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# The heterogeneity of humus profiles and earthworm communities in a virgin beech forest

J.F. Ponge · L. Delhayé

**Abstract** Thirty sites, encompassing a range of soil and vegetation conditions in the biological reserve of La Tillaie (Fontainebleau Forest, France) were investigated in April 1992. Beech (*Fagus sylvatica* L.) was the dominant tree species, with several developmental phases forming the forest patchwork. Sessile oak [*Quercus petraea* (Mattus.) Liebl.] was present but only as old relictual individuals. Gaps in the canopy cover were abundant, mostly caused by wind storms 2 years previously. The next most recent storm was 25 years before, resulting in distinct patches of full-grown trees. Humus profiles were classified and compared with the distribution of earthworm communities, canopy cover, and soil types. Geomorphology was responsible for the main part of the observed variation. Absence of lime in the substrate and direct contact with a sandstone stratum near the ground surface was associated with the absence of earthworms and the appearance of an OH horizon (moder humus). Elsewhere, earthworms were present and humus profiles did not display any OH horizon (mull or mull-like moder humus), but species composition was variable and strongly influenced by the thickness of the superficial sand deposit overlying limestone. On a thick (1 m or more) sandy substrate earthworm communities were dominated by epigeic species together with the anecic *Lumbricus terrestris* L. The species richness was higher on a shallower sandy substrate (50 cm) where lime was more accessible to tree roots and burrowing animals. The influence of the forest cycle of beech was visible in the latter case (covering most of the area), with an increase in the thickness of the OL and OF horizons and a decrease in endogeic earthworm populations during the phase of intense growth of beech. This fall in burrowing activity was apparent in gaps created by wind storms and fungal diseases within mature stands as early as 2 years after the fall of the trees.

**Key words** Virgin forest · Forest cycle · Geomorphology · Heterogeneity · Earthworms · Humus type

## **Introduction**

Previous work on mountain spruce forests (Bernier 1992; Bernier et al. 1993; Bernier and Ponge 1993, 1994; Ponge et al. 1994) has demonstrated that parallel changes occur in vegetation, humus profiles, and soil animal communities throughout the forest cycle, with alternation between phases of accumulation and incorporation of litter. These effects might be thought important for regeneration when tree seedlings are not tolerant of humus type. This is the case for spruce (Weissen 1979) and also for beech trees (Weissen 1986; Weissen et al. 1986). Amelioration of humus conditions under adult trees, preparing for the installation phase, has been demonstrated both in managed (Page 1968) and in native forests (Page 1974).

A preliminary study was conducted in a virgin beech forest to discern whether such changes occur in the case of beech and whether they can be separated from differences due to heterogeneity of the parent material. Thirty sites were investigated in the biological reserve of La Tillaie (Fontainebleau forest near Paris), encompassing the whole range of soil and vegetation conditions. Humus profiles and earthworm communities were sampled in April 1992.

The biological reserve of La Tillaie (50 km south of Paris, France), free of management since the beginning of the 16th century, has been studied time and again (Lemée 1990a). The changes that took place in the passage from the ancient woodland where oak was favoured by man to the present beech steady state and in the regeneration of the latter ecosystem have been deduced both from synchronic (Lemée 1978, 1985, 1987a, b, 1989) and diachronic (Guillet and Robin 1972; Jacquiot et al. 1973; Lemée 1981, 1990b; Faille et al. 1984a, b) analyses. The soil and vegetation types and canopy cover have been mapped (Bouchon et al. 1973) and long-term studies have been set up to follow the changes occurring in plant cover and forest architecture over time (Van Baren and Hilgen 1984; Koop and Hilgen 1987).

Studies on the forest cycle of virgin forests may be complicated by the heterogeneity of the soil substrate. This is particularly evident in the case of soil animal communities (Arpin et al. 1984) and humus profiles (Duchauffour 1980; Toutain 1987). In the present study we tried to distinguish between variations due to

geomorphological diversity and others due to forest dynamics.

### **The sites**

The study area has been described by Lemée (1978). The soil is sandy, with 0–3% clay and 2–5% silt particles in the A horizon (Robin 1970), varying from leached only to podzol soil according to the nomenclature by Duchaufour (1991). The vegetation comprises beech trees, varying in age and density, with oak present as a few senescent trees. Regeneration areas include only beech. Phases of the forest cycle have been recognized, as in other virgin forests, according to the nomenclature of Oldeman (1990), the delineation of the different eco-units being based on observations that regeneration of beech (when effective) occurs mainly when the trees are in a senescent state or dead. In some cases declining trees are always present, together with young individuals of the next generation. In others (when healthy adult trees were wind-thrown) gaps occurred before regeneration took place. The appearance of wide gaps may be delayed in time by successive storms, the first smaller gaps beginning to be filled with the growth of lateral branches of standing trees, enlarging when these trees died in turn. Trees have never been felled, and dead wood has never been removed from the ground. The biological reserve of La Tillaie covers 33.74 ha. This woody area is located at the centre of the Fontainebleau forest, 50 km south-east of Paris. The ground is fairly level, the elevation ranging from 134.8 to 139.4 m above sea level. The parent material is wind-blown sand directly overlying a sandstone base or an intercalary stratum of friable limestone. In the latter case the thickness of the sand cover is variable, ranging from 30 to 200 cm (Robin 1970).

