Comparative study of soil organic layers in two bilberry-spruce forest stands (Vaccinio-Piceetea): relation to forest dynamics

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Comparative study of soil organic layers in two bilberry-spruce forest stands *(VaccinioPiceetea)*. Relation to forest dynamics

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ABSTRACT

Morphologica1 features of twelve humus profiles demonstrating the diversity of vegetation types present in subalpine forests were compared, together with soil fauna. Two forest stands of spruce [*Picea abies* (L.) Karst.] in association with bilberry (*Vaccinium myrtillus* L.), located at 1630 and 1880 m altitude (Mâcot-La Plagne, Tarentaise valley, Savoy, France), were studied. Morphological observations of small soil volumes were made on disturbed samples by the method of Ponge, but here transformed into quantitative data. Analysis of the data gave evidence of a large degree of heterogeneity of the form of humus in a given forest stand, but most of the observed variation might be exp1ained by differences in vegetation, due to phases of the forest cycle and sylvicultural practices. Regeneration sites are characterized by the development of a herbaceous coyer under which a mull humus is built through the activity of burrowing earthworm species. During the phase of intense growth of spruce organic matter accumulates in the top few centimeters. At this stage, the Al horizon previously formed under the action of endogeous earthworms becomes inactive but its crumby structure remains stable. Anecic worms (earthworms with a high amplitude of vertical movements) appear again under adult trees. As a result, changes in the form of humus are observed, with seemingly mull formation (burying of litter) but without true incorporation of organic matter to mineral matter. This humus was named dysmull. Thus soil conditions that prevail in the regeneration sites were developed to some extent under pre-existing adult trees. A parallel

evolution of soil fauna, form of humus and vegetation may thus be described. The above mentioned sequence is not the only one possible. When small gaps in the canopy are created by unsuitable sylvicultural practices such as selection thinning, the development of ericaceous species (bilberry at the higher montane and subalpine levels) may impede the natural forest cycle. Under bilberry, dramatic changes in the form of humus occur: disappearance of the Al horizon previously formed under spruce, accumulation of undecomposed organic matter and, at the subalpine level, podzolization. Accumulation of organic matter under bilberry is mainly due to mosses.

INTRODUCTION

Surface layers of the soil are most sensitive to vegetation changes (Klinka et al., 1990). Thus it is necessary to get a better understanding of the processes affecting the development of humus forms. Several micromorphological studies were focussed on this point (Haarlov and Weis-Fogh, 1953; Zachariae, 1965; Bal, 1970; Babel, 1971, 1975; Toutain, 1981; Ponge, 1990, 1991 a, b). These studies, however, aimed only at describing a given humus profile. In order to understand the function of the form of humus in forest dynamics we need to compare samples that represent a chronosequence (synchronic analysis). This was achieved by identifying the vegetation units that compose the forest patchwork. In the case of spruce forests, regeneration is known to occur only on mull humus or on more restricted surfaces such as decaying wood (Weissen, 1979; Gensac, 1988, 1990; André et al., 1990). Given the influence of coniferous trees on soil conditions (Page, 1968; Nihlgård, 1971) and on the accumulation of organic matter, it may be asked by what processes natural spruce forests regenerate. Besides that, the development of bilberry which is common in spruce forests of the northern Alps is known to impede the establishment of spruce seedlings (Trepp, 1961) and is associated with the formation of raw humus (André and Gensac, 1989). Thus the development of the forms of humus may be considered not only as a consequence of successional patterns of vegetation, but also as a process taking an active part in the development of forest ecosystems.

STUDYSITES

Two bilberry (*Vaccinium myrtillus*) - spruce *(Picea abies)* forest stands at two different elevations were compared. They are located on a northern slope in the Alps (Tarentaise valley, Savoy, France), on the territory of the Macot-La Plagne commune, and belong to the same communal forest. The sites were studied for several years by the University of Savoy at Chambery, France (Gensac, 1988, 1989, 1990; André and Gensac, 1989; André et al., 1987, 1990). The main features of these two stands are given in Table 1.

In each stand several vegetation types have been recognized. Sampling was done in 12 sites, 7 at Macot Low and 5 at Macot High. Their main features are summarized in Table 2.

METHODS

One humus profile was studied in each of the 12 investigated sites. The sampling method was already used by Ponge (1984, 1985a, b, 1988). Humus profiles were disturbed and directly fixed in the field. Microstratification of a 5 cm X 5 cm surface was noted in the field after dressing a humus block of 10−15 cm thick with the help of a sharp knife. Each layer was provisionally identified according to the Hesselmann (1926) nomenclature, and immediately fixed in 95° ethyl alcohol to prevent fauna from escaping and fungi and roots from collapsing. Structure (crumby or compact) and colour were also noted at this stage. The vegetation of each site was described and samples of the main living species (aerial and subterranean parts) were taken and fixed in the same way to allow for identification of decaying and living plant tissues.

In the laboratory, each layer was fragmented then homogenized with the help of dissection forceps. An aliquot was taken and spread out in a thin layer in a Petri dish filled with 95° ethyl alcohol. The different components were identified under a dissecting microscope and the area occupied by each of them was estimated by eye. Thirty-three categories were recognized (Fig. 1). Among them, organo-mineral matter was observed under a light microscope with phase contrast after crushing, homogenization and mounting in chlorallactophenol (25 ml lactic acid, 50 g chloral hydrate, 25 ml phenol) and classified into 9 categories.

The layers were analysed in a random order. After a first screening of the bulk sample, layers similar to each other were observed a second time in order to assess them for differential characters, and the estimates were changed when necessary. All observations were made by the first author.

Sampling dates were September 1989 and July 1990 for the main units ("Spruce" and "Bilberry") and July 1990 for the other units. Thus the main units were sampled twice.

The distribution of the different categories in each layer was mapped and the different layers belonging to the same humus profile were plotted vertically according to their thickness and depth in the profile.

Two families of oligochete annelids were studied in some of the above mentioned vegetation units: Enchytraeidae and Lumbricidae (earthworms). This choice was made after preliminary investigations on the whole soil fauna (unpubl. data), because of the strong effect they exert on their environment, i.e. their role in the building of humus profiles (Bal, 1982).

Enchytraeids were extracted using the wet funnel method (O'Connor, 1955). Sampling was done on 88-08-11, 88-08-25, 88-09-29, 88-10-21 and 88-10-27. At each sampling date, two soil cores of 500 cm3 each were taken in the two main vegetation units of each site (“Spruce” and “Bilberry”). No attempt was made to separate species.

