 1871)
PNO	*Parisotoma notabilis* (Schäffer, 1896)
PPA	*Pseudachorutes parvulus* Börner, 1901
PSE	*Pseudisotoma sensibilis* (Tullberg, 1876)
PSS	*Pseudachorutes subcrassus* Tullberg, 1871
PSU	*Protaphorura subuliginata* (Gisin, 1956)
SAS	*Sminthurides assimilis* (Krausbauer, 1898)
SAU	*Sminthurinus aureus* (Lubbock, 1862)
SDE	*Stenaphorura denisi* Bagnall, 1935
SEL	*Sminthurinus elegans* (Fitch, 1863)
SMA	*Sminthurides malmgreni* (Tullberg, 1876)
SNI	*Sminthurus nigromaculatus* Tullberg, 1872
SPA	*Sminthurides parvulus* (Krausbauer, 1898)
SPU	*Sphaeridia pumilis* (Krausbauer, 1898)
SSC	*Sminthurides schoetti* (Axelson, 1903)
SSI	*Sminthurinus signatus* (Krausbauer, 1898)
TBO	*Tomocerus botanicus* Cassagnau, 1962
TMI	*Tomocerus minor* (Lubbock, 1862)
VAR	*Vertagopus arboreus* (Linné, 1758)
WAN	*Willemia anophthalma* Börner, 1901
WBU	*Willemia buddenbrocki* Hüther, 1959
WIN	*Willemia intermedia* Mills, 1934
WME	*Wankeliella mediochaeta* Rusek, 1975
WPO	*Wankeliella pongei* Rusek, 1978
XBR	*Xenylla brevisimilis* Stach, 1949
XGR	*Xenylla grisea* Axelson, 1900
XSC	*Xenylla schillei* Börner, 1903
XTU	*Xenylla tullbergi* Börner, 1903
XXA	*Xenylla xavieri* Gama, 1959

Appendix II: List of biotopes used as supplementary items

1 Forest earthworm mull humus: tree trunks, rocks
2 Forest earthworm mull humus: fallen wood
3 Forest earthworm mull humus: ground mosses
4 Forest earthworm mull humus: herbs
5 Forest earthworm mull humus: litter (L layer)
6 Forest earthworm mull humus: mineral soil (A horizon)
7 Forest acid mull humus: tree trunks, rocks
8 Forest acid mull humus: fallen wood
9 Forest acid mull humus: ground mosses
10 Forest acid mull humus: herbs
11 Forest acid mull humus: litter (L layer)
12 Forest acid mull humus: litter (F layer)
13 Forest acid mull humus: naked soil
14 Forest acid mull humus: mineral soil (A horizon)
15 Oak moder humus: tree trunks, rocks
16 Oak moder humus: fallen wood
17 Oak moder humus: naked soil
18 Oak moder humus: ground mosses
19 Oak moder humus: herbs
20 Oak moder humus: litter (L layer)
21 Oak moder humus: litter (F layer)
22 Oak moder humus: litter (H layer)
23 Oak moder humus: mineral soil (A horizon)
24 Pine moder humus: tree trunks, rocks
25 Pine moder humus: ground mosses
26 Pine moder humus: litter (L layer)
27 Pine moder humus: litter (F layer)
28 Pine moder humus: litter (H layer)
29 Pine moder humus: mineral soil (A horizon)
30 Forest hydro-mull: ground mosses
31 Forest hydro-mull: litter (L layer)
32 Forest hydro-mull: mineral soil (A horizon)
33 Forest hydro-moder: litter (L layer)
34 Forest hydro-moder: litter (F layer)
35 Forest hydro-moder: litter (H layer)
36 Forest hydro-moder: mineral soil (A horizon)
37 Proximity of pounds, streams
38 Pound shores, drains: ground mosses
39 Pound shores, drains: herbs
40 Pound shores, drains: litter
41 Pound shores, drains: mineral soil (gley horizon)
42 Sphagnum bogs: herbs
43 Sphagnum bogs: moss, living part
44 Sphagnum bogs: moss, dead part
45 Water surface
46 Forest paths, clearings: tree trunks, rocks
47 Forest paths: herbs
48 Forest paths: ground mosses
49 Forest paths: mineral soil (A horizon)
50 Clearings: herbs
51 Clearings: naked soil
52 Cultivated fields, meadows: herbs
53 Cultivated fields, meadows: naked soil
54 Cultivated fields, meadows: mineral soil (A horizon)
55 Rotten stumps
56 Waste products
57 Spring season
58 Summer season
59 Autumn season
60 Winter season