Table 1 indicates the main features of the 30 sites investigated. The age of the trees has not been determined but two major events (storms in 1967 and 1990) are reflected in the presence of numerous thickets of actively growing trees (aggradation phase) and numerous gaps without any vegetation (zero event, before the innovation phase). Some ancient gaps have been invaded by bracken fern [*Pteridium aquilinum* (L.)], sparse regeneration when present taking place only at their periphery. The smaller gaps (fall of individual trees) are often filled with branches growing from adjacent trees. In this case regeneration either did not take place or was aborted. Some particular cases were investigated, such as the development of beech clonal populations (suckers) issuing from the infrequent fall by wind of a pole-stage tree. Ground vegetation is sparse. The micro-scale distribution of graminaceous species (mainly *Melica uniflora* Retz.) in the gaps or of dwarf shrubs such as *Ruscus*

*aculeatus* L. under adult trees was not taken into account in the present study, although it is known to influence humus properties (Lemée 1975; Faille 1975a, b, 1977a, b). Each site was sampled repetitively (three samples for humus description, six for earthworm communities), the choice and size of study sites being based only on architectural and geomorphological features. Thus no nesting of study scale was attempted, the present work being aimed only at separating effects of the forest cycle from those of site conditions. The local influence of understory plant species will be the subject of a further study.

## **Materials and methods**

### Description of humus profiles

In each site three sample plots were selected randomly, and the soil was first trenched with a shovel down to 15 cm. Then a vertical profile was gently dressed with a sharp knife. The profiles were described by thickness of the OL, OF, OH horizons, depth of the A horizon (nomenclature according to A.F.E.S. 1992) and colour parameters (colour, chroma, value on Munsell soil colour charts) at 3, 6, and 9 cm in depth below the litter horizons. The presence or absence of white-rot fungi in the beech leaves (OL and OF horizons) was roughly estimated with the naked eye (coded as 1 or 0). Thus 14 measurements were taken on each humus profile.

### Description of earthworm communities

Each earthworm sampling area was 1.5 m<sup>2</sup> (six replicates randomly selected, each 0.5 m<sup>2</sup>) and was prepared by spraying a repellent solution on the bare ground after having sorted the OL and OF horizons by hand. The chemical repellent used was formalin, applied at 10<sup>-3</sup>, 1.5x10<sup>-3</sup>, then 2x10<sup>-3</sup> concentrations at 10-mn intervals. The worms were immediately fixed in pure formalin then transferred to the laboratory. Identification was made under a dissecting microscope. The nomenclature used was that of Sims and Gerard (1985). The species were classified into litter-dwelling and soil-dwelling species. The first group was considered synonymous with the epigeic group of Bouché (1972), but the second group included both endogeic and anecic species sensu Bouché (1972). The species are listed in Table 2, with an indication of their typical habitat according to literature. In the present study

site the sandy nature of the soil allowed the worms very easy vertical movement. Thus they were able to change habitat frequently. Most worms (including the so-called litter-dwelling species) were found living in the mineral soil, from which they were expelled very easily by formalin (no worm was found after hand-sorting of the mineral soil once the extraction was completed). Another particular feature was the unexpected lack of body pigmentation in *Dendrodrilus rubidus* and *Dendrobaena pygmaea*, two litter-dwelling species that were invariably found burrowing into the A horizon.

#### Statistical treatment

Humus profiles, described by their 14 morphological measurements, were ordinated using correspondence analysis (Greenacre 1984). The data were transformed by reweighting and focusing them so that the mean equalled 10 and the variance equalled 1 for each measurement. Two variates were associated with each measurement, the original value (transformed as above) and its complement to 20. Thus, on the graphs one point was associated with the higher values of a given measurement, the other with the lower values. Between the two a gradient from lower to higher values was displayed. Earthworm densities and biomasses and variates describing vegetation, soil types, and geomorphology were added as additional variates, without any influence on the ordination of humus profiles but giving weight to interpretation of the axes.

