

 Open access • Journal Article • DOI:10.1016/0038-0717(94)90161-9

Humus form dynamics during the sylvogenetic cycle in a mountain spruce forest

— [Source link](#) 

Nicolas Bernier, Jean-François Ponge

Published on: 01 Feb 1994 - Soil Biology & Biochemistry (Pergamon)

Topics: Humus, Picea abies, Earthworm, Forest dynamics and Forest ecology

Related papers:

- [Humus forms in terrestrial ecosystems: a framework to biodiversity](#)
- [Classification of forest humus forms: a French proposal](#)
- [The heterogeneity of humus profiles and earthworm communities in a virgin beech forest](#)
- [The Forest Regeneration Puzzle Biological mechanisms in humus layer and forest vegetation dynamics](#)
- [Towards a Taxonomic Classification of Humus Forms](#)

Share this paper:    

View more about this paper here: <https://typeset.io/papers/humus-form-dynamics-during-the-sylvogenetic-cycle-in-a-2xsynfxd0a>



HAL
open science

Humus form dynamics during the sylvogenetic cycle in a mountain spruce forest

Nicolas Bernier, Jean-François Ponge

► To cite this version:

Nicolas Bernier, Jean-François Ponge. Humus form dynamics during the sylvogenetic cycle in a mountain spruce forest. *Soil Biology and Biochemistry*, Elsevier, 1994, 26 (2), pp.183-220. 10.1016/0038-0717(94)90161-9. hal-00506004

HAL Id: hal-00506004

<https://hal.archives-ouvertes.fr/hal-00506004>

Submitted on 26 Jul 2010

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

HUMUS FORM DYNAMICS DURING THE SYLVOGENETIC CYCLE IN A MOUNTAIN SPRUCE FOREST

N. BERNIER and J. F. PONGE

Museum National d'Histoire Naturelle, Laboratoire d'Ecologie Générale, 4 avenue du Petit-Chateau, F-91800
Brunoy, France

Summary—The humus forms during the life cycle of a spruce forest are described. A significant change in humus form may be attributed to plant and soil fauna changes. This phenomenon is considered to be fundamental for the renewal of the forest ecosystem. Forest dynamics is perceived as a biphasic cycle, (i) the tree growth phase with a shift from mull towards moder humus form, as a consequence of a decline in earthworm populations and (ii) a humus form improvement from moder towards earthworm mull humus, during the second half of the life of spruce trees. This results from a succession of earthworm species. The particular role of anecic species during the second phase has been highlighted, where they allow endogeic earthworm species and young spruce seedlings to install themselves in the regeneration site, the fall of parent trees not being considered as the chief factor governing humus changes.

The life cycle of the spruce ecosystem can nevertheless be impaired by the development of a bilberry heath, with a mor humus form which is detrimental to the germination and growth of spruce seedlings. Earthworm populations of anecic and endogeic species are present in this case but without any burrowing activity.

INTRODUCTION

Most studies on changes in soil profiles associated with vegetation have supported the successional theory developed by Clements (1916, 1936). Therefore, the time scale most commonly assumed for soil dynamics is of

the order of several centuries (Duchaufour, 1968; Guillet, 1975). Moreover, soil development has been considered as only unidirectional unless a catastrophe occurs (Crocker and Dickson, 1957). As soon as the soil reaches the pedoclimax, it does not change any more. However, the time sequence of pine stands studied by Mettievier Meyer *et al.* (1986) showed that changes of organic and mineral horizons occurring within a century are also important. In this case the time scale is much shorter. Similarly, Page (1974) described a cycle, in which the soils of very young and very old plantations were quite similar. The capability of soil-forming processes to be reversed under vegetational influence has been clearly demonstrated by the work of Fisher (1928) and Dimpleby (1952).

In parallel, the forest climax appears now to be less uniform than it seemed previously. In fact, forest ecosystems may be considered as a mosaic of sylvogenetic phases (Mayer, 1976; Lemée, 1989; Koop and Hilgen, 1987; Oldeman, 1990). In a natural or near natural forest ecosystem, it should be possible to study the causal relationships between vegetation and soil dynamics. The humus profile is the result of the functional connections between primary producers (vegetation) and decomposers (soil microorganisms and saprophytic animals) in a given environment (Bal, 1982). Thus by studying the top few centimetres of the soil it should be possible to throw light on the dynamic processes taking place in forest soils.

Since the founding work of Kubiëna (1938), humus micromorphology has evolved from a descriptive science to an analysis of the functional relationships between soil components, in the frame of forest ecology (Babel, 1975; Brun, unpublished, 1978; Bal, 1982; Ponge, 1988). Attempts have been made to compare distinct humus profiles (Bal, 1970; Bernier *et al.*, 1994), so it is possible to include the dynamics of surface horizons in a study of the sylvogenetic cycle. The hypothesis we wanted to test in the present study was that a given humus profile may inform us both about the way the humus is functioning and about the state of development (or degradation) of the ecosystem to which it belongs.

STUDY SITE

The Norway spruce [*Picea abies* (L.) Karst.] forest under study is located on a northern slope in the French Alps (Tarentaise Valley, Savoy), on the territory of the Macôt-La-Plagne commune. It belongs to the *Melampyro sylvatici-Piceetum* type (Gensac, 1988). The elevation ranges between 1535 and 1575 m, that is the middle part of the montane level. The soil parent material is a colluvium made of quartzite particles of varying

size. This site has been chosen as part of a more comprehensive study dealing with altitudinal effects on forest dynamics (Bernier and Ponge, 1994).

A map of the chosen site has been prepared as a guide for sampling the different units of the forest patchwork (Fig. 1). These motifs have been named eco-units by Oldeman (1990). They are surfaces which are homogeneous from a vegetational point of view, due to a common history (in the course of the sylvogenetic cycle or other natural or man-made events). The main features of the nine eco-units selected are described in Table 1. In addition to true phases of the sylvogenetic cycle (dense spruce thickets and regeneration sites), the study area is characterized by the presence of an ericaceous heathland (André and Gensac, 1989) which is established in places where tree crowns do not join. This development of ericaceous species as a dense cover closely resembles what can be observed at a higher elevation in the *Homogyno-Piceetum* (Gensac, 1988).

METHODS

The sampling method for humus profiles was described by Ponge (1984) and Bernier *et al.* (1994). A block 25 cm² in section and 15 cm high (including the moss cover and leaf bases when present) was prepared directly in the field with a sharp knife. Then each layer was isolated and fixed immediately in 95% ethanol. The thickness of each humus layer was recorded using a correction factor to allow for the compression of the humus block. This measurement was done to an accuracy of 0.5 cm. The whole depth of the humus profile investigated has been standardized to 15 cm, which is the maximal depth of organic matter observed in neighbouring sites (Bernier *et al.*, 1994).

The samples were taken at the centre of each eco-unit described in Table 1 (see also Fig. 1) in June 1991.

Each layer was studied under a dissecting microscope after spreading it out in a Petri dish filled with 95% ethanol. The different components were identified at the magnification of $\times 40$ with samples of the main living plant species as control. From these observations a reference array was constructed (Fig. 2).

Among humus components, two were heterogeneous but could not be analysed at this magnification, (i) the holorganic faecal pellets and (ii) the organo-mineral material. These were studied at a higher magnification ($\times 400$), under a light microscope with phase contrast. To do this, an aliquot of each of these components was

crushed, homogenized, then mounted in methyl blue-lactophenol (a dye for cytoplasmic inclusions). At this magnification, it was possible to recognize the microscopic components listed in Fig. 3. As it was impossible to trace the plant species from which the observed fragments originated, only the structure of the plant material and its colour were recorded. Amorphous organic matter means that this component had lost the refringency properties of plant cell wall residues due to their microcrystalline structure (Esau, 1965). In addition, the structure of the organo-mineral material as seen under the dissecting microscope was recorded. This structure could be either crumb-like or compact. As the aggregates were made mainly by lumbricid species (faecal pellets), their degree of preservation (smooth and brilliant surface aspect for the fresh pellets, dull and rugose for old material) gave an indication of the actual or past activity of earthworm species.

The different components were quantified by the point-count method described by Jongerius (1963) and used by Bal (1970) and Rozé (1989). Under the dissecting microscope, a transparent film with a 400 point grid was laid down above the preparation. Under the light microscope, counting was made by regularly shifting the advanceable stage and with the aid of a cross reticle in the eye piece. For each light microscope slide, about 200 points were observed, distributed all over the slide. The results were expressed as percentages, corresponding to the volume ratio of each solid element.

The data thus obtained for each humus layer allowed the construction of two types of diagrams, one for what has been observed under the dissecting microscope, the other for the light microscope. They have been drawn by using the volume ratio as abscissa and the depth as ordinate. The same method has been used to represent the distribution of the different components of organo-mineral matter.

Earthworm populations were extracted from each eco-unit (Table 1), as near as possible from the sampled humus profile, according to the procedure of Bouché (1969) and Bouché and Gardner (1984): formalin application followed by hand sorting. In each eco-unit, six 0.25 m² samples were extracted, three in June 1991 and three in June 1992. The species were identified using Bouché (1972).

Nomenclature of litter layers and soil horizons follows Baize and Girard (1992).

RESULTS

The humus diagrams (Figs 4-13) show a marked heterogeneity among humus forms. Vegetation and

associated litter were not the only cause of these differences. The most prominent differences resulted from the way the organic matter had been transformed and its degree of mixing with mineral particles.

The regeneration site

Natural regeneration took place mainly within tree fall gaps, as represented by eco-unit 1 (Fig. 1, Table 1). Herb species [mainly *Luzula sylvatica* (Huds.) Gaud. and *Deschampsia flexuosa* (L.) Trin.] had grown directly in an organo-mineral substrate (Fig. 4) which had been built up recently by the lumbricid fauna, as proved by the presence of fresh aggregates down to 9 cm depth (Fig. 14). This humus form showed typical features of the mull type (Müller, 1889). Below 9 cm depth, organo-mineral faecal pellets looked older and altered, indicating that recent earthworm activity took place mainly in the top 9 cm, with traces of past activity at a lower depth. Below 13 cm the structure became partly compacted. The plant remains which were present in the studied profile did not come entirely from the aboveground herbaceous cover. Between 3 and 4 cm depth, a layer made of bark fragments from fallen trees (see tree stumps on Fig. 1) was present. The old spruce parents could be traced by the presence of a layer of dead conifer roots between 7 and 11 cm depth.

The light microscope humus diagram (Fig. 4) showed that organo-mineral faecal pellets were composed mainly of amorphous organic matter linked to thin mineral particles (quartz crystals of clay and silt size). The resulting structure seemed to be highly stable (Fig. 15). This assemblage could be related to the dominance of endogeic earthworm species such as *Allolobophora icterica* (Savigny, 1826) and *Nicodrilus caliginosus* (Savigny, 1826) (Fig. 19), given our knowledge on their life habits (Bouché, 1972; Lavelle, 1981). Below 11 cm depth, the amorphous organic matter was no longer linked entirely to mineral crystals. This material was now present mainly as *ca* 50 μm coherent pellets (Fig. 16). This change in the appearance of amorphous organic matter coincided with a structural shift from aggregation to compaction of the organo-mineral material (Fig. 14).

The young growth phase, before and after canopy closure

In an approx. 30-yr-old eco-unit of growing spruce (eco-unit 2, Fig. 1, Table 1), the regeneration process was complete. Crowns were distributed unevenly so that two different kinds of situation occurred.

Before the canopy closure, the soil surface was covered with a thick moss layer (Fig. 5). This moss

cover had produced dead litter, which was present even at the bottom of the profile. The abundance of herbaceous remains increased with depth, giving evidence of a previous herbaceous cover. Below 12 cm depth, dead spruce roots (from parents) were surmounted by the living roots of young trees. In fact, the bottom of the profile closely resembled the humus form of the regeneration site.

After canopy closure, the soil was covered mainly by a layer of spruce needles (Fig. 6). Just under it, an important moss litter was present, which was the dead equivalent of the living moss layer which was present before canopy closure (Fig. 5). The two humus forms also possess a bark layer of about 9–12 cm depth, originating from the fall of old spruce trees. This event was also indicated by the presence of herbaceous remains, just above the bark layer. As in the previous humus profile, dead and living roots of spruce were not found at the same depth. Starting from the fall of the trees, indicated by the bark deposit, the humus profile had been built up by the successive deposition of different plant remains. The actual development of roots seemed to be very superficial, and thus living roots (of actual trees) were found at a lower depth than dead roots (of parent trees).

The building of the humus profile by soil animals during this phase of the sylvogenetic cycle was always due to burrowing earthworm species, mostly endogeic (same species as above) and anecic [*Nicodrilus nocturnus* (Evans, 1946), *Lumbricus terrestris* Linné, 1758], even though the density of endogeic species was considerably lower (Figs 19 and 20). The structure of the organo-mineral material (Fig. 14) showed that the lower level of deposition of fresh faecal pellets was at 12 cm depth before canopy closure and at 10 cm depth after canopy closure, i.e. in the two cases just above the old root litter layer. Below that, the structure was made of old earthworm casts which were always separated in the first humus profile but compacted in the second one. The old structure depicted by these humus profiles below 10–12 cm depth was probably the one which had been active at the time of regeneration. Since then, the importance of plant remains increased as earthworm densities decreased, producing an imbalance between litter production and consumption by fauna.

The results of this dynamic process were also perceptible in the light microscope humus diagram (Figs 5 and 6). Indeed, organo-mineral faecal pellets were richer in plant material and poorer in fine amorphous organic matter than during the regeneration phase. Nevertheless the organo-mineral linkage was always as firm. The two humus profiles of the young growth phase belonged to the mull type.