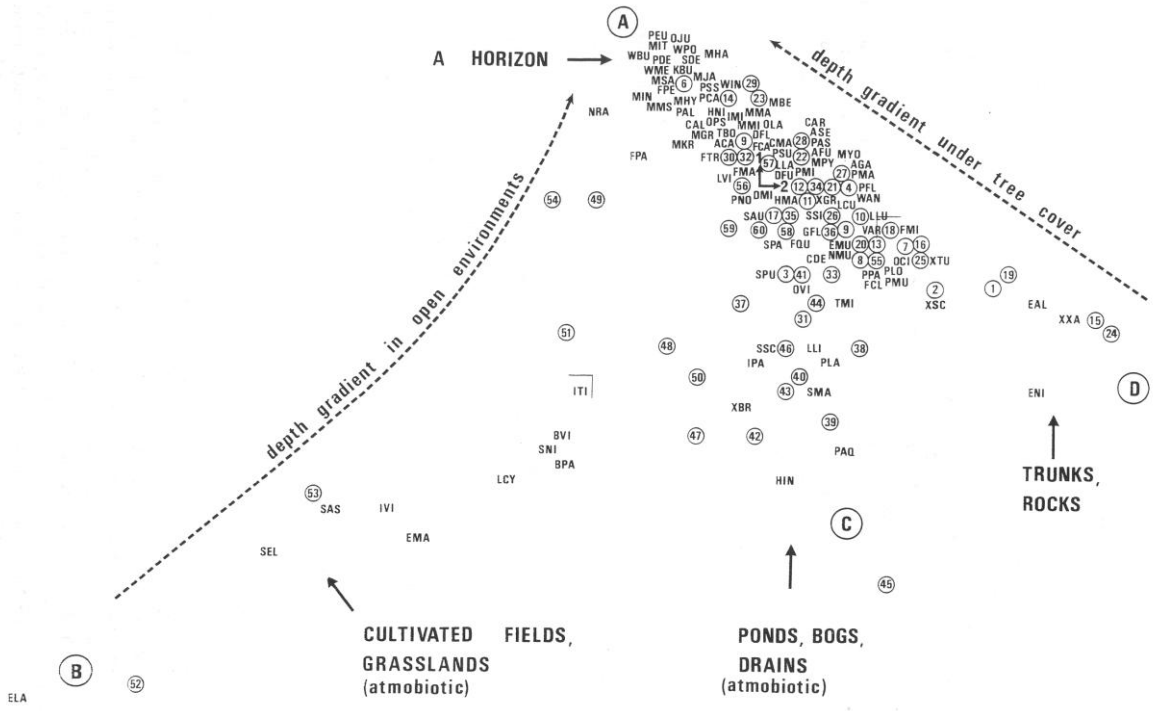
A
A HORIZON
depth gradient under tree cover
depth gradient in open environments
TRUNKS, ROCKS
CULTIVATED FIELDS, GRASSLANDS (atmobiotic)
PONDS, BOGS, DRAINS (atmobiotic)
B
C
D

Fig. 1

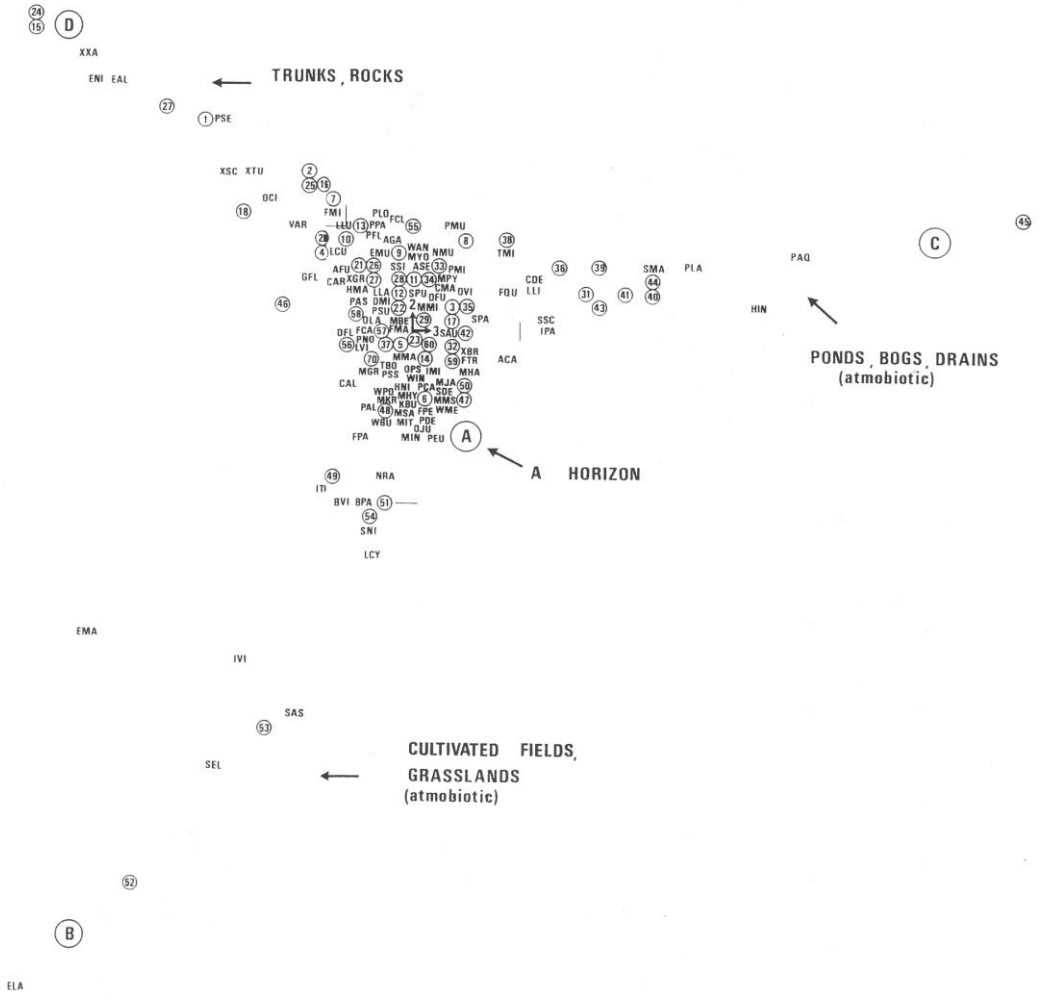
TRUNKS, ROCKS
PONDS, BOGS, DRAINS
(atmobiotic)
A HORIZON
CULTIVATED FIELDS,
GRASSLANDS
(atmobiotic)