The humus measurements and densities and biomass of earthworm species and categories were compared between the different sites. These were grouped according to geomorphological features or phases of the forest cycle. Heterogeneity among means was tested by one-way analysis of variance (Sokal and Rohlf 1969; Rohlf and Sokal 1969) with the different samples taken in a given group as replicates. The different sites (Table 1) were chosen randomly within the study area and immediately classified into sylvogenetical or geomorphological groups with the help of tree architecture (Oldeman 1990) and maps of the study area (Bouchon et al. 1973). In each site, six (for earthworms) and three (for humus profiles) sample plots were selected randomly. It might have been necessary to test the differences between sites within a given group; in this case the residual error would have been the variation within sites. Since we had no reason to expect the variation between sites (within a group) to be greater than the variation within sites, all samples within a group were considered as replicates, thus taking the risk of increasing the residual error but providing more confidence in the answer to the

question is there a geomorphology or a forest cycle effect on humus profiles and earthworm communities in the study area? Significant differences between means were calculated a posteriori using the Student-Newman-Keuls procedure for unbalanced groups (Sokal and Rohlf 1969; Rohlf and Sokal 1969). Earthworm densities and biomasses were transformed into  $\log(x + 1)$  in order to ensure that the effects were additive. All earthworm species were tested, except *Eisenia fetida* and *Lumbricus eiseni*, which were each represented by only one individual in the data matrix.

## Results and discussion

### Influence of geomorphology

Ordination of the 90 samples by correspondence analysis (Fig. 1) indicated that the parent geology was the main factor in the variation of humus types. Three groups were easily separated on the basis of morphological features. The humus profiles in sites with free access to lime were separated from the two other groups by axis 1. They were characterized by a thin A horizon, light yellow in colour, and the absence of the OH horizon (acid mull humus; Toutain 1981). The two other groups were separated by axis 2 according to the presence or absence of a sandstone layer at the base of the superficial sand cover. When sandstone was present the humus profiles were characterized by the presence of an OH horizon (moder humus; Toutain 1981) and a dark reddish A horizon. When limestone was present, but under a deep sand cover, the humus profile was characterized by the absence of the OH horizon and a deep and dark yellow A horizon (mull-like moder humus; Kubiěna 1953). In the latter case the soils were always podzols or at least podzolic soils (Bouchon et al. 1973); the other soils have been described as varying from leached acidic (mostly represented in shallow sand overlying limestone) to ochrous podzolic (mostly represented in shallow sand overlying sandstone).

The analysis of variance of morphological features (Table 3) indicated that while the OL and OF horizons were not discriminant the OH horizon was thicker on sandstone and the depth of the A horizon was higher on a deep sand cover, this feature being accompanied by a weaker presence of white-rot fungi. According to the Munsell code, the A horizon was redder on sandstone. Munsell hue and chroma were autocorrelated, being higher (lighter and more strongly coloured A horizon) on shallow sand cover overlying limestone. Thus most

traits depicted by correspondence analysis seemed to discriminate significantly between the three geomorphological groups.

Earthworm communities differed significantly between these three groups (Table 3). Total earthworm biomasses followed a decreasing order from the shallow sand cover overlying limestone to the deep one and last to the thin sand cover overlying sandstone, but total densities were higher in the middle case. This latter phenomenon was mainly due to the increased abundance of litter-dwelling species, except *Lumbricus castaneus*. The soil-dwelling species *Allolobophora chlorotica*, *Aporrectodea caliginosa*, and *Lumbricus terrestris* followed a similar order, being absent on sandstone and present but to a lesser extent on deep sand cover with limestone. The only species (excluding rare species) that seemed ubiquitous between the three groups was the litter-dwelling *Lumbricus castaneus*, which was nevertheless more abundant on a deep sand cover with limestone. Thus shallow sand sites with limestone were characterized by the presence and the dominance of soil-dwelling species (mainly *Lumbricus terrestris* and *Aporrectodea caliginosa*), deep sand sites with limestone by the presence and the dominance of litter-dwelling species. These two groups contained the two ecological categories of earthworms but in a different ratio. Sandstone was characterized by the near absence of earthworms, except the litter-dwelling *Lumbricus castaneus*.

The shallow sand cover (50–100 cm) overlying limestone was thus characterized by an acid mull humus with a complete earthworm community (both litter- and soil-dwelling species) and fairly good incorporation of litter. The structure of the A horizon was crumby at the time of full earthworm activity (spring, autumn), but this structure was unstable throughout the year given the absence of clay particles (Robin 1979) and the rapid mineralization of organic matter (Lemée 1967, 1978), both important agents stabilizing earthworm aggregates (Shipitalo and Protz 1989). The thick sand cover (more than 1 m) overlying limestone was characterized by the presence of a mull-like moder, with an earthworm community dominated by litter-dwelling species. The OH horizon was absent and the incorporation of litter was not as efficient as in the shallow sand cover. The behaviour of the so-called litter-dwelling species, which have been observed to burrow through the sandy A horizon (highly porous because of the even particle size), might explain the absence of an accumulation layer of holorganic faecal material. Mineralization was not so good (Lemée 1967, 1978), which might explain the darker A horizon. When limestone was absent, with the sand cover directly overlying a sandstone layer, the humus form was of the moder



type, with a near absence of earthworm species. The OH horizon was present. The A horizon was dark, as in the thick sand cover over limestone, but its ground colour was red, perhaps due to a more intense mobilization of iron (Toutain and Duchaufour 1970; Delecour 1972).