The phase of intense growth, at 50 and 60 years age

In the 50-yr-old spruce stand (eco-unit 3, Fig. 1, Table 1), the humus form was markedly different (Fig. 7). The humus profile could be separated easily into two parts. The top 3 cm were wholly organic, but in contrast the deeper horizons were rich in mineral matter. The organic layers were characterized by the presence of holorganic faecal pellets. This humus form was being built up by epigeic fauna, which were the main features of the moder type (Ramann, 1911). The shift towards an epigeic functioning was recent, the holorganic faecal pellets were just beginning to accumulate in an OH horizon (Hesselmann, 1926). In fact, an endogeic residual activity was perceptible in the structure of the organo-mineral material (Fig. 14). From 5 to 15 cm depth, this structure was constant. Part of the organo-mineral matter was compact but most of it was in the form of old earthworm aggregates. Microscopic examination of the organo-mineral material (Fig. 7) gave evidence of a disruption of the linkages between organic and mineral matter. These features did not match with the results of earthworm sampling (Figs 18, 19 and 20). The densities of endogeic and anecic earthworm species were not typical of the moder type. This phenomenon had already been observed at a lower elevation (unpublished data). Our hypothesis is that the 50-yr-old spruce stand was subjected to selective thinning a few years before (a lot of cut stems are visible), so that the effects of spruce on the soil system decreased temporarily. On the other hand, part of the soil fertility had been restored by decomposition of slash. Nevertheless, this enrichment could be considered as only provisional.

The hypothetical affiliation of this humus form with those of the 30-yr-old spruce stand (eco-unit 2) was confirmed by the presence of moss and herbaceous remains under the holorganic horizon of the moder humus profile. Therefore, despite a temporary increase in earthworm population, the imbalance between endogeic faunal consumption and litter production drove the system towards a moder humus form.

Moder features (Kubišna, 1953) were more evident (Fig. 8) under a 60-yr-old spruce stand (eco-unit 4, Fig. 1, Table 1), when trees had grown to a height about twice those in the 50-yr-old stand (eco-unit 3). The holorganic faecal pellets had built a 5 cm thick OH horizon under the thin OL and OF horizons (2 cm in bulk). Only the upper part of this OH horizon was permeated by the thin mycorrhizal root system of spruce, as has been observed in pine stands (Ponge, 1990). Below 6 cm depth, no sign of earthworm activity was perceptible. This humus form is a leptomoder (Klinka *et al.*, 1981). Earthworm densities reinforce the idea that this humus profile had been built up only by epigeic species such as *Dendrobaena subrubicunda* Eisen, 1874 (Fig. 18). The first organo-mineral layer (7–8 cm depth) was virtually devoid of organic matter, apart from some root and bark litter

(Fig. 8). Pure quartz particles (Fig. 17) gave a white aspect to this layer. Below 8 cm depth the soil was rich in free amorphous organic matter (Fig. 16) in the form of small organic pellets that gave the horizon its red-brown colour. The properties of these two mineral horizons provided evidence of current podzolization. The bleached horizon between 7 and 8 cm depth was an eluviated level or E horizon (Brady, 1984), while the underlying horizon was an illuviated level or B horizon. At this stage, the soil was a micropodzol, given the thin depth of the E horizon layer.

The mature phase, at 160 and 190 years age

In the 160-yr-old spruce stand investigated (eco-unit 5, Fig. 1, Table 1), the leptomoder humus form was almost destroyed (Fig. 9). In fact, holorganic faecal pellets were as abundant as in the leptomoder humus but they did not form an OH horizon. This material was distributed throughout the entire humus profile. In fact, this apparent feature was due to casting activity within surface horizons (Fig. 14). This subterranean activity was due to a small population of the anecic earthworm species *Lumbricus terrestris* (Fig. 20). This species is able to burrow deeply into the soil but feeds on surface litter. As a consequence, the E and B horizons had disappeared and the stratification of the profile was less obvious. In fact, if we neglect the organo-mineral material that had been deposited in the first 13 cm, we find the same holorganic layers as in the leptomoder of the eco-unit 4 (60 yr). For instance the shallow position of fine mycorrhizal roots (2–7 cm depth) when compared to large and dead roots (7–11 cm depth) was typical of a moder humus profile (Meyer and Götttsche, 1971). Organo-mineral faecal pellets brought up to surface layers were poor in organic matter (Fig. 9), like the organo-mineral material present in deeper horizons. Most organic matter was not linked to mineral particles (Fig. 6). The association of moder features (absence of association of organic matter to mineral particles, shallow development of fine roots) and mull features (deep burrowing of the plant material, surface deposition of mineral matter) corresponded to the mull-like moder humus described by Kubiěna (1953), except that this form was attributed by Kubiěna himself to the activity of small animal species and not, as here, to earthworms.

This humus form was fully developed in a small relict stand consisting of a few 190-yr-old spruce trees (eco-unit 6, Fig. 1, Table 1). Features of the former leptomoder profile were no longer distinguishable at this stage of development. The holorganic faecal pellets were far less abundant and they were spread all over the humus profile (Fig. 10). This was also the case for spruce needles. Thus, this humus form was not only built by surface deposition of organo-mineral earthworm faeces but also by the burying behaviour of *Lumbricus*

terrestris (Darwin, 1881, experimentally verified with spruce needles by Bernier, unpublished, 1992). Mull features were hidden by a thick spruce needle litter layer, which prevented the earthworm casts from being seen on the soil surface. The accumulation of spruce litter might be related to the high level of foliage production due to the free growth of the single dominant tree. Increase in litter production has been demonstrated elsewhere not to change the activity of soil fauna (David *et al.*, 1991). The organo-mineral material had recently acquired an aggregated structure, due to the activity of anecic and, to a lesser extent, endogeic earthworm populations (Figs 10, 19 and 20). Organo-mineral faecal pellets were still poorly cemented, although a greater proportion of amorphous organic matter was now linked to mineral particles (Fig. 10). We propose the name of *earthworm mull-like moder* for this humus form which exhibits the main features of the mull-like moder type (Kubiëna, 1953), but is built up mainly by anecic earthworm species. Their faeces were recognizable in the 0.5 cm Φ aggregates.

The collapse stage

The eco-unit 7 (Fig. 1, Table 1) was located in the vicinity of a 215-yr-old larch tree, with stem remains of adjacent spruce trees of similar age which had probably fallen during the previous winter. The density of the endogeic earthworm population was nearly as large as the population in the regeneration site (Fig. 19). Despite this activity, the humus form still had features of the earthworm mull-like moder (Fig. 11). The few holorganic faecal pellets were dispersed over the whole profile. Deep-burrowing earthworm species (Fig. 20) had buried needles down to 14 cm depth. Half of the amorphous organic matter was now linked to mineral particles (Fig. 11). Fresh earthworm faecal pellets were present mostly in the top 11 cm (Fig. 14). Thus, this humus profile was the first step towards the formation of a true earthworm mull profile. The A horizon between 4 and 11 cm depth was being built up by endogeic earthworm species, probably using as food the anecic earthworm faeces in the previous mull-like moder.

The bilberry heath and its genesis

The eco-unit 8 was chosen in a mossy patch between adult trees with an open canopy (Fig. 1, Table 1). Living moss parts and moss remains, together with larch and spruce needles (OL and OF horizons, Fig. 12), overlaid a network of bilberry (*Vaccinium myrtillus* L.) rhizomes. Thus this ericaceous species was invading this

eco-unit at the time of sampling. The lower layers were rich in dead conifer roots which might come from the trees that had been present on the site. The faunal activity was mainly epigeic, and earthworm species were scarce (Figs 18, 19 and 20). Aggregate analysis (Fig. 14, see also Fig. 12 for estimation of percentages) showed that fresh organo-mineral faecal pellets were more or less absent. Some old organo-mineral faecal pellets were present, together with compacted material, down to 15 cm depth. Under moss cover, the epigeic faunal activity was depicted by the presence of a small quantity of holorganic faecal pellets. This could be taken as indicating the formation of an OH horizon. Observation under the light microscope (Fig. 12, right side) showed a sharp transition between this layer and the underlying organo-mineral horizons. The structure of the latter horizons was mainly compact, with a few old aggregates (Fig. 14). The organic matter was mainly present in a free amorphous form (Fig. 12, right side). The presence of old organo-mineral aggregates, together with deeply buried spruce needles, fits with the features depicted by the earthworm mull-like moder (see above). Nevertheless anecic earthworm species were no longer present (Fig. 20). Thus these features were relicts. The current earthworm activity was mainly epigeic.

In the bilberry heath (eco-unit 9, Fig. 1, Table 1), the humus profile had a 5 cm thick OH horizon, underlying a thick moss layer (Fig. 13). In this humus profile, plant remains had not accumulated, thus the OF horizon was not fully developed. Most of the plant remains originated from the moss layer, but they had been incorporated rapidly into the holorganic faecal material. The composition of this material was particular (Fig. 13). It was composed not only of plant cell or tissue remains (as under 60-yr-old spruce trees), but also contained a great quantity of amorphous organic matter, cementing the plant remains. It looked like organo-mineral material. We may suppose that this was the consequence of a longer residence time of plant organic matter. A corollary of this hypothesis would be that the humus form under bilberry was more stable than any other observed in the same site. No trace of past vegetation was visible, contrary to what was observed under spruce stands. The hypothesis of the high stability of this profile was confirmed by the massive structure of the OH horizon (field data). This hypothesis was not the only possible one. Amorphous organic matter might also have come from intra-cellular tannin-protein complexes that are known to be rapidly released after the death of bilberry leaves (Gallet, unpublished, 1992). In any case, the presence of unlinked amorphous organic matter was a feature shared by holorganic and organo-mineral horizons. Thus amorphous organic matter, which was found deeper in the B horizon, probably arose from the leaching of holorganic layers. According to the nomenclature of Klinka *et al.* (1981), this humus profile shared many features with the humimor humus form. In this case the humus profile developed under the bilberry heath would belong to a different order (mor order) from those

developed under spruce trees (mull and moder orders).

DISCUSSION

These results indicate that cyclic patterns of humus and soils are connected strongly with the life cycle of the spruce forest ecosystem. The importance of this fact for the sustainability of spruce forests is due mainly to the exacting nature of this tree species at the beginning of its life. The mull humus form in the natural regeneration site of Norway spruce was documented by Weissen and Jacqmain (1978), Weissen (1979), Gensac (1989), André *et al.* (1990), Bernier *et al.* (1994) and by Eis (1965) and Christy and Mack (1984) on other spruce species. Another favourable substrate for the establishment of conifer seedlings is decaying wood (Christy and Mack, 1984; Harmon and Franklin, 1989; Gensac, 1990; Hofgaard, 1994). The most commonly recognized environmental conditions associated with the narrow regeneration niche of spruce are suitable water content and temperature regimes (Eis, 1965; Ott, 1966), non-toxic litter (Daniel and Schmidt, 1972; Gallet, unpublished, 1992) and high nutrient content (Mousain; 1975; Weissen and Jacqmain, 1987). Intense regeneration may be observed in clearings where there is a high probability of occurrence of the above-mentioned factors (Ponge *et al.*, 1994).

On the other hand, coniferous trees are well-known for their acidifying effects (Shleynis, 1965; Noirfalise and Vanesse, 1975), driving humus towards a moder or mor form (Noirfalise and Vanesse, 1975; Bonneau, 1978; Babel, 1981; Mettievier Meyer *et al.*, 1986). Our results show the same shift when spruce growth is maximal, but without any change in pH (Ponge *et al.*, 1994). It seems that pH reached a minimum value (pH = 4) in our study site and therefore cannot change any more. The key point is the disappearance of the moder humus during the mature phase, so that the inconsistency between regeneration requirements and accumulation of raw humus under spruce trees is no longer valid. The same observation was made by Bernier *et al.* (1994) in the same forest, but without knowledge of the steps essential for this transformation of the humus profile. Page (1968, 1974) found a similar improvement of humus condition in a series of coniferous stands of increasing age. It must be noted that most studies dealing with coniferous effects on soil took place in young plantations of species that were out of their natural range (Shleynis, 1965; Nihlgard, 1971; Bonneau, 1978).

In this study, earthworm species play a leading role because of their strong influence upon the development of the humus profile (Bal, 1982). For example, typical mull is observed only when endogeic

earthworms are abundant (see also Bernier *et al.*, 1994) and the depth of the mull humus form (10 cm) fits well with the maximal burrowing depth of these animals (Bal, 1982; Tomlin *et al.*, 1992). In the course of the forest cycle, data on earthworm populations undoubtedly describe a species succession. This succession begins when spruce trees are adult, with the installation of an anecic earthworm species (*L. terrestris*) which progressively transforms the humus form previously built up by epigeic animals. This vigorous earthworm species brings an intense modification of the humus profile which in the course of time becomes favourable to endogeic earthworm species, such as *N. caliginosus* and *A. icterica*. In the regeneration site (a tree fall gap) both epigeic, endogeic and *L. terrestris* populations increase, and the action of the latter species is reinforced by another anecic (*N. nocturnus*). Similar successions in earthworm communities have been investigated by Scheu (1992) in the course of an old field succession. He described similarly *L. terrestris* as a pioneer species. On the other hand, Dunger (1969) demonstrated that the first species which was able to colonize a new substrate such as a coal mine spoil was *N. caliginosus*, and the last was *L. terrestris*.

In our study, endogeic earthworms were never found in the absence of anecic species. Anecic and endogeic populations collapsed simultaneously, when spruce was in an intense growth phase. These two earthworm ecological categories behave similarly after selective thinning (50-yr-old stand). At this time both populations increase (Figs 19 and 20), but this effect was of a short duration. The improvement of casting activity after selective thinning was documented by Ott (1966). After that stage, an earthworm collapse takes place again and only epigeic species can maintain themselves but at a low density.