Earthworms were extracted according to Bouché (1969) and Bouché and Gardner (1984): water with formaldehyde and hand sorting. Given the slope and poor wettability of mountain soils, the method was modified to increase its efficiency. After a first extraction according to the above mentioned procedure, water with formaldehyde was spread on the soil after shovelling away the surface material to a depth of 20 cm. In each vegetation unit, 4 to 6 extractions were made, each on 1/4 m^2 , according to earthworm densities. Sampling dates were 89-07-12 and 89-07-17.

RESULTS

The 12 humus profiles have been mapped (Figs. 2 to 13). Each profile is characterized both by the composition of the litter and by the form of humus.

The main discontinuities are between the layers L, F, H and the horizons Al, A2 (as established visually in the field). In some cases major differences, not perceived in the field, were noted within these layers and the nomenclature was changed accordingly. For instance, large dissimilarities were seen in the field between the two humus profiles “Spruce” in Macot High (Figs. 8 and 9). After examination of the different layers in the laboratory, it appears that the main vertical discontinuity was at 5.5 cm depth, i.e. between the H1 and the H2 layers in the first sample, and between the H layer and the A horizon in the second sample. In fact the change in the two cases was due to the appearance of an organo-mineral fraction, which was dominant if the root system of spruce (more developed in the first sample) was not taken into account. Thus the H2 layer of the first sample belonged to the A horizon but this was not perceptible in the field due to the confusion between dead fine roots and holorganic animal faeces. Examination under a binocular microscope thus seems necessary for a more reliable identification of the different layers.

The profiles “Herbaceous”, in Macot Low and Macot High, are both characterized by the following features (Figs. 2 and 3):

- absence of F and H layers, i.e. rapid disappearance of litter, mainly made of herbaceous (dominant), moss and needle litter;
- sharp transition from the L layer to the A1 horizon;
- absence of the root system of spruce, presence of herb roots in the A1 horizon;
- adsorption of amorphous organic matter to mineral particles in the Al horizon, recognizable plant fragments being of minor importance in the organo-mineral material.

The profile “Prenanthes” in Macot Low (Fig. 4) is characterized by similar features of the Al horizon, except that living and dead roots of spruce are present together with herb roots. Other features are:

- abundance of living moss in the surface vegetation;
- presence of a thin (0.5 mm) F layer, mainly made of unincorporated dead moss.

The profile “Regeneration” in Macot Low (Fig. 5) is characterized by similar features of the A1 horizon, but a thick (4 cm) litter layer is present, with L (1 cm), F (2 cm) and H (1 cm) layers. The F layers are mainly made of decaying needles, the H layer of holorganic faeces. Herbs are absent, the root system of spruce being present in the F layers (living only), the H layer (living and dead) and the A1 horizon (mainly dead).

The profiles “Spruce” in Macot Low (Figs. 6 and 7) may be distinguished from the profiles described above by differences in the A1 horizon:

- decrease of the proportion of organic matter adsorbed to mineral particles, greater abundance of plant pieces juxtaposed to mineral particles;
- presence of twig and bark pieces and (in “Spruce 1”) of incorporated needles;
- weak development of the root system of spruce;

− presence of holorganic faeces besides organo-mineral material.

The H layer is present (1 cm thick); it consists of organo-mineral material mixed with holorganic faeces and decaying needles. Organo-mineral material may be observed even in the F and L layers. Subterranean parts of bilberry are present in the A1 horizon of the “Spruce 1” profile.

The profiles “Spruce” in Macot High (Figs. 8 and 9) have Al horizons with features similar to those of Macot Low “Spruce”, except that the root system of spruce is here much more developed, dead roots being dominant. The H layer is thicker (2 to 3 cm thick) but its composition is different in the two studied profiles. In “Spruce 1” organo-mineral material is present together with holorganic faeces and decaying needles, on the contrary in “Spruce 2” the H layer is made of holorganic faeces, decaying needles and spruce roots (living in H1, dead in H2 and H3). The presence or organo-mineral material may be observed in the F and L layers of “Spruce 1”, too. Holorganic faeces are dispersed throughout the A1 horizon of the “Spruce 2” site.

The profiles “Bilberry” in Macot Low (Figs. 10 and 11) exhibit marked differences from the profiles described above, the main one being the absence of organic matter adsorbed to mineral particles in the A1 horizon. Presence of an H layer is highly variable: 10 cm thick in “Bilberry 1”, absent in “Bilberry 2”, but in the two cases we may notice the presence of a layer made of a dense network of roots and rhizomes of bilberry together with organo-mineral matter. In the case of “Bilberry 1” this layer is mixed with an appreciable amount of holorganic faeces (thus justifying the name “H” for this layer), in the case of “Bilberry 2” the amount of free holorganic faeces is negligible; faecal material is incorporated in organo-mineral aggregates. Mosses are present as living vegetation in the surface layer (L layer), and as dead vegetation in the 0.5 cm thick F layer.

The profiles “Bilberry” in Macot High (Figs. 12 and 13) are characterized by the presence of an A2 horizon beginning at 6 to 6.5 cm depth, indicating podzolisation. The thick (3 cm) holorganic layer surmounting the thin (0.2 to 1 cm) A1 layer with a sharp transition is difficult to assign either to a F or an H layer. The presence of a great quantity of dead moss (undecayed) may justify calling it an F layer but in the case of “Bilberry 1” organo-mineral material (with comminuted plant pieces dominant) and in the case of “Bilberry 2” holorganic faeces are also major components. Our choice was to call it F/H. Its main feature is that dead moss material is accumulating at this place. Living moss is the main component of the L layer.

Earthworm species are not evenly distributed among the vegetation types (Fig. 14). The endogeic species *Allolobophora icterica* and *Nicodrilus caliginosus* are dominant under herbaceous cover, both in Macot Low and

Macot High. The anecic (i.e. with a wide amplitude of vertical movements) species *Lumbricus terrestris* is dominant under adult spruce, both in Macot Low and Macot High (together with another anecic species *Nicodrilus nocturnus* in the latter stand). Epigeic species (*Dendrobeana octaedra* and *Lumbricus castaneus*) are present both under herbaceous cover and under bilberry. In the Macot High stand, only epigeic earthworms are present under bilberry, but in Macot Low the three ecological categories are present under this vegetation, epigeic earthworms being dominant. The same is true of soil without vegetation (road slope).

Enchytraeid worm densities (Fig. 15) exhibit a marked influence of elevation and of vegetation. A considerable increase in the number of individuals occurs in Macot High compared to Macot Low and under bilberry compared to spruce in these two stands. Most animals live in the surface layers L, F, H.

DISCUSSION

From the observation of the different humus profiles we can say that two main types of organic matter distribution are present on the studied sites: (i) organic layers directly overlying a mineral substrate, ii) coexistence of mineral and organic matter within a Al horizon. These two types are not necessarily exclusive of each other. They result from the activity of different animal groups.