#### Influence of the forest cycle

This effect was tested using three groups, the mature stage (biostasis), the tree-fall gaps (zero-event), and the pole stage (aggradation). Only the shallow sand cover with limestone was used for this study, given the restricted area covered by the other two geomorphological types. Table 4 indicates that the main effect on humus profiles was in the depth of the A horizon and to a lesser extent (although significant) in the thickness of the OL and OF horizons. The depth of the A horizon fell sharply after a gap had been created (reduced to about one-half), while the OL and OF horizons remained unchanged. Thus a considerable lack of organic matter occurred in the surface horizons of the soil within 2 years. The development of a new tree stand (aggradation phase) was accompanied by an increase in the thickness of the OL and OF horizons, the depth of the A horizon remaining unchanged. Thus an accumulation process occurred, but only in the litter. Maturation of the stand was characterized by a strong decrease in the thickness of the OL (reduced to one-half) and OF (reduced to one-third) horizons and an increase in the depth of the A horizon. Thus incorporation of litter was better under adult trees (Fig. 2). The OH horizon was nearly absent throughout the forest cycle and no significant change was observed in the colour parameters of the A horizon. However, although changes in the thickness of the OH horizon and colour of the A horizon were far more pronounced according to geomorphology, the forest cycle had a more marked influence on the thickness of the OL and OF horizons and depth of the A horizon.

These results were reflected in changes in earthworm communities (Table 4). The total number of earthworms decreased after a tree-fall gap occurred; the number of litter-dwelling worms was reduced to one-half (insignificant, due to a high inter-sample variation) while the number of soil-dwelling worms was decreased to one-third (highly significant). The species that contributed most to the decrease in soil-dwelling populations was *Aporrectodea longa*, a true anecic species (Bouché 1972). Its density dropped to one-tenth. Other soil-dwelling species decreased but not significantly. The growth phase of the beech stand was not accompanied by significant changes in earthworm communities, except for a threefold increase in *Dendrodrilus rubidus* populations (a

litterdwelling species). The dominant litter-dwelling *Lumbricus castaneus* increased, too, but only slightly. Maturation of the stand was characterized by a doubling in total earthworm numbers. Soil-dwelling species were principal contributors, increasing fourfold, the most striking being *Aporrectodea longa* (20-fold). Densities of litter-dwelling species remained stable overall, but those of *Dendrodrilus rubidus* decreased sharply to one-third. These changes were visible on biomass measurements (Table 4) but most were less significant, given the high variability of the weight of individual worms (mainly due to variations in age). An exception was the increase in biomass of *Allolobophora chlorotica* (soil-dwelling) during maturation of the beech stand, which was not reflected in numbers. This indicated that the individuals were bigger in the last phase of the forest cycle.

Thus no change in the humus type was observed, contrary to findings in spruce forests at the higher montane level (Bernier and Ponge 1993, 1994; Ponge et al. 1994), but quantitative changes occurred in some important soil features. Two years after a tree-fall gap had been created a strong fall in the depth of the A horizon and maintenance of the thickness of the litter layers (OL and OF horizons, OH being absent) despite the lack of litter input were observed. These changes were accompanied by a sharp decline in earthworm populations, which was more important for soil- than for litter-dwelling species. In particular, these changes applied to soils with a poor ground vegetation. Since that time we have observed (unpublished data, 1994) that the fate of the humus profile was highly dependent on the appearance of a graminaceous cover (mainly *Melica uniflora*). In the absence of grasses the A horizon seems more compact and darker than in their presence. These features were observed previously on the same site by Lemée (1975) and Faille (1977b) after wind storms in 1967. The disappearance of organic matter in the topsoil (deduced from the fall in depth of the A horizon) could be due to mineralization or to leaching. Climate conditions were different in the gaps, with higher temperature maxima and a higher water content in the top horizons (Pontailier 1979); thus more intense mineralization may be expected, even in the absence of ground vegetation. This effect might be reinforced by reduced inputs of organic matter from the litter layers, which remained untouched by earthworms as judged by the constancy of their thickness. An increase in leaching might be expected, too, due to an increase in incident rain and a fall in the activity of soil-dwelling earthworm populations (as long as there was no ground vegetation). Changes in soil conditions and in biological activity following dear-cutting have been measured repeatedly, but an examination of the literature did not give a clear picture of what might happen in the absence of understory vegetation or slash burning. Considering only the effects of the absence of litterfall (and not climatic effects due to the absence of a canopy cover), we compared

these results with experimental effects of litter deprivation on a similar humus type (David et al. 1991). These authors, too, observed a sharp decline in earthworm populations.