Our hypothesis is that *L. terrestris* is the main species changing humus from a moder to a mull form. The effects of this burrowing species on the humus profile are probably amplified by epigeic species such as *D. subrubicunda*, *L. castaneus* and *L. rubellus* which are able to ingest a lot of mineral particles when present in a soil with a thin litter layer (Pearce, 1978; Bal, 1982; Judas, 1992). We assume that the installation phase of endogeic populations is possible only when a critical mass of organo-mineral faeces has been deposited by anecic earthworms close to the soil surface. Endogeic earthworms are unable to burrow deeply and need organo-mineral material (Bal, 1982). Once a true earthworm mull has developed, endogeic worms will always depend on anecic species for the excavation of mineral matter and on both epigeic (not only earthworms) and anecic (earthworm) species for their fresh organic matter requirements. This dependence is first on *L. terrestris*, and later on *N. nocturnus* as well. Such a synergistic association between earthworm species was suggested by Shaw and Pawluk (1986) for the soil fabric and by Scullion and Ramshaw (1988) for casting activity. According to our observations, it may be said (i) that a high earthworm diversity is correlated with a typical mull profile (Staaf,

1987) and (ii) that other humus forms result from the absence of some earthworm species rather than from the presence of others. Likewise, David *et al.* (1993) observed that a higher macro-faunal diversity was associated with typical mull humus.

As has been assumed for a long time, the analysis of humus profiles depicts a narrow relationship between the status of soil organic matter and earthworm activity (Rafidison, unpublished, 1982; Hayes, 1983; Shipitalo and Protz, 1989; Martin, 1991). When epigeic species are alone, the humus profile belongs to the moder form (Bornebusch, 1930; Staaf, 1987) and the soil organic matter is leached from the top of the mineral profile (E horizon) and accumulates in a B horizon. The microscopic appearance of organic matter in the B horizon suggests that organic coherent assemblages are filling the soil micropores with a poor adherence to quartz grains. Babel (1975) described the microstructure of podzol B horizons as a sandy skeleton coated with a thin layer of amorphous matter. We never found such coatings on silt particles in our humus profiles. These discrepancies could be attributed either to the drying of the samples and subsequent retention of the plasma before resin embedding in Babel's work or to a possible difference in the nature of the parent rock.

The shift from a moder to a mull humus form by the activities of anecic earthworms is a stepwise process. Soil organic matter does not change in appearance immediately after its first inclusion into earthworm faeces. In spite of its crumbly structure the humus profile built up by *L. terrestris* (the earthworm mull-like moder) is probably made of the O, E and B horizons which have been indiscriminately mixed together.

The most important shift in organo-mineral assemblages is observed in the humus profile built up by endogeic earthworm species. In this case soil organic matter seems to be better linked with mineral particles. This may be due to a more intense mixing of the soil by endogeic species. According to this hypothesis, endogeic earthworms would then be able to create new chemical links, in particular between mineral and organic matter.

The evolution towards a moder form does not first affect soil organic matter. In the 30- or 50-yr-old spruce stands, the structure becomes more-and-more compact while organic matter is still linked with mineral matter (see Bernier *et al.*, 1994). Thus it is possible, by help of micromorphology, to distinguish mull-forming and mull-destroying phases where structure and organo-mineral assemblages do not evolve at the same rate. The stabilization of the structure by organic matter would then be the result of a more advanced transformation of the soil by burrowing species, in particular when both anecic and endogeic earthworms are present (Shaw and Pawluk, 1986).

For each humus profile, morphological features may be ascribed either to past or present building actions. They offer more solid arguments to valid time sequences based only on the study of present vegetation. The relationships between the history of mosaic elements of the forest patchwork (e.g. eco-units) and soil biological activity allow us to address a hypothetical trend about forest dynamics.

In the forest cycle, mull conditions that are necessary for the renewal of spruce forest are developed a long time before the trees actually die. The detrimental effects of coniferous stands on the soil are thus in fact restricted to their growth phase. In this case the soil may recover its original properties only if adapted populations of anecic earthworm species are able to recolonize the sites they have abandoned temporarily. This colonization may be effected by horizontal movements of migrating animals through an heterogeneous environment (Fig. 1) or by an increase in the size of relict standing populations. If the former is true, then a mosaic pattern of developmental phases of the spruce ecosystem may offer more opportunities than a pure stand of even-aged trees.

The bilberry heath has a particular status in this forest. Negative effects of ericaceous or related species on coniferous regeneration are well-known (Handley, 1963; André and Gensac, 1989; Gallet, unpublished, 1992; Nilsson and Zackrisson, 1992). The forest cycle is then broken. The genesis and development of heath in this forest were unclear (Bernier *et al.*, 1994) until we analysed the moss eco-unit (Fig. 12). Ericaceous species have a vegetative development which is mainly centrifugal (Flower-Ellis, 1971). This has been observed at the periphery of herbaceous tree fall gaps (André, unpublished data) or in small openings occurring in adult spruce stands (the moss ecounit). In the first case (colonization of herbaceous gaps), spruce regeneration is already achieved when moss and bilberry development is obvious, so in this case the future development of bilberry heath is curtailed. In the second case (colonization of adult spruce stands), the improvement of the humus form usually observed under the mature stand is arrested. Instead of creating favourable conditions for regeneration, old spruce eco-units are then progressively fragmented, inducing the development of a dense bilberry heath between the trees. In this way wide gaps appear between the trees, filled with heath, and then there is no hope for spruce regeneration. Mor humus form is closely associated with ericaceous species, bilberry being among them (Dimbleby and Gill, 1955; Låg, 1959, 1961). This looks like a regressive succession pattern with, at the end, an autogenic lockup (Watt, 1947; Bournérias, 1979; Leparand Escarré, 1983). We assumed that heath genesis took place after intense thinning of mature spruce stands with the aim of stimulating regeneration. This forestry practice, rather common in mountain forests until the last

decade, permitted the bilberry heath to spread itself at an elevation far lower than expected (Bernier, unpublished, 1992; Ponge *et al.*, 1994). The humus form we observed under bilberry (humimor) shows

original features such as a considerable amount of amorphous organic matter included in the OH horizon, which was not observed in the leptomoder humus under spruce. This is a supportive argument for our hypothesis concerning the consequences of the development of bilberry in the site we studied. The building of a completely different humus profile, with distinct biological activities, is the sign of the birth of the bilberry heath ecosystem within a spruce forest. These two ecosystems would then be in close competition, the outcome of which would depend on human activities.

REFERENCES

- André J. and Gensac P. (1989) *Vaccinium myrtillus* et la régénération dans les pessières d'altitude: cas de deux stations dans les Alpes françaises septentrionales. *Acta Biologica Montana* **9**, 135–142.
- André J., Gensac P. and Gautier M. (1990) La régénération dans la pessière à myrtille. Description préliminaire de deux stations dans les Alpes septentrionales internes. *Bulletin d'Ecologie* **21**, 51–61.
- Babel U. (1975) Micromorphology of soil organic matter. In *Soil Components. I. Organic Components* (J.E. Gieseking, Ed.), pp. 369–473. Springer, Berlin.
- Babel U. (1981) Humusmorphologische Untersuchungen in Nadelholzbeständen mit Wuchsstörung. *Mitteilungen des Vereins für Forstliche Standortskunde und Forstflanzenzüchtung* **29**, 7–20.
- Baize D. and Girard M.C. (1992) *Référentiel Pédologique. Principaux Sols d'Europe*. INRA, Paris.
- 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.
- Bernier N. and Ponge J. F. (1994) Dynamique et stabilité des humus au cours du cycle sylvogénétique d'une pessière d'altitude. *Comptes-Rendus des Séances de l'Académie des Sciences de Paris, Série 3, Sciences de la Vie* **316**, 647–651.

- Bernier N., Ponge J. F. and André J. (1994) Comparative study of soil organic layers in two bilberry-spruce forest stands (*Vaccinio-Piceetea*). Relation to forest dynamics. *Geoderma* **51**. In press.
- Bonneau M. (1978) Conséquences pédologiques des enrésinements en forêt. *Comptes-Rendus des Séances de l'Académie d'Agriculture de France* **64**, 931–942.
- Bornebusch C.H. (1930) The fauna of forest soil. *Det Forstlige Forsøgsvaesen* **11**, 1–158.
- Bouché M.B. (1969) Comparaison critique de méthodes d'évaluation des populations de lombricidés. *Pedobiologia* **9**, 26–34.
- Bouché M.B. (1972) *Lombriciens de France. Ecologie et Systématique*. INRA, Paris.
- Bouché M.B. and Gardner R. H. (1984) Earthworm functions. VIII.—Population estimation techniques. *Revue d'Ecologie et Biologie du Sol* **21**, 37–63.
- Bournérias M. (1979) *Guide des Groupements Végétaux de la Région Parisienne*. SEDES, Paris.
- Brady N.C. (1984) *The Nature and Properties of Soils*, 9th Edn. Macmillan, New York.
- Christy E.J. and Mack R. (1984) Variation in demography of juvenile *Tsuga heterophylla* across the substratum mosaic. *Journal of Ecology* **72**, 75–91.
- Clements F.E. (1916) *Plant Succession. An Analysis of the Development of Vegetation*. The Carnegie Institution, Washington.
- Clements F.E. (1936) Nature and structure of the climax. *Ecology* **24**, 252–284.
- Crocker R.L. and Dickson B.A. (1957) Soil development on the recessional moraines of the Herbert and Mendenhall glaciers, South-Eastern Alaska. *Journal of Ecology* **45**, 169–185.
- Daniel T.W. and Schmidt J. (1972) Lethal and nonlethal effects of the organic horizons of forested soils on the germination of seeds from several associated conifer species of the Rocky Mountains. *Canadian Journal of Forest Research* **2**, 179–184.
- Darwin C.R. (1881) *The Formation of Vegetable Mould Through the Action of Worms, with Observation on Their Habits*. Murray, London.

- David J.F., Ponge J.F. and Delecour F. (1993) The saprophagous macrofauna of different types of humus in beech forests of the Ardenne (Belgium). *Pedobiologia* **37**, 49–56.
- David J.F., Ponge J.F., Arpin P. and Vannier G. (1991) Reactions of the macrofauna of a forest mull to experimental perturbations of litter supply. *Oikos* **61**, 316–326.
- Dimbleby G.W. (1952) Soil regeneration on the North-East Yorkshire moors. *Journal of Ecology* **40**, 331–341.
- Dimbleby G.W. and Gill J.M. (1955) The occurrence of podzols under deciduous woodland in the New Forest. *Forestry* **28**, 95–106.
- Duchaufour P. (1968) *L'Evolution des Sols. Essai sur la Dynamique des Profils*. Masson, Paris.
- Dunger W. (1969) Fragen der natürlichen und experimentellen Besiedlung kulturfeindlicher Boden durch Lumbriciden. *Pedobiologia* **9**, 146–151.
- Eis S. (1965) Development of white spruce and alpine fir seedlings on cut-over areas in the Central Interior of British Columbia. *Forestry Chronicle* **41**, 419–431.
- Esau K. (1965) *Plant Anatomy*. Wiley, New York.
- Fisher R.T. (1928) Soil changes and silviculture on the Harvard Forest. *Ecology* **9**, 6–11.
- Flower-Ellis J.G.K. (1971) Age structure and dynamics in stands of bilberry (*Vaccinium myrtillus* L.). Department of Forest Ecology and Forest Soils, Royal College of Forestry, Research Note No. 9.
- Gensac P. (1988) Types de pessière et régénération en Moyenne Tarentaise (Savoie). *Revue Forestière Française* **40**, 285–296.
- Gensac P. (1989) Régénération de l'épicéa sur les terrassements des pistes de ski. *Bulletin de la Société Botanique de France* **136**, 327–334.
- Gensac P. (1990) Régénération en altitude de l'épicéa (*Picea abies* (L) Karst.) sur les souches dans les Alpes françaises. *Annales des Sciences Forestières* **47**, 173–182.
- Guillet B. (1975) Les podzols forestiers et les podzols de dégradation: relation entre l'histoire de la végétation et l'évolution des podzols sur grès vosgien triasique. *Revue d'Ecologie et Biologie du Sol* **12**, 405–414.

- Handley W.R.C. (1963) Mycorrhizal associations and *Calluna* heathland afforestation. Forestry Commission Bulletin No. 36.
- Harmon M.E. and Franklin J.F. (1989) Tree seedlings on logs in *Picea-Tsuga* forests of Oregon and Washington. *Ecology* **70**, 48–59.
- Hayes M.H.B. (1983) Darwin's "vegetable mould" and some modern concepts of humus structure and soil aggregation. In *Earthworm Ecology* (J. E. Satchell, Ed.), pp. 19–33. Chapman & Hall, London.
- Hesselmann H. (1926) Studier over barrskogens humustacke. *Meddelanden från Statens Skogsforskningsanstalt* **22**, 169–552.
- Hofgaard A. (1994) Structure and regeneration pattern of a virgin *Picea abies* forest in Northern Sweden. *Journal of Vegetation Science* **3**. In press.
- Jongorius A. (1963) Optic-volumetric measurements on some humus forms. In *Soil Organisms* (J. Doeksen and J. Van Der Drift, Eds), pp. 137–148. North-Holland, Amsterdam.
- Judas M. (1992) Gut content analysis of earthworms (Lumbricidae) in a beechwood. *Soil Biology & Biochemistry* **24**, 1413–1417.
- Klinka K., Green R.N., Trowbridge R.L. and Lowe L.E. (1981) Taxonomic classification of humus forms in ecosystems of British Columbia. First Approximation. Province of British Columbia, Ministry of Forests, Land Management Report No. 8.
- Koop H. and Hilgen P. (1987) Forest dynamics and regeneration mosaic shifts in unexploited beech (*Fagus sylvatica*) stands at Fontainebleau (France). *Forest Ecology and Management* **20**, 135–150.
- Kubiëna W.L. (1938) *Micropedology*. Collegiate Press, Ames.
- Kubiëna W.L. (1953) *The Soils of Europe*. Murby and Company, London.
- Låg J. (1959) Influence of forest stand and ground cover vegetation on soil formation. *Agrochimica* **4**, 72–77.
- Låg J. (1961) Studies on quantitative relationships between soil and soil-forming factors in Norwegian forests. In *Transactions of the 7th International Congress in Soil Science*, pp. 152–156. Madison, Wisconsin.
- Lavelle P. (1981) Stratégies de reproduction chez les vers de terre. *Acta Oecologica, Oecologia Generalis* **2**,

117–133.