The form of humus in the “Herbaceous” sites, both in Macot Low and Macot High, is a typical earthworm mull humus (Kubiëna, 1953), with rapid disappearance of litter (even moss litter, Fig. 2) and rapid incorporation of organic matter to mineral particles. Those sites where regeneration of spruce occurs in Macot Low are the seat of an intense activity of endogeic earthworm species. It is not possible to ascribe the building of such a form of humus to this particular category of species, since they coexist with other earthworm species. Literature on the food and behaviour of endogeic species gives contradictory results (Bal, 1982), but we must emphasize the fact that true incorporation of organic matter to mineral particles was only registered where endogeic species were present.

The form of humus in the site “Prenanthes” in Macot Low, with young spruce trees 10−25 years old, exhibits a trend towards moder formation (appearance of an F layer made of dead moss) but is always of the mull type. Endogeic earthworm species are always present.

The form of humus in the “Regeneration” site in Macot Low, with spruce 50−70 years old, exhibits features of the moder type (Kubiëna, 1953), for instance the presence of an H layer made of holorganic faeces, but also of the mull type, such as the incorporation of organic matter to mineral particles in the A1 horizon. This form could be named amphimullmoder following the rules of classification proposed by Klinka et al. (1981). Earthworms have not been sampled in this site but we may observe in the humus profile that (i) litter is no longer incorporated into the A1 horizon, (ii) holorganic faeces are deposited under decaying needles, thus no activity of burrowing earthworm species is exhibited by the humus profile. On the contrary, the presence of incorporated organic matter should be the result of such an activity. The only possible explanation is that the A1 horizon is a relict of the mull humus of the regeneration site.

The form of humus in the “Spruce” sites, both in Macot Low and Macot High, exhibits features of both mull and moder types. To the mull type could be ascribed the presence of organo-mineral material in the Land F layers (except in “Macot High Spruce 2”), the incorporation of litter elements (needles, holorganic faeces) in the A1 horizon (except in “Macot High Spruce 1”) and the presence of a fraction made of organic matter adsorbed to mineral particles. To the moder type could be ascribed the presence of a layer where holorganic faeces are dominant (H layer). The perturbation of the horizons (imperfect H and A1 layers) is due to the activity of anecic earthworms which were repeatedly collected under old spruce trees. The difference with the previous form of humus is that all the morphological features may be explained by the present faunal activity. We hypothesize that anecic earthworm species, when alone, are unable to build a typical earthworm mull, at least with spruce needles as food. This litter component is burrowed before being consumed, probably due to the need for conditioning by microorganisms. This humus form may be called dysmull according to Delecour (1980).

The form of humus in the “Bilberry” sites is better exemplified in Macot High compared to Macot Low: accumulation of dead moss in the F/H layer, together with holorganic faeces or organo-mineral material rich in undecomposed plant material, presence of an A2 horizon without organic matter. The sharp transition with the A2 horizon is characteristic of the mor type (Delecour, 1980). But other characters are highly variable and F and H layers can hardly be distinguished. Thus it is difficult to name unambiguously this form of humus. The absence of burrowing earthworm species and the abundance of enchytraeid worms known to ingest mosses (Ponge, 1991a) and deposit their fecal pellets where they eat (Ponge 1991b) explain why there is such a sharp transition between a thick organic layer and the mineral part of the soil. In Macot Low the thin F layer (made of dead moss) is underlain by a horizon made of organo-mineral material (where plant remains are dominant), holorganic faeces and subterranean parts of bilberry. Earthworm species are present (the three ecological categories), but their numbers are low. Their role in the building of this form of humus, where undecomposed organic matter accumulates mixed with mineral particles, is unclear at this stage of our study.

The form of humus is an essential part of the regeneration niche (Collins and Good, 1987) and is thus a key component of forest dynamics. Studies on the same sites by André and Gensac (1989), André et al. (1990), Gensac (1990) and on spruce in Belgium by Weissen (1979) and Weissen and Jacqmain (1978) established that young spruce seedlings were exacting in relation to the form of humus, mull humus and decaying wood being favoured.

Synchronic analysis gave evidence of a shift in the form of humus when young spruce trees were growing in dense thickets, as is the case in sites where natural regeneration occurs. The first step is the development of a true earthworm mull humus under graminaceous cover ("Herbaceous" sites). The following step is a vegetation type dominated by taller herbs and by mosses ("Prenanthes" site), where moss decomposition seems to be impeded (formation of a F layer made of dead moss). During the following phase L and F layers increase their thickness and an H layer is built, the moss-herb cover disappearing after canopy closure ("Regeneration" site). Under this vegetation type, spruce needles replace moss in the accumulation process of dead organic matter. Earthworms become far less abundant and fungi become more abundant in accumulated litter. A similar phenomenon was observed by Page (1968) and Babel (1981) under spruce. The crumby structure of the A1 horizon (built under a herbaceous cover) becomes fossil but is always present under accumulated litter. Under adult spruce trees the incoming of anecic earthworms decreases the thickness of the litter layer and buries spruce needles. Despite this activity, there is no true incorporation of organic to mineral matter but organic matter is placed in contact with mineral matter (especially fine particles), due to burrowing, and leaching of the soil is counteracted (due to casting activity near or at the surface and aggregation of mineral matter). Possibly the small part of organic matter adsorbed on minerals which is present at this stage may be a relict, but this cannot be demonstrated without more sophisticated techniques. Under adult spruce, the form of humus is favourable to regeneration, but other factors (poor light and poor water availability) impede the development of young seedlings. This can be overcome after windthrow or timber cropping.

Under bilberry the above developmental cycle is rendered impossible, given the nature of the form of humus. The negative effects of ericaceous species on spruce regeneration (André and Gensac, 1989) and biological activity of humus profiles (Handley, 1954) have been documented. Organic matter accumulates (although primary production is weak) and the activity of fauna (except enchytraeid worms) is low. This is a transitional form towards mor humus and associated podzols (podzolisation is visible in the Macot High site).

We observed that accumulation of organic matter was mainly due to the slow decomposition of moss under bilberry, contrary to what was observed under herbaceous cover. Thus bilberry seems to act upon the decomposition process of other plant species. This lock effect cannot be overcome without the fall of surrounding trees and appearance of regeneration on dead wood (and further disappearance of bilberry as the trees grow). We observed that bilberry was present in the smallest gaps of the spruce canopy; the gaps are generally the result of selection thinning by foresters du ring the growth of dense spruce thickets. Our hypothesis is that the mode of dissemination of bilberry (mostly by vegetative growth), compared to herbaceous plants (mostly by seed dispersal), is responsible for the differences in vegetation between the small and the large gaps.