During the growth phase of the beech stand we observed an accumulation of organic matter at the ground surface (increase in the thickness of the OL and more of the OF horizon, but no build-up of an OH layer) without any significant change either in the A horizon or in earthworm populations. It is remarkable that the increase in litter input was not followed by an increase in earthworm populations, that relied on litter or products derived from litter for their food. In this case, too, we compared these results with those from an experimental increase in litterfall, which did not result in any increase in litter-feeding earthworm populations but in a quite similar accumulation of OL and OF litter (David et al. 1991). The question is whether the earthworm populations reached saturation point with the increase in food or whether there were other factors. In this case positive effects, e.g., an increase in food resources and habitat, might be counterbalanced by negative effects such as impoverishment and acidification of mineral soil horizons. The improved humus conditions (increase in the depth of the A horizon, decrease in the thickness of the OL and OF horizons) observed under adult trees might be an argument in favour of the second hypothesis.

Earthworm populations (mainly soil-dwelling) were stimulated to a large extent by cessation of tree growth (adult stage). Since foliage production per unit ground surface did not seem to be affected by the passage from the pole to the adult stage (Lemée 1978), the principal changes must occur in the soil system. Current knowledge of nutrient cycles in tree plantations of varying age (Miller 1984), especially the translocation of nutrients from older to younger tissues in adult trees, suggests that nutrient uptake by trees in the soil system might decrease once growth has ceased. Thus the laws outlined by Ulrich (1984) for the establishment, steady state and destruction of whole forest ecosystems may be applied to a forest cycle. In particular, the phase of humus disintegration that accompanies the (postulated) death of forest ecosystems closely resembles the improvement in humus conditions and the enrichment of earthworm communities observed under adult trees in the present study. Similar findings have been reported previously for virgin forests (Page 1974) and man-made forests grown to the adult stage (Bernier and Ponge 1993, 1994; Ponge et al. 1994), and thus seems to be a general law of the forest cycle, at least for climax species that are not tolerant of humus conditions, such as spruce or beech.

## Conclusion

Whether humus profiles and soil animal communities are better indicators of site quality than a simple list of plant species is not the question we sought to answer in the present study. However, in the light of our results and as pointed out by Miles (1985), these features are key components of terrestrial ecosystems and therefore need to be studied not only as passive but also as active agents of ecosystem dynamics.

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**Legends of figures**

**Fig. 1** Analysis of correspondences (30 x 90 samples,  $14 \times 2 = 28$  measurements), projection in the plane of the two first axes (*OL*, *OF*, *OH* thickness of the OL, OF, OH horizons, *A* depth of the A horizon, *WR* white-rot fungi in the OF horizon, *C03 C06 C09* Munsell colour of the A horizon at 3, 6, 9 cm beneath the O horizon, *CH3, CH6, CH9* idem for Munsell chroma; *VA 3, VA 6, VA 9* idem for Munsell hue, + and – denote higher and lower value for a given measurement, respectively)

**Table 1** Vegetation and soil features of the 30 study sites. Trees are beech unless otherwise indicated

Site	Phase of the forest cycle	Soil	Sand cover	Limestone
1	Tree-fall gap (zero-event)	Leached acidic	Thin	Present
2	Pole stage 45 years (aggradation)	Leached acidic	Thin	Present
3	Full-grown stage (biostasis)	Leached acidic	Thin	Present
4	Tree-fall gap (zero-event)	Leached acidic	Thin	Present
5	Pole stage 35 years (aggradation)	Leached acidic	Thin	Present
6	Senescent individual oak	Leached acidic	Thin	Present
7	Bracken heath (collapse)	Ochrous podzolic	Thin	Absent
8	Sparse beech (20 years) + bracken	Ochrous podzolic	Thin	Absent
9	Pole stage 20 years (aggradation)	Leached acidic	Thin	Present
10	Pole stage 45 years (aggradation)	Leached podzolic	Thin	Present
11	Pole stage 20 years (aggradation)	Ochrous podzolic	Thin	Present
12	Tree-fall gap (zero-event)	Leached podzolic	Thin	Present
13	Full-grown stage (biostasis)	Leached acidic	Thin	Present
14	Gap filled by adjacent trees	Leached acidic	Thin	Present
15	Sapling stage 15 years (innovation)	Ochrous podzolic	Thin	Present
16	Senescent individual oak	Podzol	Thick	Present
17	Bracken heath (collapse)	Podzol	Thick	Present
18	Pole stage 25 years (aggradation)	Podzolic	Thick	Present
19	Full-grown stage (biostasis)	Podzol	Thick	Present
20	Gap filled by adjacent trees	Podzol	Thick	Present
21	Clonal suckers	Podzol	Thick	Present
22	Tree-fall gap (zero-event)	Podzolic	Thick	Present
23	Pole stage 45 years (aggradation)	Podzol	Thick	Present
24	Gap filled by adjacent trees	Podzolic	Thick	Present
25	Full-grown stage (biostasis)	Podzolic	Thin	Absent
26	Gap filled by adjacent trees	Podzolic	Thin	Absent
27	Gap filled by adjacent trees	Leached podzolic	Thin	Absent
28	Bracken heath	Podzolic	Thin	Absent
29	Full-grown stage (biostasis)	Ochrous podzolic	Thin	Absent
30	Pole stage 45 years (aggradation)	Ochrous podzolic	Thin	Present