- Lemée G. (1989) Structure et dynamique de la hêtraie des réserves biologiques de la forêt de Fontainebleau: un cas de complexe climacique de forêt feuillue monospécifique tempérée. *Acta Oecologica, Oecologia Generalis* **10**, 155–174.
- Lepart J. and Escarré J. (1983) La succession végétale, mécanismes et modèles: analyse bibliographique. *Bulletin d'Ecologie* **14**, 133–178.
- Martin A. (1991) Short- and long-term effects of the endogeic earthworm *Millsonia anomala* (Omodeo) (Megascopidae, Oligochaeta) of tropical savannas, on soil organic matter. *Biology and Fertility of Soils* **11**, 234–238.
- Mayer H. (1976) *Gebirgswaldbau. Schutzwaldpflege. Ein Waldbaulicher Beitrag zur Landschaftsökologie und zum Umweltschutz*. Fischer, Stuttgart.
- Mettivier Meyer H.J.B., Van Berghem J.W., Sevink J. and Verstraten J.M. (1986) Studies on organic soil profiles. I. Methodology and its application in the Hulshorsterzand. In *Forest Dynamics Research in Western and Central Europe* (J. Fanta, Ed.), pp. 77–102. PUDOC, Wageningen.
- Meyer F.H. and Götsche D. (1971) Distribution of root tips and tender roots of beech. In *Ecological Studies. Analysis and Synthesis*, (H. Ellenberg, Ed.), Vol. 2, pp. 48–52. Springer, Berlin.
- Mousain D. (1975) Effet de deux facteurs édaphiques (teneur en phosphore et qualité de la matière organique des sols) sur l'établissement de la symbiose ectomycorhizienne du pin maritime (*Pinus pinaster* Soland in Ait.). *Revue d'Ecologie et Biologie du Sol* **12**, 239–259.
- 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 Française et Etrangère* **6**, 85–423.
- Nihlgård B. (1971) Pedological influence of spruce planted on former beech forest soils in Scania, South Sweden. *Oikos* **22**, 302–314.
- Nilsson M.C. and Zackrisson O. (1992) Inhibition of Scots pine seedling establishment by *Empetrum hermaphroditum*. *Journal of Chemical Ecology* **18**, 1857–1870.
- Noirfalise A. and Vanesse R. (1975) *Conséquences de la monoculture des conifères pour la conservation des*

sols et pour le bilan hydrologique. Association des Espaces Verts (ASBL), Bruxelles.

Oldeman R.A.A. (1990) *Forests: Elements of Silvology*. Springer, Berlin.

Ott E. (1966) Über den Einfluss der Durchforstung auf ökologische Faktoren. *Zeitschriften des Schweizerischen Forstvereins*, Beiheft No. 40.

Page G. (1968) Some effects of conifer crops on soil properties. *Commonwealth Forestry Review* **47**, 52–62.

Page G. (1974) Effects of forest cover on the properties of some Newfoundland forest soils. Canadian Forestry Service, Department of the Environment, Publication No. 1332.

Pearce T.G. (1978) Gut contents of some lumbricid earthworms. *Pedobiologia* **18**, 153–157.

Ponge J.F. (1984) Etude écologique d'un humus forestier par l'observation d'un petit volume, premiers résultats. I. La couche L1 d'un moder sous pin sylvestre. *Revue d'Ecologie et Biologie du Sol* **21**, 161–187.

Ponge J.F. (1988) Etude écologique d'un humus forestier par l'observation d'un petit volume. III. La couche F1 d'un moder sous *Pinus sylvestris*. *Pedobiologia* **31**, 1–64.

Ponge J.F. (1990) Ecological study of a forest humus by observing a small volume. I. Penetration of pine litter by mycorrhizal fungi. *European Journal of Forest Pathology* **20**, 290–303.

Ponge J.F., Andre J., Bernier N. and Gallet C. (1994) La régénération naturelle: connaissances actuelles. Le cas de l'épicéa en forêt de Mâcot (Savoie). *Revue Forestière Française* **45**. In press.

Ramann E. (1911) *Bodenkunde*. Springer, Berlin.

Rozé F. (1989) Mise au point d'une méthode d'échantillonnage par points pour l'interprétation de lames minces: application à la comparaison de deux humus de landes après incendie. *Revue d'Ecologie et Biologie du Sol* **26**, 189–196.

Scheu S. (1992) Changes in the lumbricid coenosis during secondary succession from a wheat field to a beechwood on limestone. *Soil Biology & Biochemistry* **24**, 1641–1646.

Scullion J. and Ramshaw G.A. (1988) Factors affecting surface casting behaviour in several species of earthworm. *Biology and Fertility of Soils* **7**, 39–45.

- Shaw C. and Pawluk S. (1986) The development of soil structure by *Octolasion tyrtaeum*, *Aporrectodea turgid* and *Lumbricus terrestris* in parent materials belonging to different textural classes. *Pedobiologia* **29**, 327–339.
- Shipitalo M.J. and Protz R. (1989) Chemistry and micromorphology of aggregation in earthworm casts. *Geoderma* **45**, 357–374.
- Shleynis R.I. (1965) Difference in soil formation beneath spruce and oak forests in the Northwestern USSR. *Soviet Soil Science* **1965**, 226–234.
- Staaf H. (1987) Foliage litter turnover and earthworm populations in three beech forests of contrasting soil and vegetation types. *Oecologia* **72**, 58–64.
- Tomlin A.D., McCabe D. and Protz R. (1992) Species composition and seasonal variation of earthworms and their effect on soil properties in Southern Ontario, Canada. *Soil Biology & Biochemistry* **24**, 1451–1457.
- Watt A.S. (1947) Pattern and process in the plant community. *Journal of Ecology* **35**, 1–22.
- Weissen F. (1979) La régénération naturelle de l'épicéa en Ardenne. *Bulletin de la Société Royale Forestière de Belgique* **88**, 115–123.
- Weissen F. and Jacqmain M. (1978) Perspectives de régénération naturelle de l'épicéa après fumure. *Bulletin des Recherches Agronomiques de Gembloux* **13**, 353–371.

LEGENDS OF FIGURES

Fig. 1. Map of the study site. The numbers indicate the nine eco-units investigated.

Fig. 2. Humus components visible at $\times 40$ magnification under the dissecting microscope.

Fig. 3. Components of holorganic and organo-mineral material visible at the $\times 400$ magnification under the light microscope.

Fig. 4. Diagrammatic humus profile of eco-unit 1 (regeneration site). To the left, bulk humus material observed at $\times 40$ magnification, with depth on the ordinate and cumulate percentages on the abscissa. To the right, fine material observed at $\times 400$ magnification, with the same conventional features. In the right profile, the thick black line delineates the border between holorganic (to the left) and organo-mineral material (to the right), the total percentage of the two categories being fixed at 100.

Fig. 5. Humus profile of eco-unit 2 (young growth phase, before canopy closure). Same comments as for Fig. 4.

Fig. 6. Humus profile of eco-unit 2 (young growth phase, after canopy closure). Same comments as for Fig. 4.

Fig. 7. Humus profile of eco-unit 3 (intense growth phase of spruce at 50 yr). Same comments as for Fig. 4.

Fig. 8. Humus profile of eco-unit 4 (intense growth phase of spruce at 60 yr). Same comments as Fig. 4.

Fig. 9. Humus profile of eco-unit 5 (mature phase of spruce at 160 yr). Same comments as for Fig. 4.

Fig. 10. Humus profile of eco-unit 6 (mature phase of spruce at 190 yr). Same comments as for Fig. 4.

Fig. 11. Humus profile of eco-unit 7 (collapse stage of spruce, age unknown). Same comments as for Fig. 4.

Fig. 12. Humus profile of eco-unit 8 (moss). Same comments as for Fig. 4.

Fig. 13. Humus profile of eco-unit 9 (bilberry). Same comments as for Fig. 4.

Fig. 14. Diagrammatic representation of the organo-mineral material observed under the dissecting microscope ($\times 40$). \circ , Recent lumbricid faecal pellets (smooth and brilliant aggregates). \bullet , Old lumbricid faecal pellets (dull and rugose aggregates). Black surface: unaggregated structure.

Fig. 15. Organo-mineral material coming from the earthworm mull humus of eco-unit 1 (5–7 cm depth). Silt (arrow 1) and clay particles (arrow 2) are cemented by amorphous organic matter (arrow 3). Phase contrast microscopy, $\times 400$. Bar = 10 μm .

Fig. 16. Free amorphous particulate organic matter from the B horizon of eco-unit 4 (10–12 cm depth). Phase contrast microscopy, $\times 400$. Bar = 10 μm .

Fig. 17. Bleached mineral material from the E horizon of eco-unit 4 (7–8 cm depth). Phase contrast microscopy, $\times 400$. Bar = 50 μm .

Fig. 18. Densities of epigeic earthworm species during the developmental phases of spruce, compared with moss and bilberry patches.

Fig. 19. Densities of anecic earthworm species during the developmental phases of spruce, compared with moss and bilberry patches.

Fig. 20. Densities of endogeic earthworm species during the developmental phases of spruce, compared with moss and bilberry patches.

Table 1. Vegetation features of the nine eco-units investigated

	Herbaceous	Spruce (30 years)	Spruce (50 years)	Spruce (60 years)	Spruce (160 years)	Spruce (190 years)	Larch (215 years)	Moss	Bilberry
Eco-unit	1	2	3	4	5	6	7	8	9
Moss layer	+	++	0	0	0	±	+	++	++
Herb layer									
<i>Luzula sylvatica</i>	++	0	0	0	0	0	+	±	±
<i>Deschampsia flexuosa</i>	++	±	0	0	0	0	+	±	±
<i>Melampyrum sylvaticum</i>	++	+	0	0	0	±	++	±	
<i>Prenanthes purpurea</i>	++	0	0	0	0	0	+	±	0
<i>Oxalis acetosella</i>	±	+	0	0	+	+	±	++	±
Shrub layer									
<i>Vaccinium myrtillus</i>	±	±	0	0	0	±	±	+	++
<i>V. vitis idaea</i>	±	±	0	0	0	+	+	+	++
Trees									
Mean age (yr)	10	30	45	53	171	190	215	—	—
Oldest	25	35	55	62	193	190	215	—	—
Youngest	0	30	35	40	137	190	215	—	—
Maximal height (m)	1.5	3	11	19	30	28	31		

0= absent; ± = scarce; + = fairly abundant; ++ = abundant.

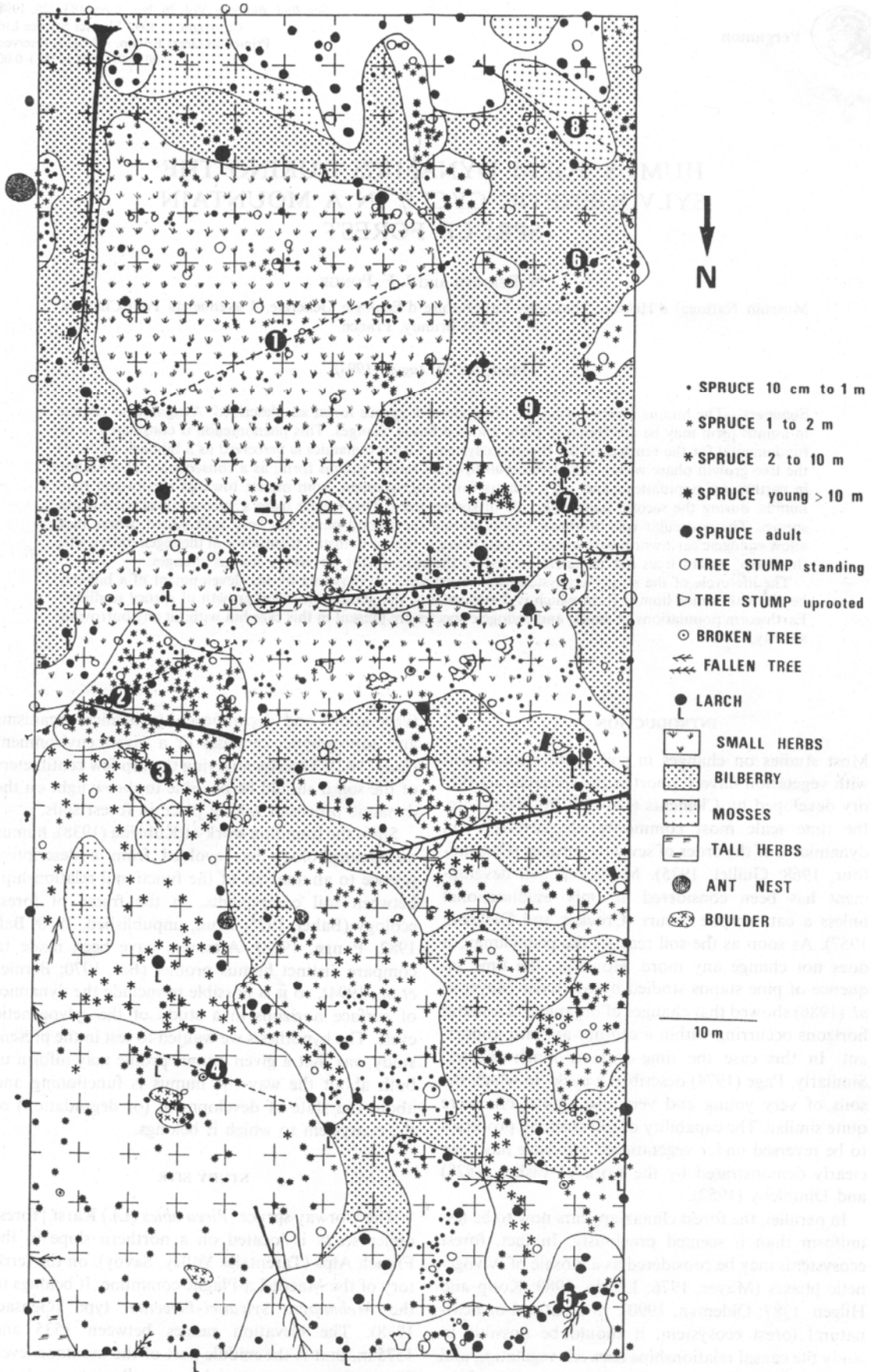


Fig. 1


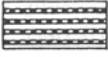



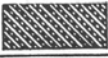


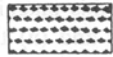

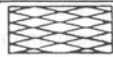

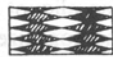





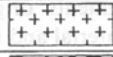








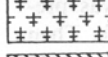


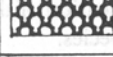




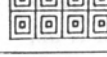
	SPRUCE	intact needles		ERICACEAE	twigs
		modified needles			rhizomes
		fragmented needles			roots
		twigs		WOOD SORREL	
	CONIFER	aerial parts misc.		WOOD RUSH	leaves + foliar bases
	LARCH	intact needles			roots
		modified needles		HAIR GRASS	leaves + foliar bases
		fragmented needles			roots
	HOLORGANIC	FAECES		COW WHEAT	
	ORGANO-MINERAL			PRENANTHES	
	MOSS	<i>Hylocomium splendens</i>		LICHEN	
		<i>Rhytidiadelphus triquetrus</i>		CONIFER	large roots
		dead moss			fine roots (long roots)
	LIVERWORT				fine roots (mycorrhizae)
	WHORTLEBERRY	intact leaves			dead roots
		modified leaves			bark
	BILBERRY	intact leaves			wood
		modified leaves		STONE	