ACKNOWLEDGEMENTS

The authors are greatly indebted to Prof. K. Klinka, The University of British Columbia, Vancouver, Canada, and the journal reviewers for careful comments and revision of the English language.

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Legends of figures

Fig. 1. Symbolic representation of the thirty-three components identified in the twelve humus profiles.

Fig. 2. Diagrammatic representation of the humus profile “Macot Low Herbaceous”. A 2 mm transition from one layer to another was arbitrarily drawn in order to follow more easily each component along the whole profile.

Fig. 3. Diagrammatic representation of the humus profile “Macot High Herbaceous”. See Figs. 1 and 2 for key and comments.

Fig. 4. Diagrammatic representation of the humus profile “Macot Low Prenanthes”. See Figs. 1 and 2 for key and comments.

Fig. 5. Diagrammatic representation of the humus profile “Macot Low Regeneration”. See Figs. 1 and 2 for key and comments.

Fig. 6. Diagrammatic representation of the humus profile “Macot Low Spruce 1”. At the right of the profile the nomenclature of the different layers, successively in the field and after examination in the laboratory, is indicated. See also Figs. 1 and 2 for key and comments.

Fig. 7. Diagrammatic representation of the humus profile “Macot Low Spruce 2”. See also Figs. 1, 2 and 6 for key and comments.

Fig. 8. Diagrammatic representation of the humus profile “Macot High Spruce 1”. See also Figs. l, 2 and 6 for key and comments.

Fig. 9. Diagrammatic representation of the humus profile “Macot High Spruce 2”. See also Figs. 1, 2 and 6 for key and comments.

Fig. 10. Diagrammatic representation of the humus profile “Macot Low Bilberry 1”. See also Figs. 1, 2 and 6 for key and comments.

Fig. 11. Diagrammatic representation of the humus profile “Macot Low Bilberry 2”. See also Figs. 1, 2 and 6 for

key and comments.

Fig. 12. Diagrammatic representation of the humus profile “Macot High Bilberry 1”. See also Figs. 1, 2 and 6 for key and comments.

Fig. 13. Diagrammatic representation of the humus profile “Macot High Bilberry 2”. See also Figs. 1, 2 and 6 for key and comments.

Fig. 14. Densities of earthworm species in some of the investigated sites. A road slope site was sampled for comparison.

Fig. 15. Densities of enchytraeid worms in the two main vegetation types of each stand.

TABLE 1

Main characteristics of the two studied forest stands

	Macot Low	Macot High
Elevation	1630 m	1880 m
Exposure	N−NW	NW
Precipitation	1300 mm/yr	1800 mm/yr
Soil (Europ. class.)	Colluvial Ranker	Podzol with stagnogley
Soil (Soil Taxonomy)	Umbrept	Aquod
Regeneration	By spots	Poor (decaying stumps)

TABLE 2

Vegetation characteristics of the twelve investigated sites

Name	Tree cover	Shrubs	Herbaceous species	Mosses
Macot Low				
Spruce I, II	Spruce (200 yr)	Nil	Nil	Nil
Regeneration	Spruce (60 yr)	Nil	Nil	Nil
Prenanthes	Spruce (10-25 yr)	Nil	*Prenanthes purpurea* *Deschampsia flexuosa* *Luzula sylvatica*	*Hylocomium splendens* *Rhytidiadelphus triqueter*
Herbaceous	Spruce (5-15 yr)	Nil	*Deschampsia flexuosa* *Luzula sylvatica*	*Hylocomium splendens* *Rhytidiadelphus triqueter*
Bilberry I, II	Nil	*Vaccinium myrtillus*	*Deschampsia flexuosa* *Luzula sylvatica*	*Hylocomium splendens* *Rhytidiadelphus triqueter*
Macot High				
Spruce I, II	Spruce (200 yr)	Nil	Nil	Nil
Herbaceous	Nil	Nil	*Deschampsia flexuosa* *Luzula sylvatica*	*Hylocomium splendens* *Rhytidiadelphus triqueter*
Bilberry I, II	Nil	*Vaccinium myrtillus*	*Homogyne alpina* *Luzula sylvatica*	*Hylocomium splendens* *Rhytidiadelphus triqueter*

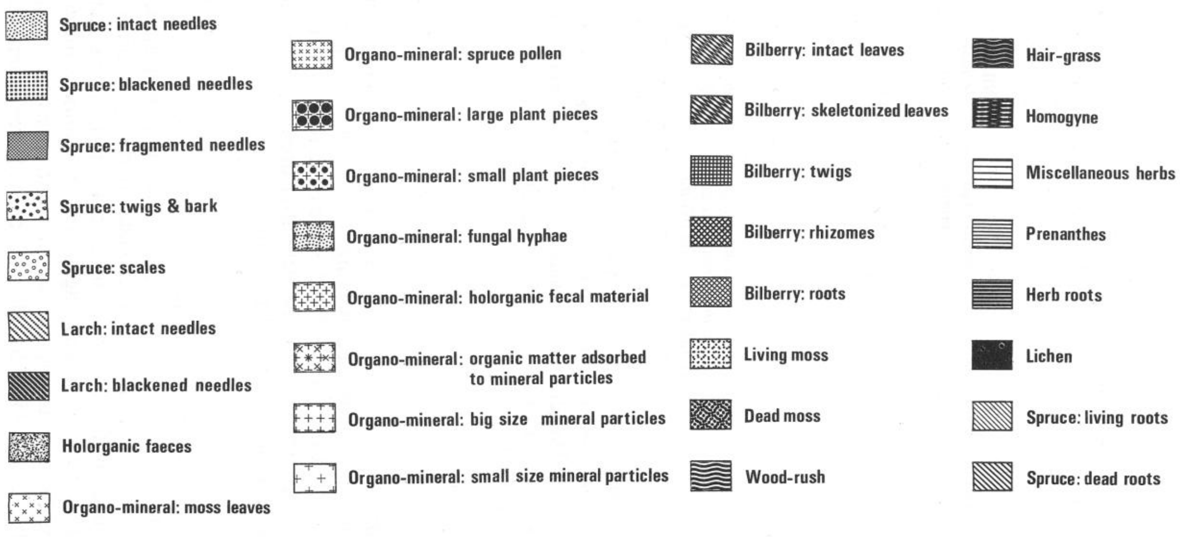

Spruce: intact needles
Spruce: blackened needles
Spruce: fragmented needles
Spruce: twigs & bark
Spruce: scales
Larch: intact needles
Larch: blackened needles
Holorganic faeces
Organo-mineral: moss leaves
Organo-mineral: spruce pollen
Organo-mineral: large plant pieces
Organo-mineral: small plant pieces
Organo-mineral: fungal hyphae
Organo-mineral: holorganic fecal material
Organo-mineral: organic matter adsorbed to mineral particles
Organo-mineral: big size mineral particles
Organo-mineral: small size mineral particles
Bilberry: intact leaves
Bilberry: skeletonized leaves
Bilberry: twigs
Bilberry: rhizomes
Bilberry: roots
Living moss
Dead moss
Wood-rush
Hair-grass
Homogyne
Miscellaneous herbs
Prenanthes
Herb roots
Lichen
Spruce: living roots
Spruce: dead roots