**Table 2** List of the 11 earthworms species present in the sites investigated

Habitat	Species
Soil	<i>Allolobophora chlorotica</i> (Savigny, 1826)
Soil	<i>Aporrectodea caliginosa</i> (Savigny, 1826)
Soil	<i>Aporrectodea longa</i> (Ude, 1885)
Litter	<i>Dendrobaena octaedra</i> (Savigny, 1826)
Litter	<i>Dendrobaena pygmaea</i> (Savigny, 1826)
Litter	<i>Eisenia fetida</i> (Savigny, 1826)
Litter	<i>Lumbricus castaneus</i> (Savigny, 1826)
Litter	<i>Lumbricus eiseni</i> (Levinsen, 1884)
Soil	<i>Lumbricus terrestris</i> (Linnaeus, 1758)
Soil	<i>Octolasion cyaneum</i> (Savigny, 1826)

**Table 3** Analysis of variance according to geomorphology with morphological measurements of humus profiles and earthworm communities

	F ratio	Probability	Shallow sand limestone	Deep sand limestone	Shallow sand sandstone
<b>Humus profile</b>					
OL thickness (cm)	0.21	0.82 NS	1.80	1.64	1.65
OF thickness (cm)	2.05	0.13 NS	1.36	1.60	1.97
OH thickness (cm)	14.18	0.0000 ***	0.06b	0.04b	0.41a
A depth (cm)	6.69	0.0021 **	6.71b	8.37a	6.02b
Presence of white-rot	4.84	0.010 *	0.67a	0.37b	0.76a
Munsell colour at 3 cm	44.47	0.0000 ***	10.0 YRa	10.0 YRa	7.1 YRb
Munsell colour at 6 cm	43.55	0.0000 ***	10.0 YRa	10.0 YRa	7.1 YRb
Munsell colour at 9 cm	48.01	0.0000 ***	10.0 YRa	10.0 YRa	7.1 YRb
Munsell hue at 3 cm	11.47	0.0001 ***	4.1/a	3.0/b	3.3/b
Munsell hue at 6 cm	7.56	0.0011 **	4.6/a	3.9/b	4.2/b
Munsell hue at 9cm	0.31	0.74 NS	5.1/	4.9/	5.1/
Munsell chroma at 3 cm	14.29	0.0000 ***	/1.7a	/1.1b	/1.1b
Munsell chroma at 6 cm	13.63	0.0000 ***	/2.0a	/1.2b	/1.5b
Munsell chroma at 9 cm	10.12	0.0001 ***	/2.6a	/1.8b	/2.4a
<b>Earthworm density (number m<sup>-2</sup>)</b>					
Total earthworms	12.51	0.0000 ***	17.04a	20.61a	7.02b
Total litter-dwelling	9.49	0.0002 ***	9.25b	16.75a	6.84b
Total soil-dwelling	22.85	0.0000 ***	6.05a	3.11b	0.06c
<i>Allolobophora chlorotica</i>	6.34	0.0024 **	0.69a	0.06b	0.00b
<i>Aporrectodea caliginosa</i>	14.68	0.0000 ***	3.31a	1.76b	0.00c
<i>Aporrectodea longa</i>	2.57	0.077 NS	0.50	0.10	0.00
<i>Dendrobaena octaedra</i>	20.92	0.0000 ***	0.46b	3.00a	0.70b
<i>Dendrobaena pygmaea</i>	7.76	0.0007 ***	0.50b	1.74a	0.32b
<i>Dendrodrilus rubidus</i>	8.23	0.0005 ***	2.70a	3.94a	0.97b
<i>Lumbricus castaneus</i>	0.62	0.55 NS	4.77	6.09	4.91
<i>Lumbricus terrestris</i>	8.94	0.0003 ***	1.73a	0.98a	0.06b
<i>Octolasion cyaneum</i>	0.57	0.57 NS	0.06	0.00	0.00
<b>Earthworm biomass (g m<sup>-2</sup>)</b>					
Total earthworms	15.13	0.0000 ***	3.96a	2.55b	0.91c
Total litter-dwelling	1.84	0.16 NS	1.06	1.33	0.89
Total soil-dwelling	17.55	0.0000 ***	2.73a	1.22b	0.02c
<i>Allolobophora chlorotica</i>	4.05	0.019 *	0.18a	0.02b	0.00b
<i>Aporrectodea caliginosa</i>	12.07	0.0000 ***	1.11a	0.54b	0.00c
<i>Aporrectodea longa</i>	3.89	0.022 *	0.25a	0.01b	0.00b
<i>Dendrobaena octaedra</i>	9.54	0.0002 ***	0.03b	0.16a	0.07b
<i>Dendrobaena pygmaea</i>	7.78	0.0007 ***	0.01b	0.06a	0.01b
<i>Dendrodrilus rubidus</i>	6.09	0.0029 **	0.35a	0.43a	0.10b
<i>Lumbricus castaneus</i>	0.02	0.98 NS	0.68	0.69	0.71
<i>Lumbricus terrestris</i>	7.43	0.0009 ***	1.27a	0.59b	0.02b
<i>Octolasion cyaneum</i>	0.57	0.57 NS	0.06	0.00	0.00