Fig. 2

	PLANT TISSUES	hyaline
		yellow
		red
		brown to black
	CONIFER POLLEN	
	MOSS LEAVES	
	FUNGAL HYPHAE	hyaline
		melanized
	MICROCRISTALLINE FRAGMENTS	hyaline
		yellow
		red
		brown to black
	AMORPHOUS ORGANIC MATTER	free
		mineral bonded
	MINERAL PARTICLES	< 25 μm
		> 25 μm

Fig. 3

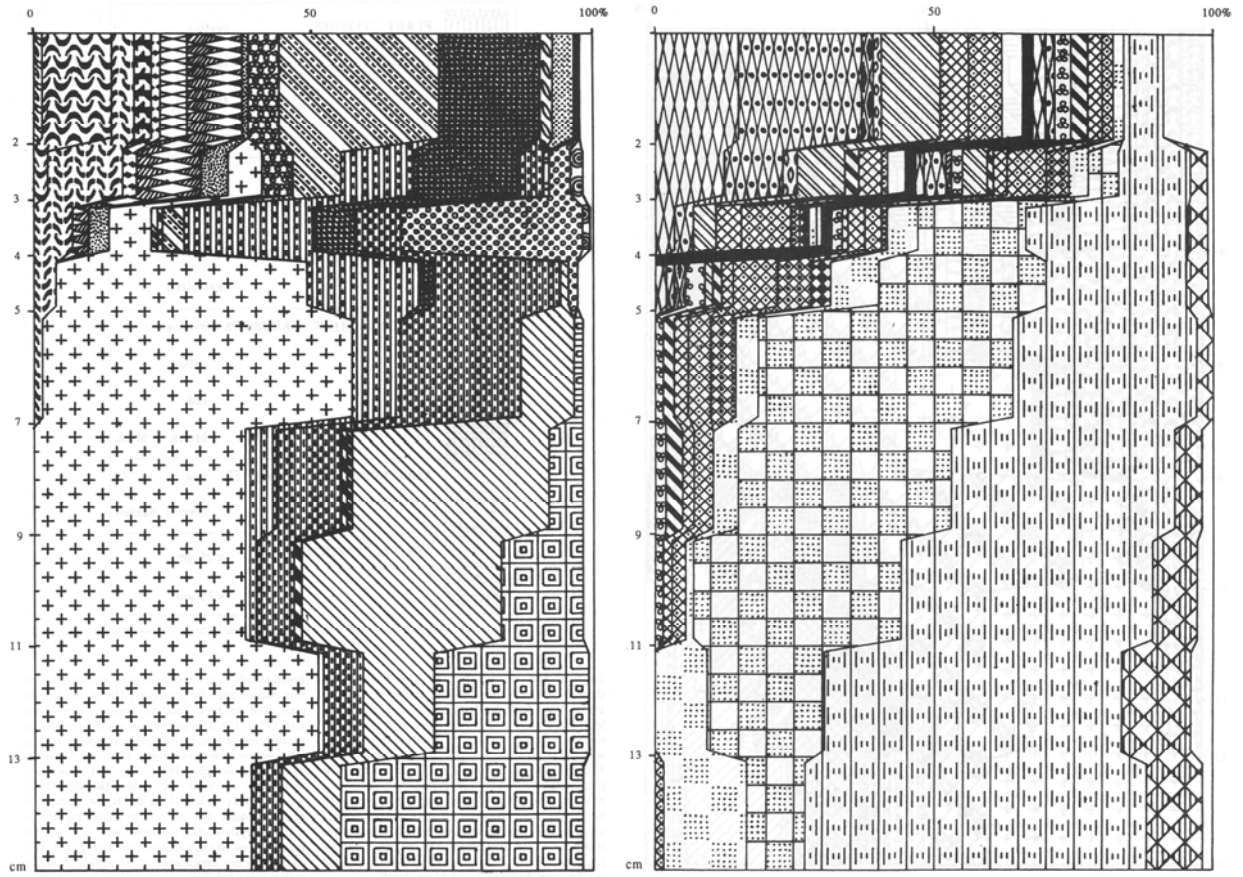


Fig. 4

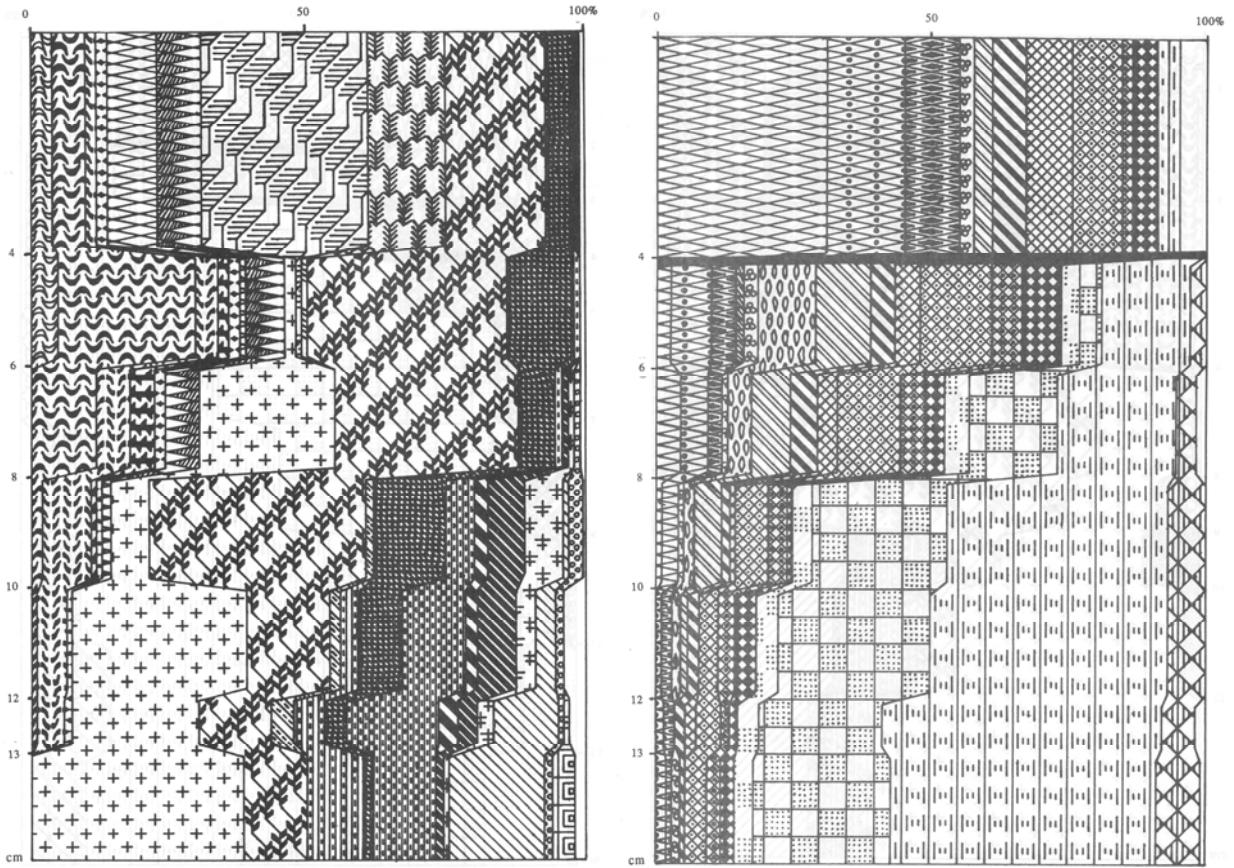


Fig. 5

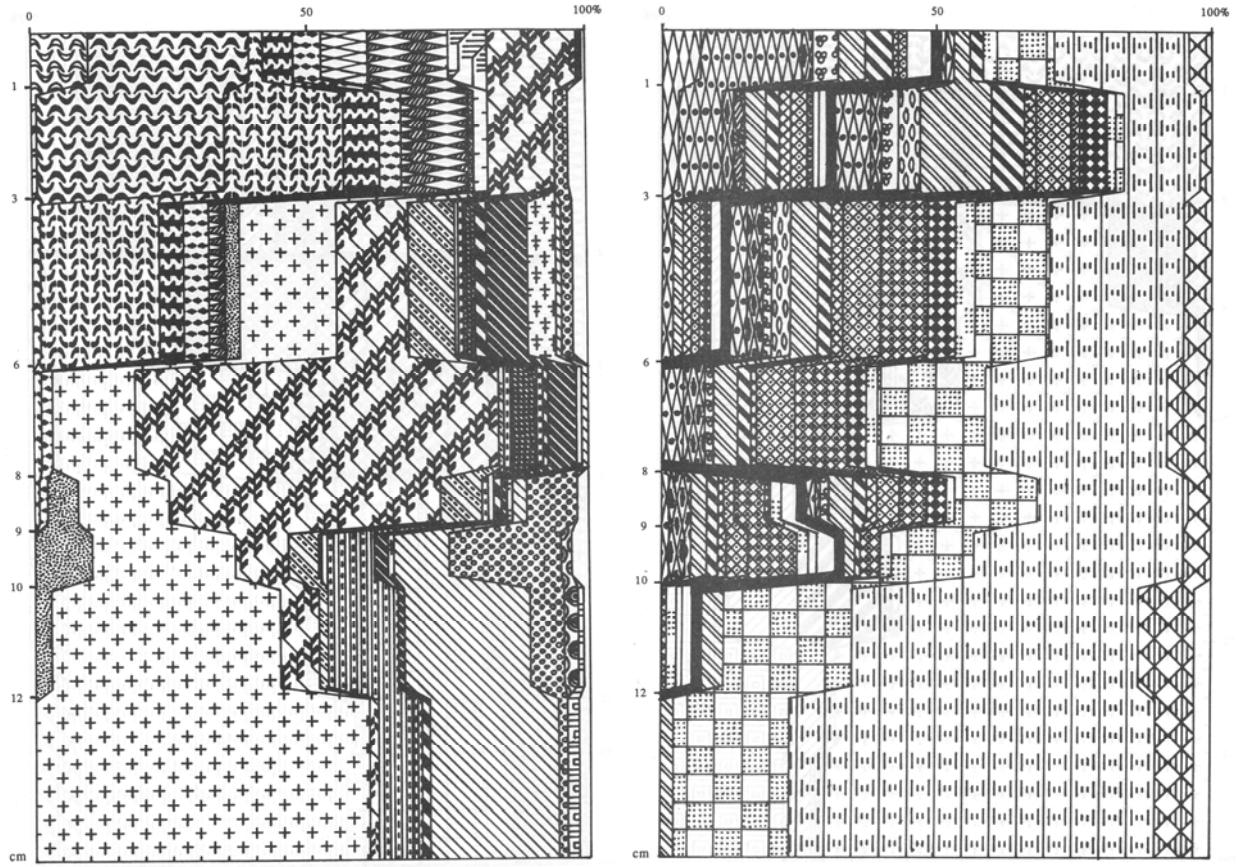


Fig. 6

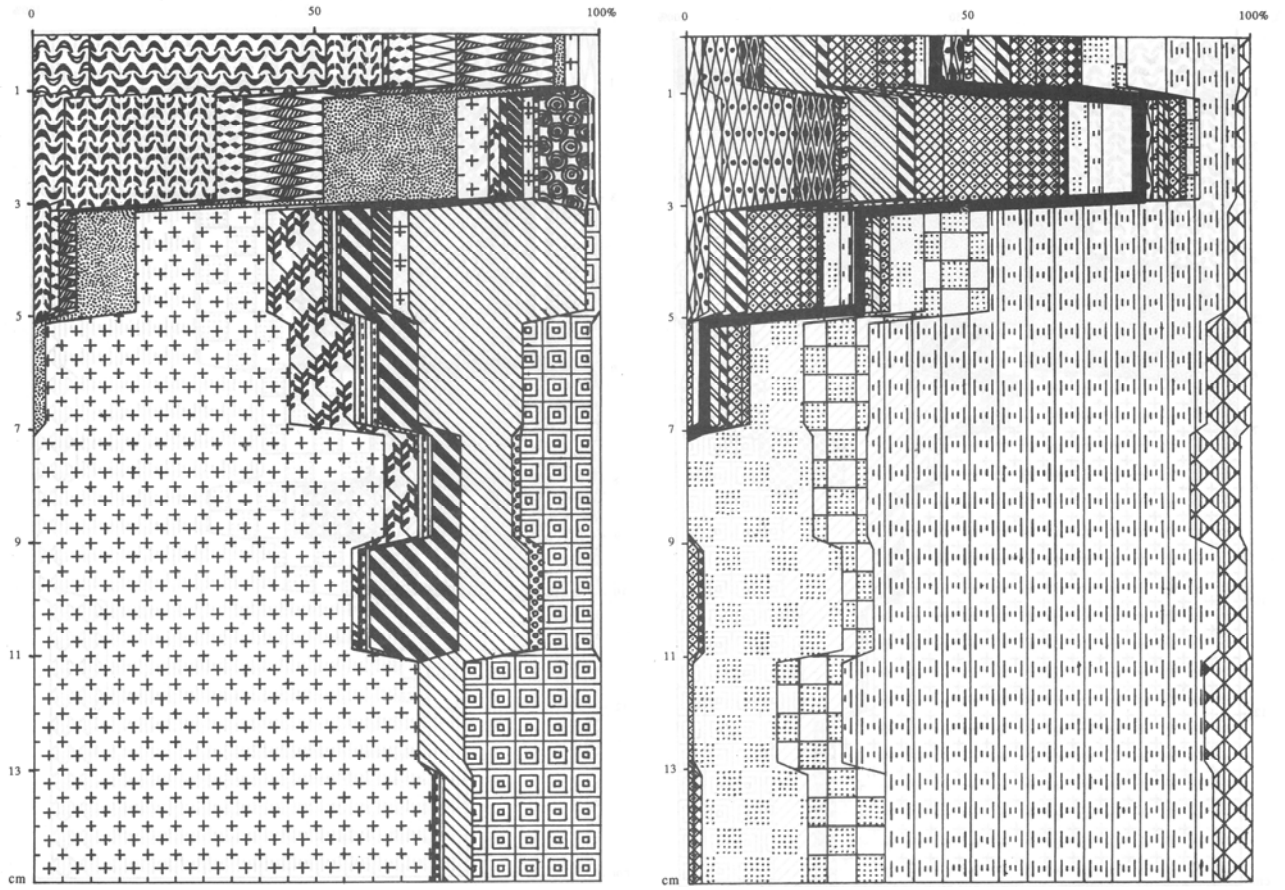


Fig. 7



Fig. 8

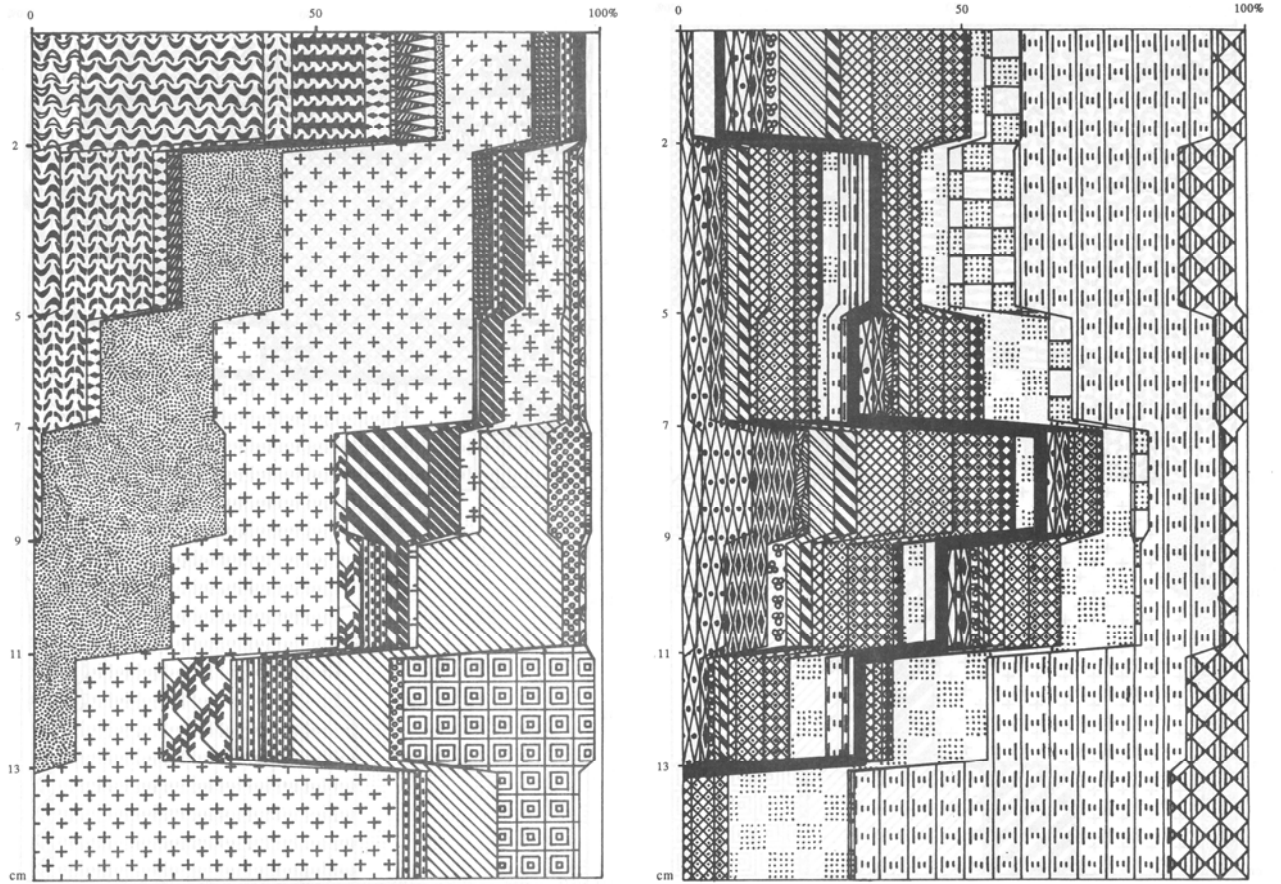


Fig. 9