Fig. 2

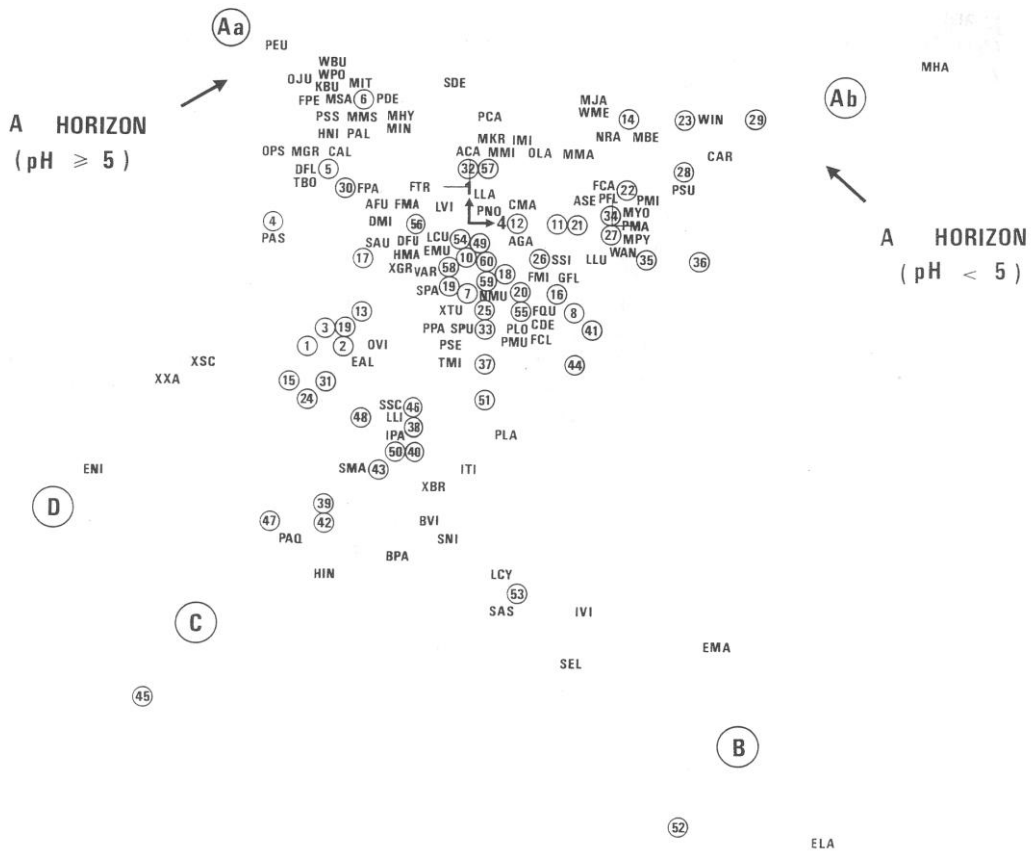
Aa
A HORIZON
(pH ≥ 5)
Ab
A HORIZON
(pH < 5)
B
C
D
PEU
WBU
WPO
OJU
KBU
MIT
SDE
FPE
MSA
PDE
PSS
MMS
MHY
MIN
HNI
PAL
OPS
MGR
CAL
DFL
TBO
FPA
FTR
AFU
FMA
LVI
DMI
PAS
SAU
DFU
HMA
XGR
VAR
SPA
XTU
PPA
SPU
OVI
EAL
PSE
TMI
XSC
XXA
SSC
LLI
IPA
SMA
ITI
XBR
ENI
PAQ
BVI
SNI
BPA
HIN
LCY
SAS
IVI
SEL
EMA
ELA
PCA
MKR
IMI
ACA
MMI
OLA
MMA
LLA
PNO
CMA
LCU
EMU
AGA
SSI
LLU
FMI
GFL
NMU
FQU
CDE
PLO
PMU
FCL
PLA
MJA
WME
NRA
MBE
WIN
CAR
PSU
FCA
ASE
PFL
PMI
MYO
PMA
MPY
WAN
MHA

Fig. 3