Fig. 1

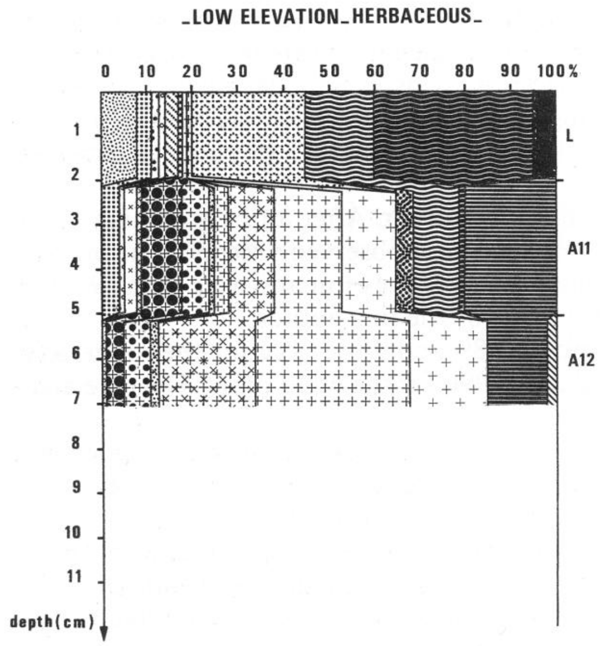

-LOW ELEVATION-HERBACEOUS-
0 10 20 30 40 50 60 70 80 90 100%
1
2
3
4
5
6
7
8
9
10
11
depth(cm)
L
A11
A12

Fig. 2

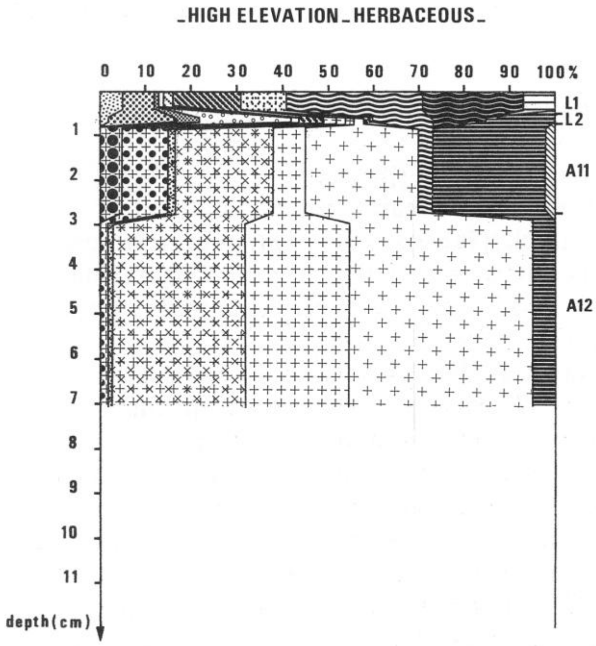

_HIGH ELEVATION_HERBACEOUS_
0 10 20 30 40 50 60 70 80 90 100%
L1
L2
A11
A12
1
2
3
4
5
6
7
8
9
10
11
depth(cm)

Fig. 3

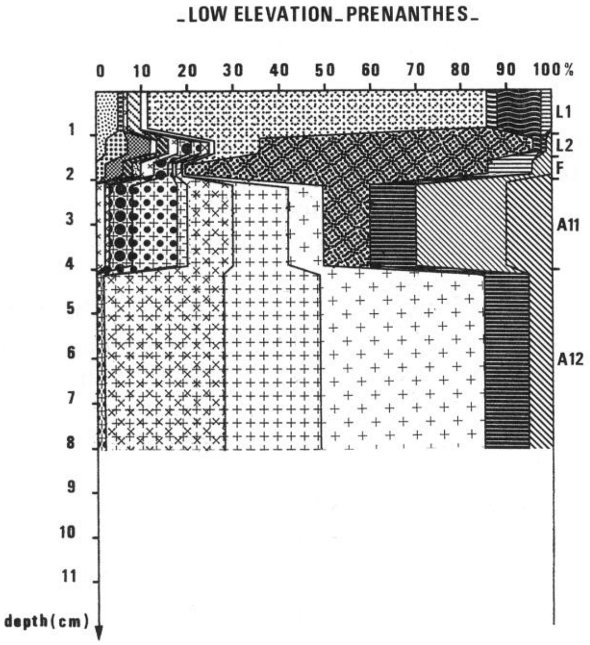
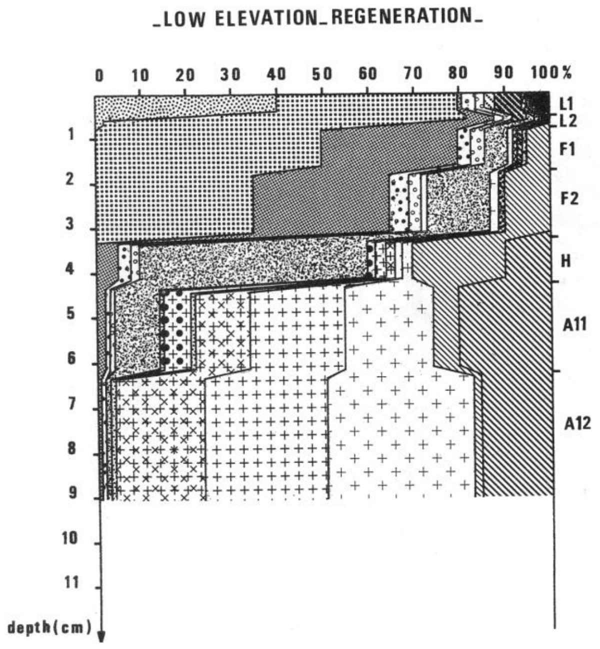
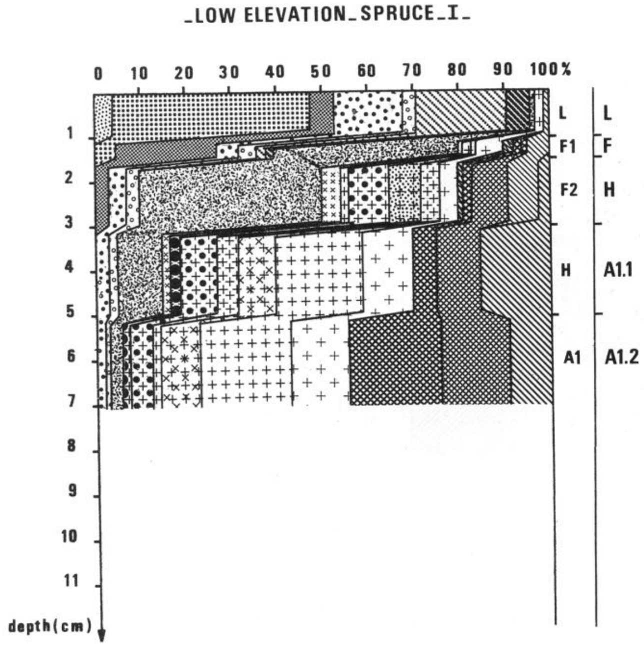