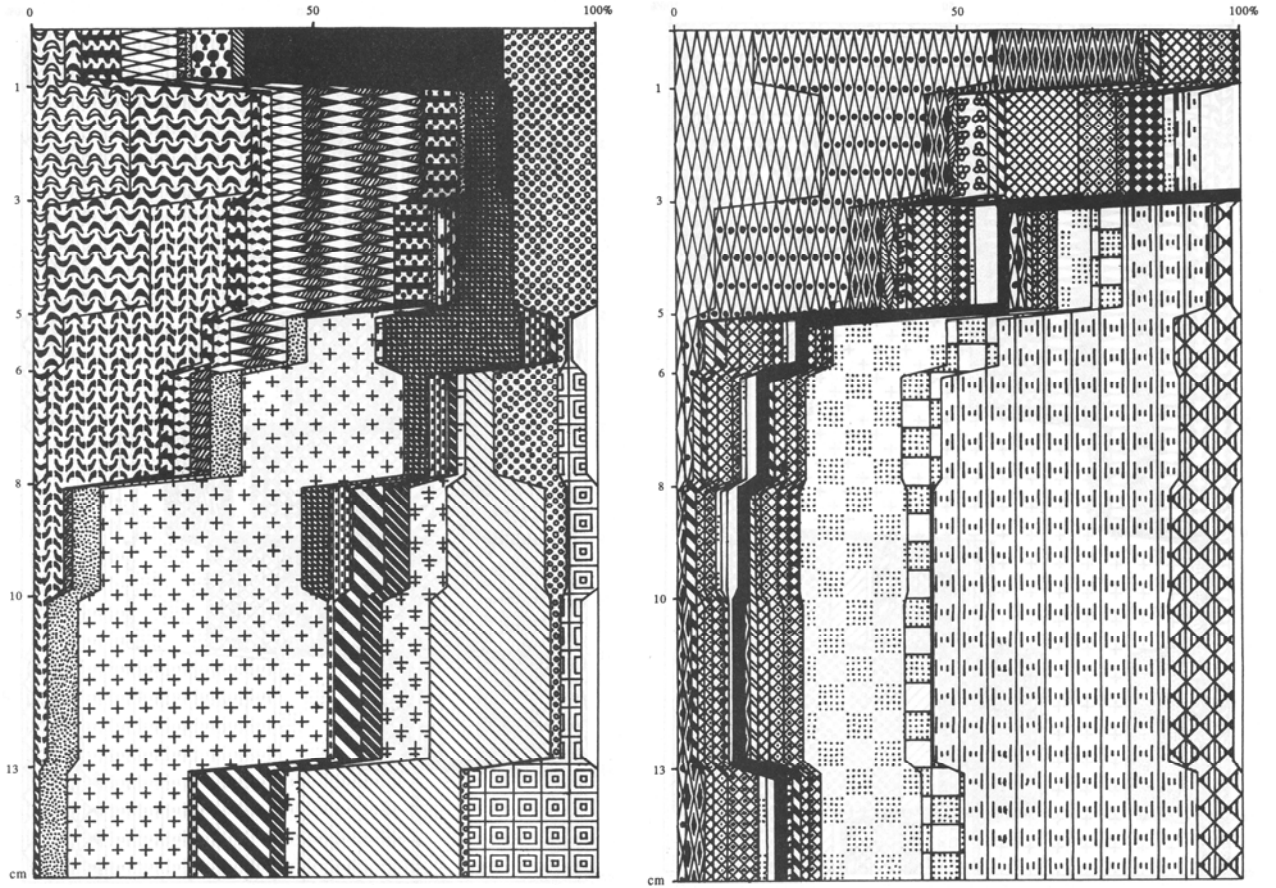


Fig. 10

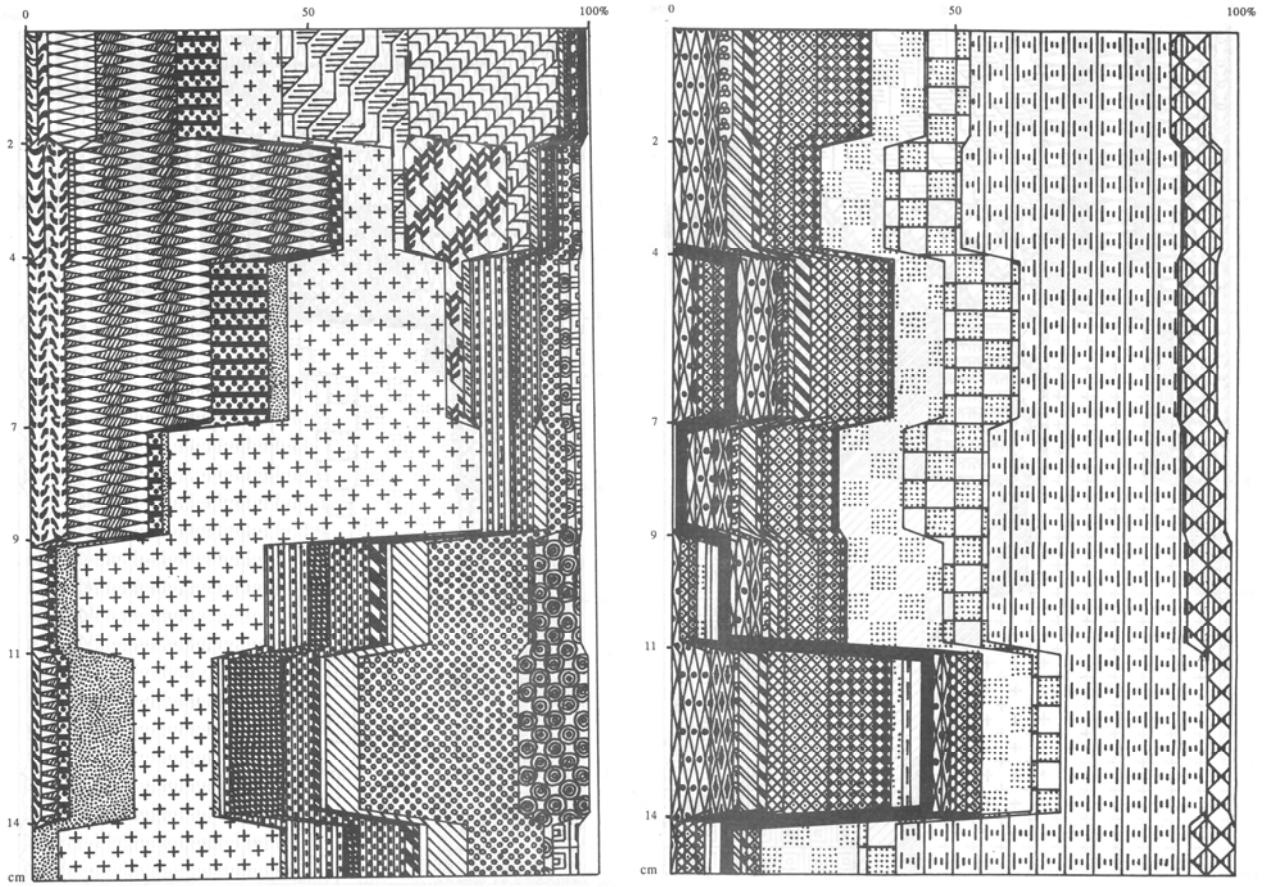


Fig. 11

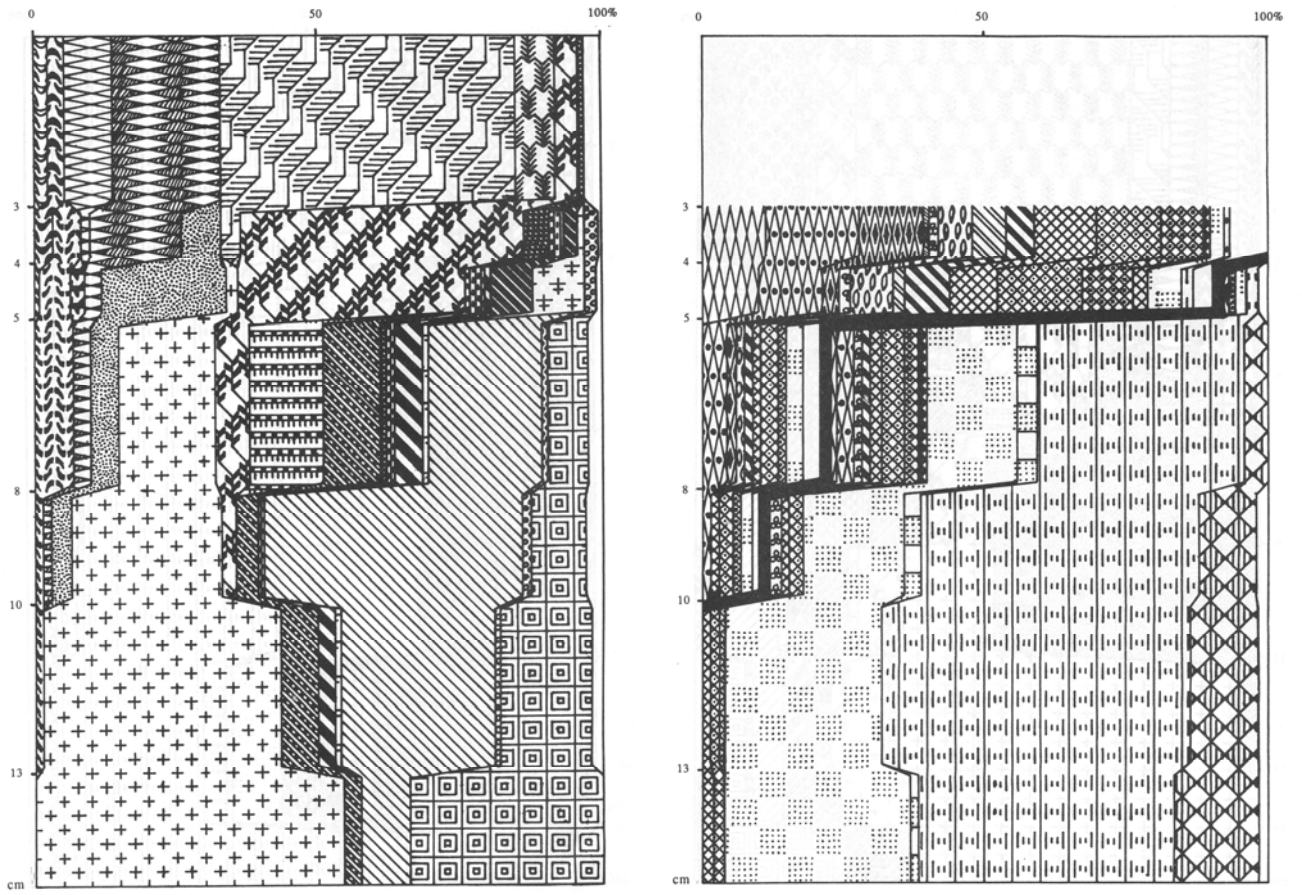


Fig. 12

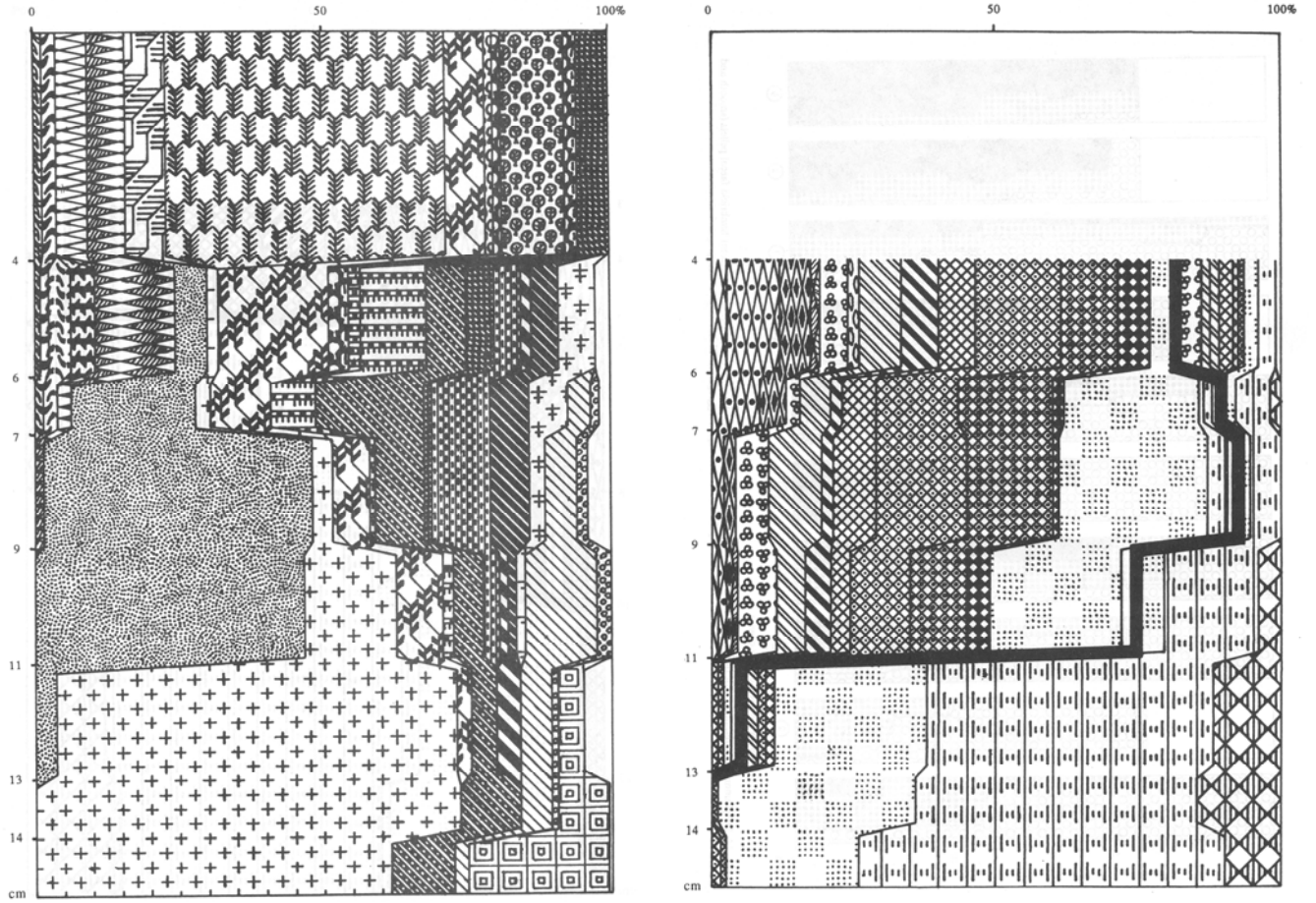


Fig. 13

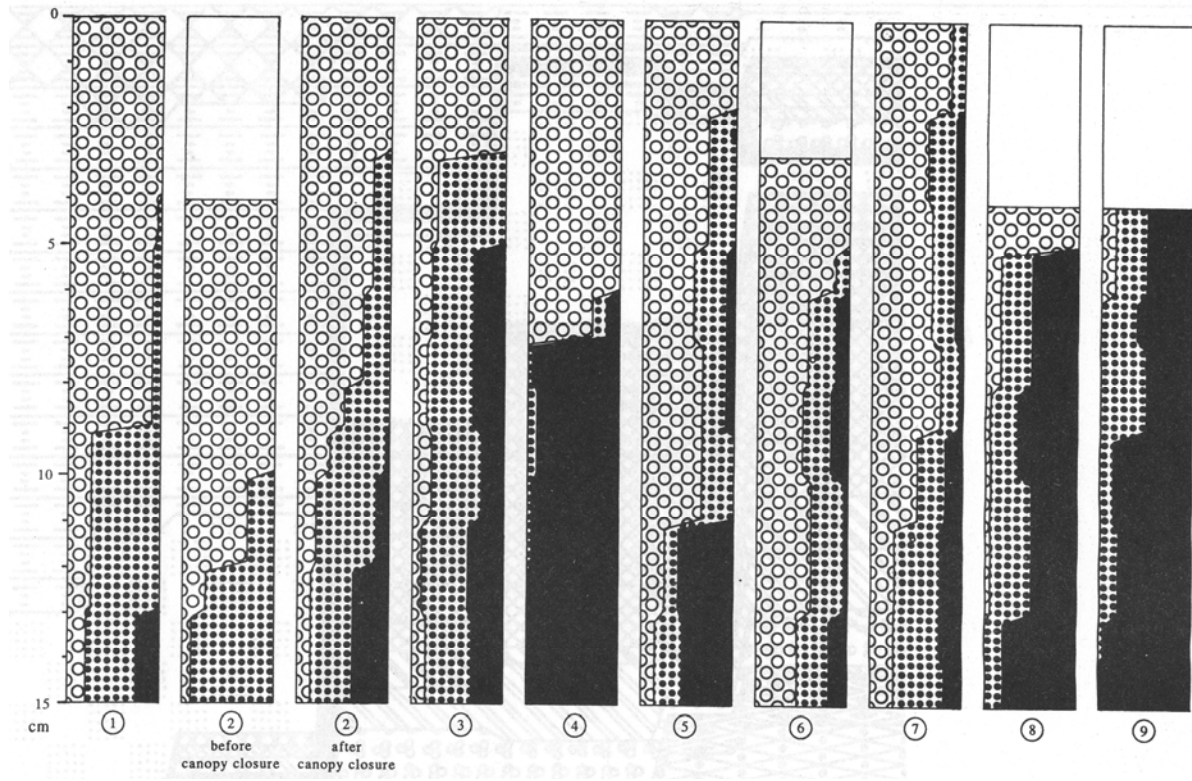


Fig. 14

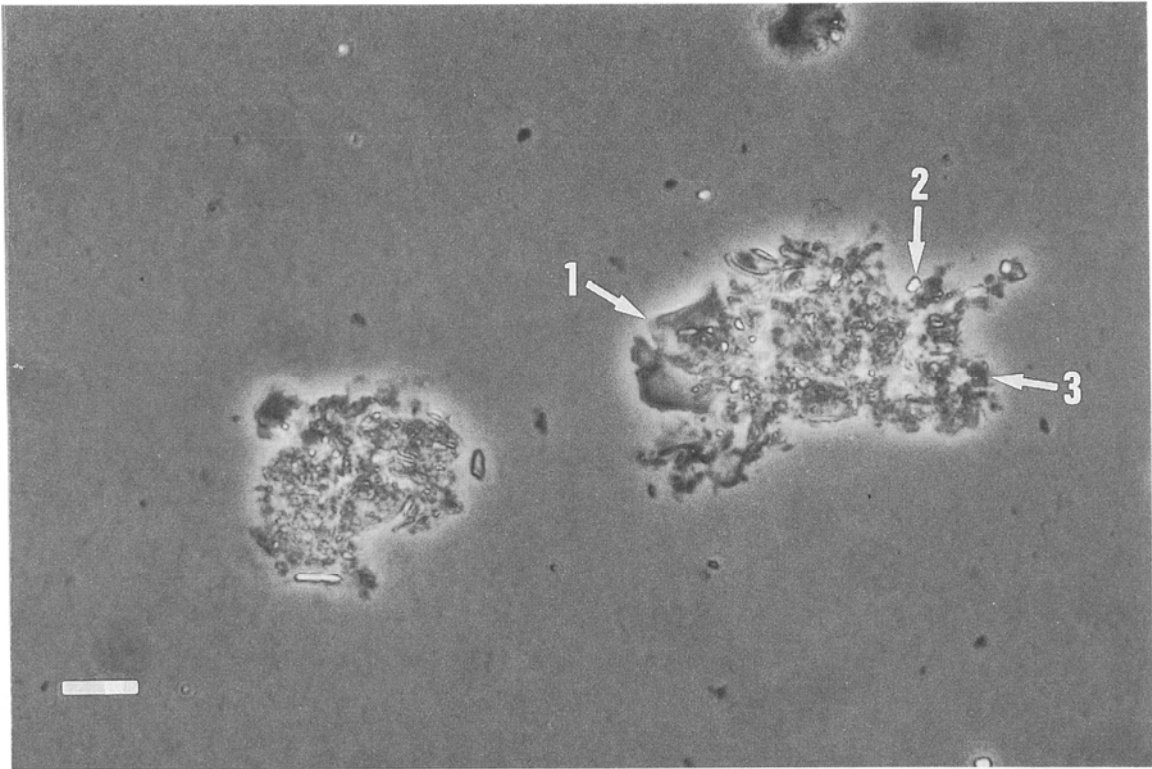