\*p < 0.05, \*\*p < 0.01, \*\*\*p < 0.001. Means from the same homogeneous group (SNK procedure) are followed by the same letter, *df* 2/87 for humus profiles, 2/177 for earthworms

**Table 4** Analysis of variance according to phases of the forest cycle, with morphological measurements of humus profiles and earthworm communities

	F ratio	Probability	Mature stage	Tree-fall gap	Pole stage
<b>Humus profile</b>					
OL thickness (cm)	3.44	0.044 *	1.21b	1.38b	2.44a
OF thickness (cm)	4.52	0.019 *	0.67b	0.92b	2.03a
OH thickness (cm)	1.28	0.29 NS	0.00	0.03	0.13
A depth (cm)	26.92	0.0001 ***	11.58a	5.28b	5.97b
Presence of white-rot	1.36	0.27 NS	1.00	0.67	0.83
Munsell colour at 3 cm	0.00	1.00 NS	10.0 YR	10.0 YR	10.0 YR
Munsell colour at 6 cm	0.00	1.00 NS	10.0 YR	10.0 YR	10.0 YR
Munsell colour at 9 cm	0.00	1.00 NS	10.0 YR	10.0 YR	10.0 YR
Munsell hue at 3 cm	1.29	0.29 NS	4.5/	3.8/	3.9/
Munsell hue at 6 cm	1.62	0.21 NS	4.5/	4.2/	4.8/
Munsell hue at 9 cm	3.28	0.051 NS	4.5/	4.7/	5.4/
Munsell chroma at 3 cm	2.92	0.068 NS	/2.2	/1.8	/1.4
Munsell chroma at 6 cm	0.52	0.61 NS	/2.0	/1.8	/2.1
Munsell chroma at 9 cm	2.70	0.082 NS	/2.0	/2.3	/2.9
<b>Earthworm density (number m<sup>-2</sup>)</b>					
Total earthworms	3.49	0.036 *	31.24a	11.78b	16.28b
Total litter-dwelling	2.82	0.065 NS	9.09	4.81	10.16
Total soil-dwelling	5.61	0.0058 **	18.60a	6.28b	4.36b
<i>Allolobophora chlorotica</i>	2.44	0.093 NS	1.98	0.96	0.37
<i>Aporrectodea caliginosa</i>	2.14	0.12 NS	6.21	4.28	2.32
<i>Aporrectodea longa</i>	7.11	0.0018 **	3.25a	0.32b	0.16b
<i>Dendrobaena octaedra</i>	0.78	0.47 NS	0.24	0.00	0.24
<i>Dendrobaena pygmaea</i>	0.16	0.85 NS	0.24	0.49	0.41
<i>Dendrodrilus rubidus</i>	4.59	0.014 *	1.72b	1.57b	4.59a
<i>Lumbricus castaneus</i>	1.86	0.16 NS	5.08	2.07	4.63
<i>Lumbricus terrestris</i>	0.84	0.44 NS	3.23	2.07	1.70
<i>Octolasion cyaneum</i>	1.35	0.27 NS	0.00	0.32	0.00
<b>Earthworm biomass (g m<sup>-2</sup>)</b>					
Total earthworms	2.43	0.094 NS	7.46	3.71	3.67
Total litter-dwelling	2.21	0.12 NS	0.99	0.56	1.19
Total soil-dwelling	2.90	0.061 NS	6.21	3.00	2.27
<i>Allolobophora chlorotica</i>	3.84	0.026 *	0.62a	0.23ab	0.06b
<i>Aporrectodea caliginosa</i>	1.78	0.18 NS	1.70	1.42	0.76
<i>Aporrectodea longa</i>	3.70	0.030 *	1.06a	0.13b	0.19b
<i>Dendrobaena octaedra</i>	1.02	0.37 NS	0.03	0.00	0.01
<i>Dendrobaena pygmaea</i>	0.42	0.67 NS	0.00	0.02	0.01
<i>Dendrodrilus rubidus</i>	3.68	0.030 *	0.19b	0.20b	0.56a
<i>Lumbricus castaneus</i>	1.04	0.36 NS	0.74	0.35	0.62
<i>Lumbricus terrestris</i>	0.74	0.49 NS	2.49	1.46	1.32
<i>Octolasion cyaneum</i>	1.35	0.27 NS	0.00	0.32	0.00