_LOW ELEVATION_PRENANTHES_
0 10 20 30 40 50 60 70 80 90 100%
1
2
3
4
5
6
7
8
9
10
11
depth(cm)
L1
L2
F
A11
A12

Fig. 4



_LOW ELEVATION_REGENERATION_
0 10 20 30 40 50 60 70 80 90 100%
L1
L2
F1
F2
H
A11
A12
1
2
3
4
5
6
7
8
9
10
11
depth(cm)

Fig. 5



_LOW ELEVATION_SPRUCE_I_
0 10 20 30 40 50 60 70 80 90 100%
1
2
3
4
5
6
7
8
9
10
11
depth (cm)
L
F1
F2
H
A1
L
F
H
A1.1
A1.2

Fig. 6

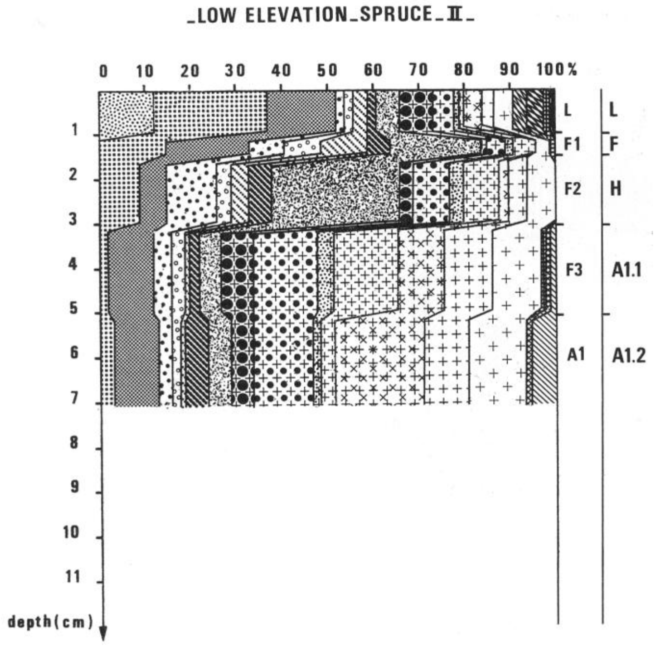

_LOW ELEVATION_SPRUCE_II_
0 10 20 30 40 50 60 70 80 90 100%
1
2
3
4
5
6
7
8
9
10
11
depth(cm)
L
F1
F2
F3
A1
L
F
H
A1.1
A1.2

Fig. 7

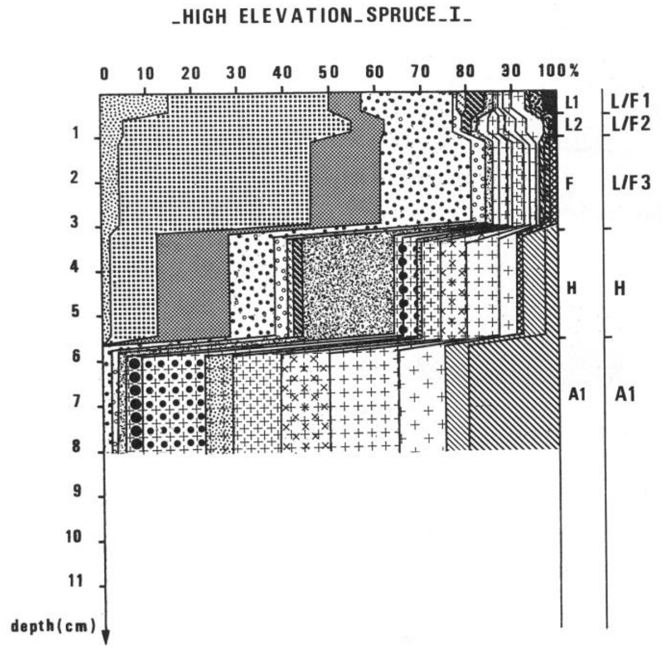

_HIGH ELEVATION_SPRUCE_I_
0 10 20 30 40 50 60 70 80 30 100%
1
2
3
4
5
6
7
8
9
10
11
depth(cm)
L1
L2
F
H
A1
L/F1
L/F2
L/F3
H
A1

Fig. 8

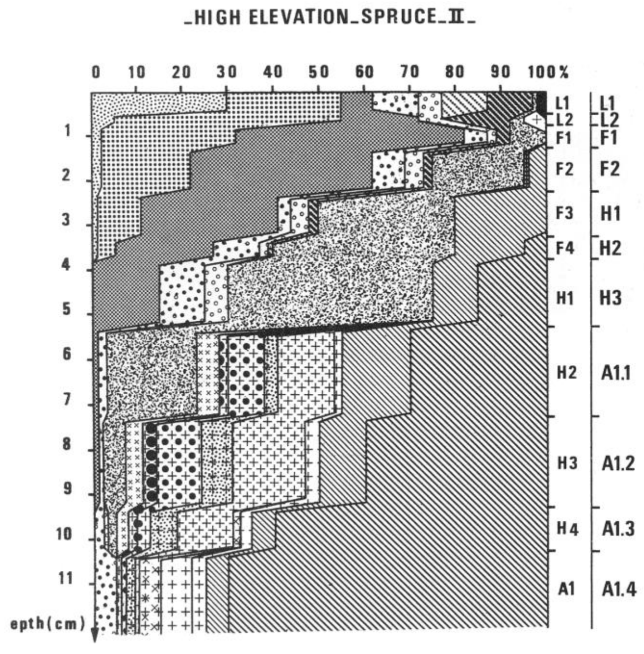
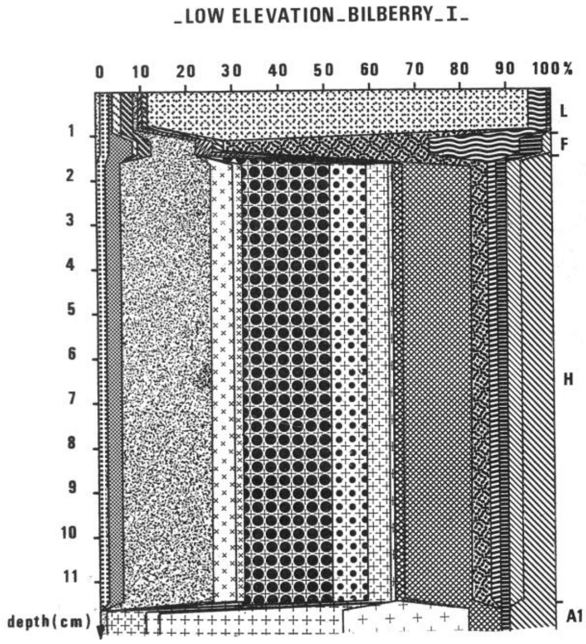