Fig. 15

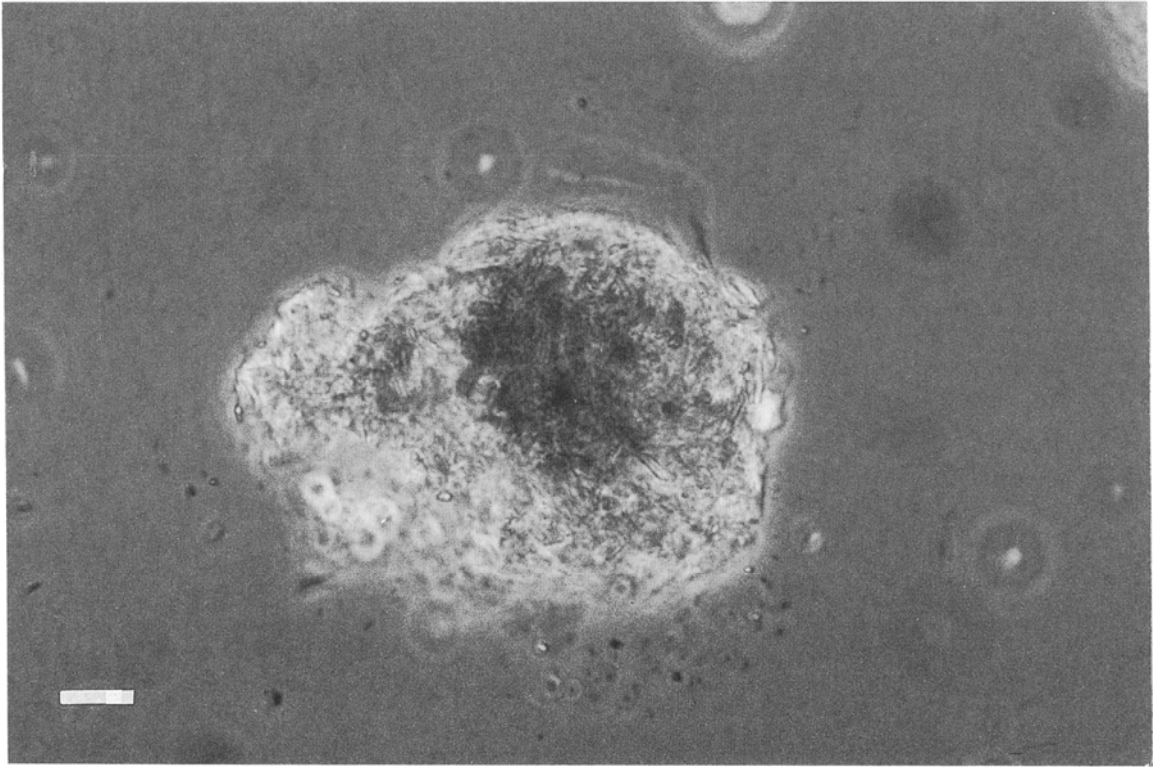


Fig. 16

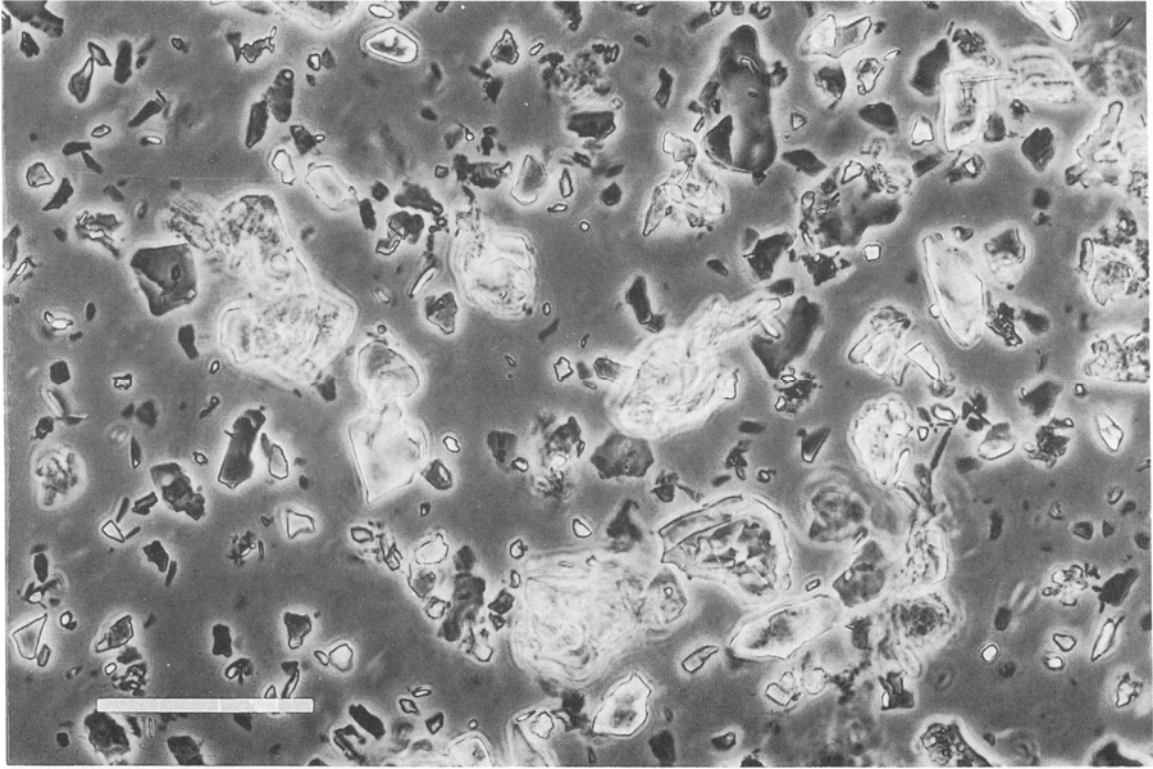


Fig. 17

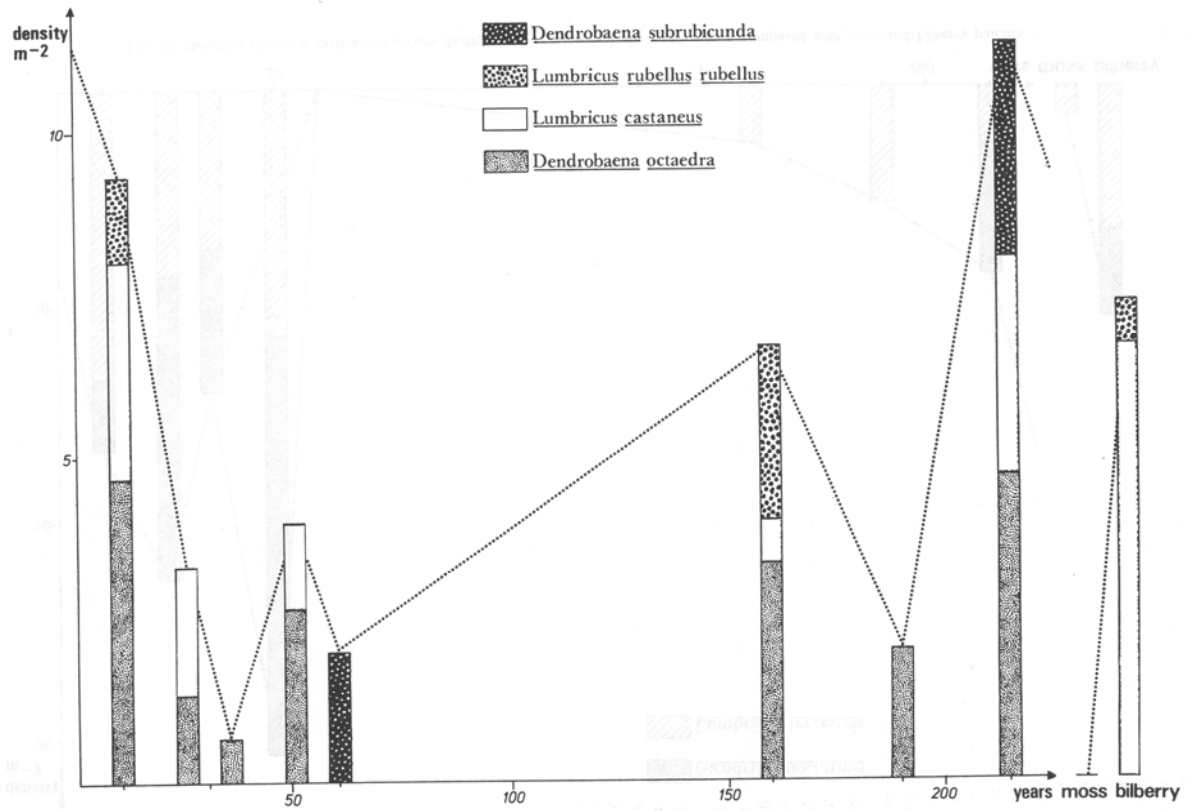


Fig. 18

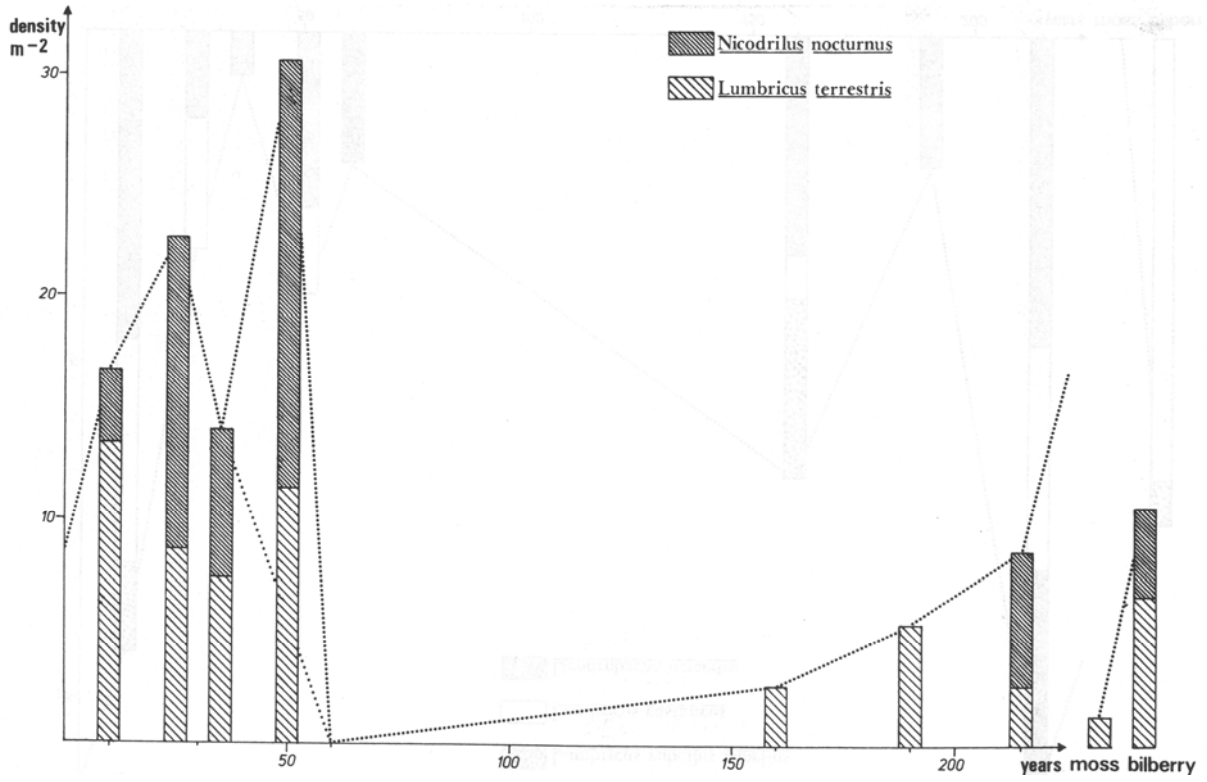


Fig. 19

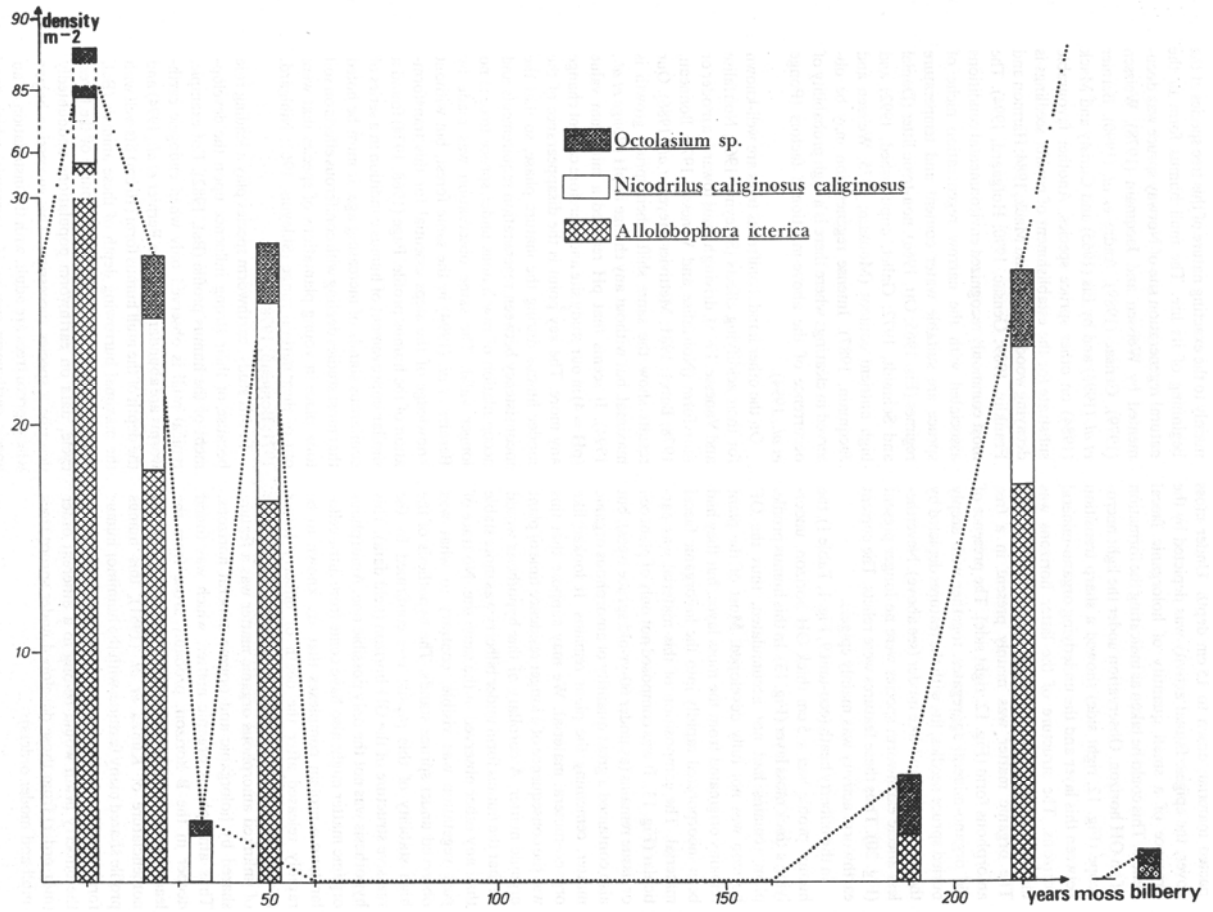


Fig. 20