See footnotes to Table 3

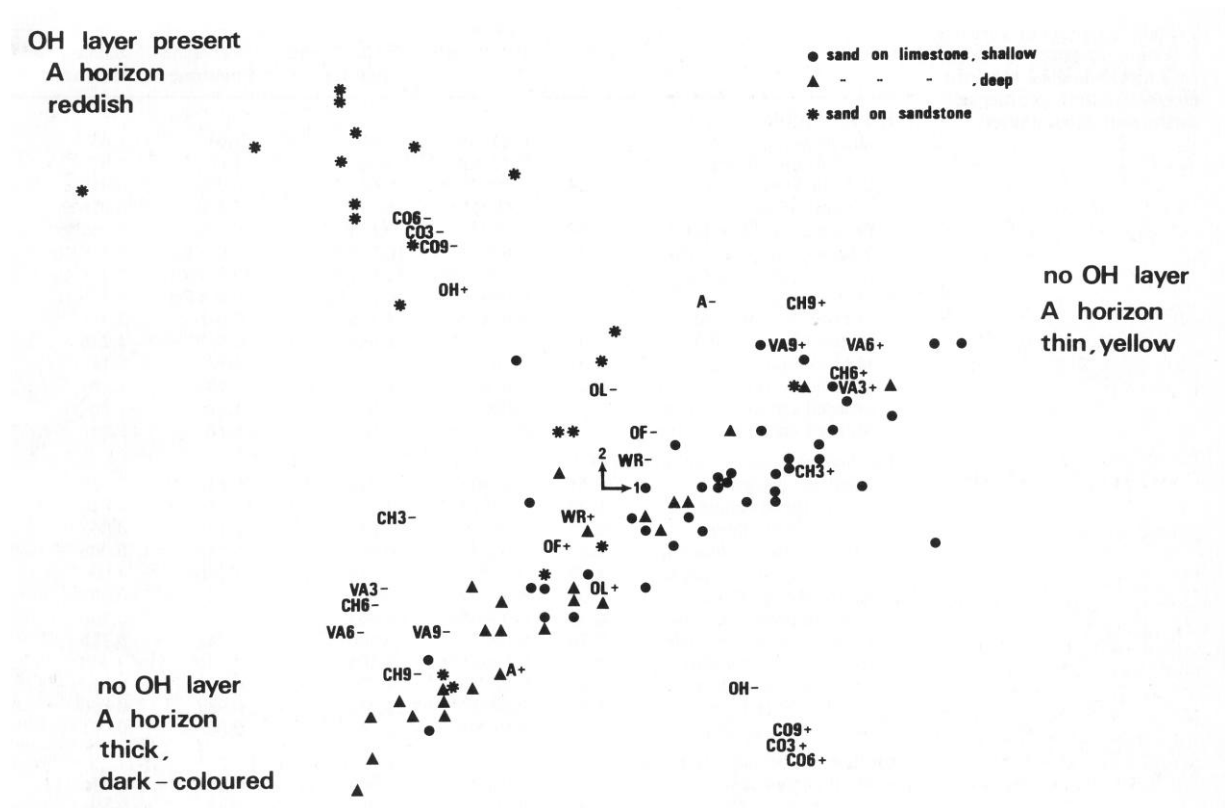


Fig. 1

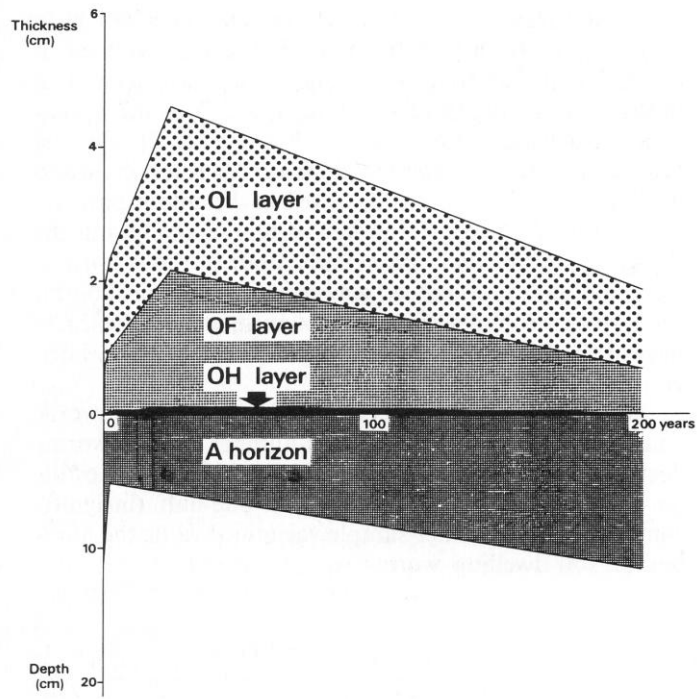


Fig. 2