_HIGH ELEVATION_SPRUCE_II_
0 10 20 30 40 50 60 70 80 90 100%
1
2
3
4
5
6
7
8
9
10
11
epth(cm)
L1
L2
F1
F2
F3
F4
H1
H2
H3
H4
A1
L1
L2
F1
F2
H1
H2
H3
A1.1
A1.2
A1.3
A1.4

Fig. 9



_LOW ELEVATION_BILBERRY_I_
0 10 20 30 40 50 60 70 80 90 100%
L
F
H
A1
1
2
3
4
5
6
7
8
9
10
11
depth(cm)

Fig. 10

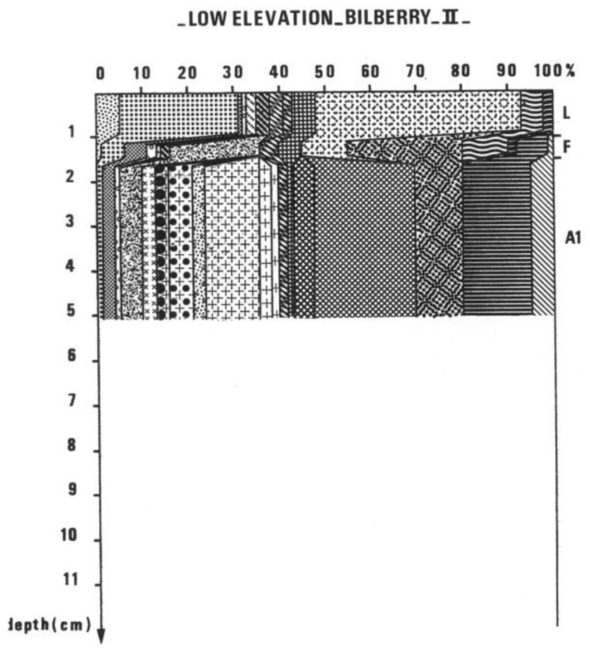

_LOW ELEVATION_BILBERRY_II_
0 10 20 30 40 50 60 70 80 90 100%
L
F
A1
1
2
3
4
5
6
7
8
9
10
11
depth(cm)

Fig. 11

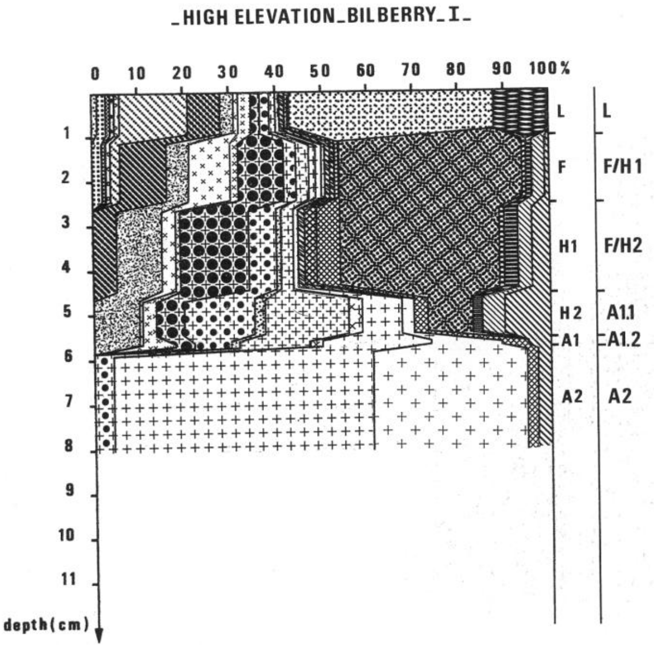

_HIGH ELEVATION_BILBERRY_I_
0 10 20 30 40 50 60 70 80 90 100%
1
2
3
4
5
6
7
8
9
10
11
depth(cm)
L
F
H1
H2
A1
A2
L
F/H1
F/H2
A1.1
A1.2
A2

Fig. 12

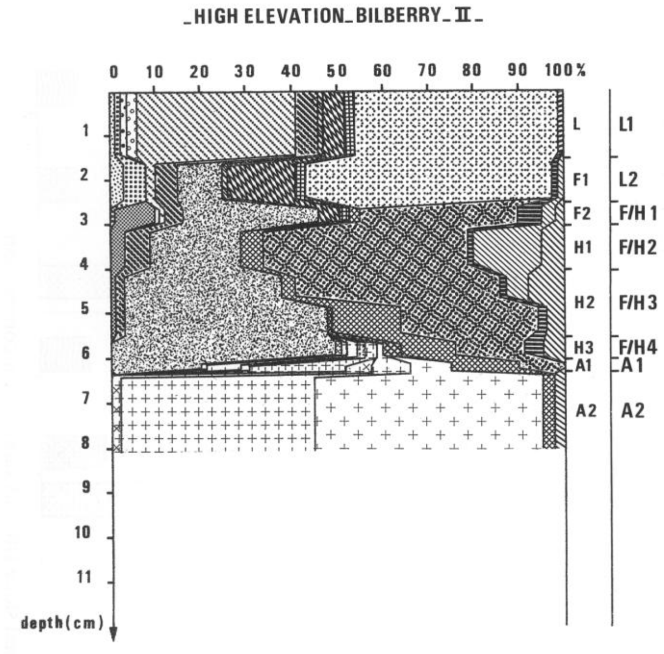

_HIGH ELEVATION_BILBERRY_II_
0 10 20 30 40 50 60 70 80 90 100%
1
2
3
4
5
6
7
8
9
10
11
depth(cm)
L
F1
F2
H1
H2
H3
A1
A2
L1
L2
F/H1
F/H2
F/H3
F/H4
A1
A2

Fig. 13

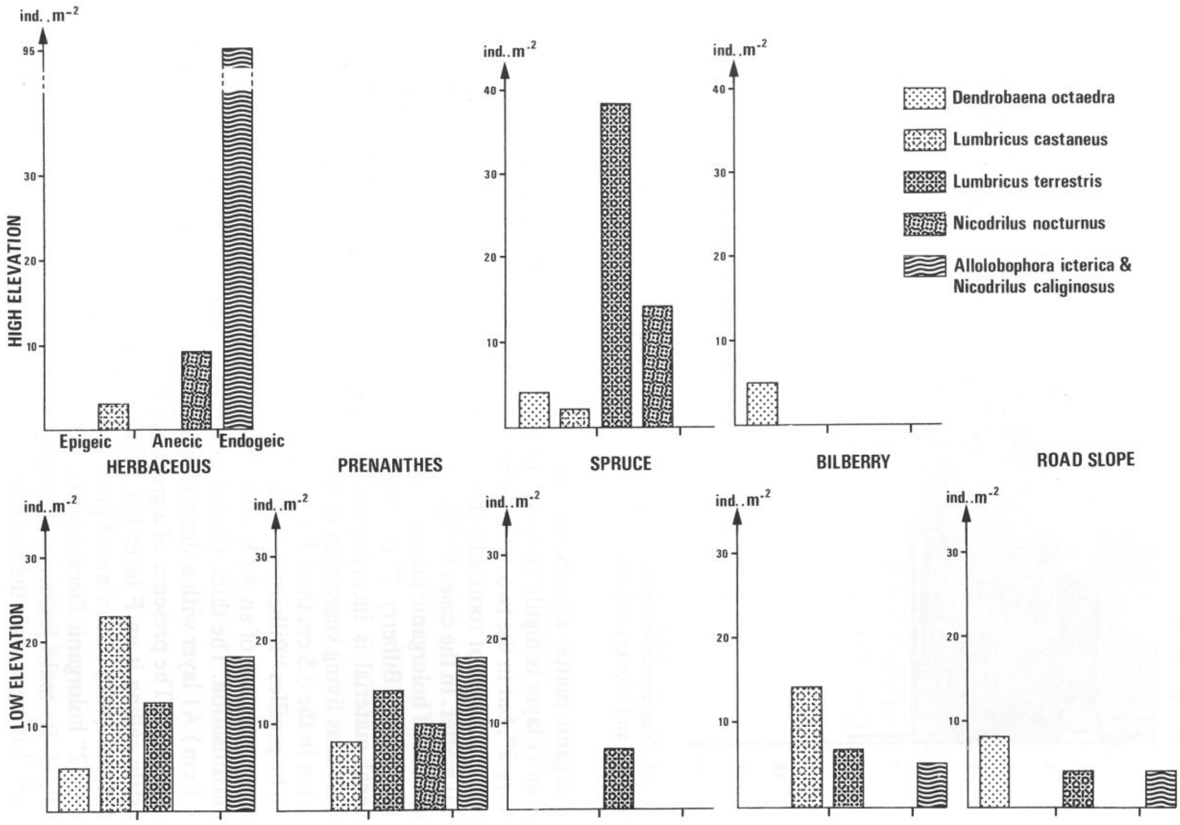

ind. .m-2
HIGH ELEVATION
LOW ELEVATION
Epigeic
Anecic
Endogeic
HERBACEOUS
PRENANTHES
SPRUCE
BILBERRY
ROAD SLOPE
Dendrobaena octaedra
Lumbricus castaneus
Lumbricus terrestris
Nicodrilus nocturnus
Allolobophora icterica &
Nicodrilus caliginosus

Fig. 14

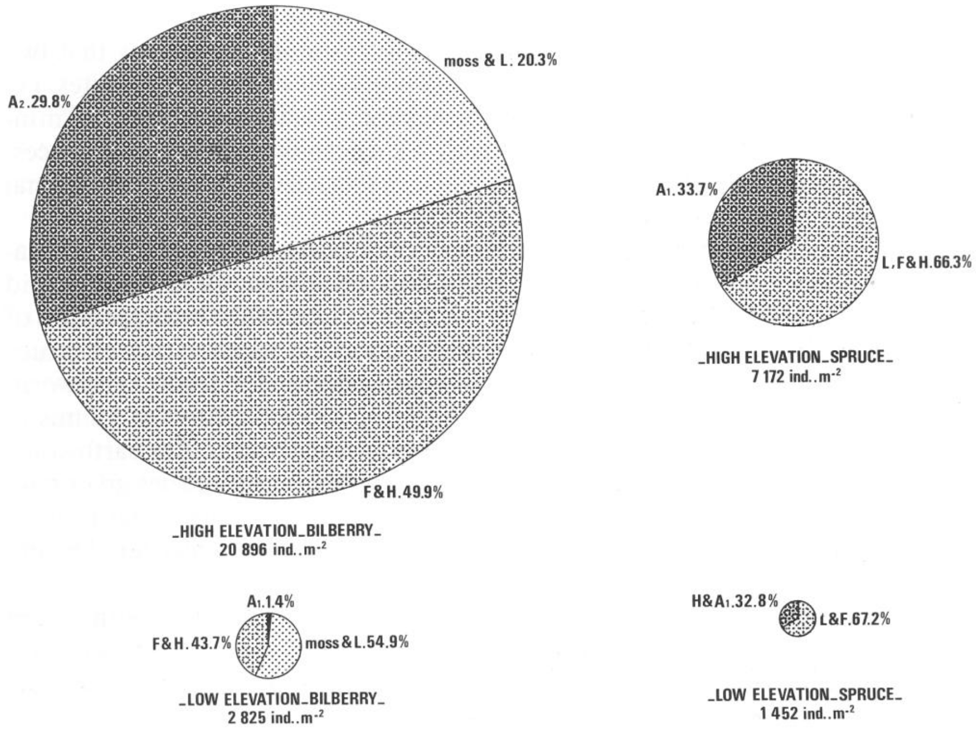

moss & L. 20.3%
A2.29.8%
F&H.49.9%
_HIGH ELEVATION_BILBERRY_
20 896 ind..m-2
A1.33.7%
L,F&H.66.3%
_HIGH ELEVATION_SPRUCE_
7 172 ind..m-2
A1.1.4%
F&H. 43.7%
moss&L.54.9%
_LOW ELEVATION_BILBERRY_
2 825 ind..m-2
H&A1.32.8%
L&F.67.2%
_LOW ELEVATION_SPRUCE_
1 452 ind..m-2

Fig. 15