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Jean-François Ponge

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HETEROGENEITY IN SOIL ANIMAL COMMUNITIES AND HUMUS FORMS: PATTERNS IN SPACE AND TIME

PONGE Jean-François, *Museum National d'Histoire Naturelle, Laboratoire d'Ecologie Générale, 4 avenue du Petit-Château, 91800 Brunoy (France), tel. +33 1 60479213, fax +33 1 60465009, E-mail: Jean-Francois.Ponge@wanadoo.fr*

Running title: SOIL ANIMAL COMMUNITIES AND HUMUS FORMS

Abstract

Two examples are given of strong relationships between the activity of soil animals and the development of humus forms in a mountain spruce forest and a lowland Scots pine stand. Both were based on field distributions of fauna and humus components. The vertical heterogeneity of soil animal communities in a moder humus profile under Scots pine is related to successional processes occurring during litter decomposition. Accumulation of faecal pellets by litter-dwelling animals influences in turn the development of the root system of pine and associated ectomycorrhizal fungi. The heterogeneity of humus forms in a mountain spruce forest is related to the developmental phases of spruce stands. Typical earthworm mull humus forms are restricted to regeneration sites with a low herbaceous vegetation. Typical moder humus forms with a thick OH horizon (dysmoder) are restricted to the pole phase of spruce stands. Between these two stages of the forest successional cycle, intermediary humus forms are found. They correspond to changes in soil animal communities, mostly burrowing earthworms, occurring together with changes in vegetation. These observations are discussed in terms of feed-back loops involving humus forms, soil animal and plant communities.

Introduction

Bornebusch described animal communities living in a variety of beech forest soils (1). Since that time soil animal ecologists put most emphasis on the influence of environmental conditions, in particular humus forms, upon the entire soil fauna community (2, 3, 4) or particular animal groups (5, 6, 7). In addition, the action of soil fauna on the establishment of humus forms has been fully recognized for a long time by soil micromorphologists (8, 9, 10, 11). This relationship was experimentally established using selected species (12, 13). The idea that humus forms and soil animal communities could be involved in feed-back loops (reciprocal interactions), and that these interactions could

explain a great part of the observed heterogeneity, has not been questioned until recently (14, 15, 16, 17).

The purpose of this paper is to present some results, originating from our previous efforts (18, 19, 20, 21, 22), that support the claim that the ecology of soil animal communities cannot be understood without accounting for their interrelationships with the development of humus forms and plant communities. Two examples, drawn from widely different scales, will be given, one concerning the vertical organization of a moder humus profile, the other concerning the forest successional patchwork (23).

Soil animals and plant litter decomposition: a trip through a humus profile

In a forest humus profile of the moder type, the composition of the different litter horizons OL, OF and OH (24) is indicative of their age, due to above-ground shedding of dead foliage. Thus investigating the humus profile from upper to lower positions may help to understand the fate of litter components through soil food webs. The development of the fine root system of trees, and the corresponding turnover, are also influenced by this ageing process. Fine roots are mostly concentrated in zones where more nutrients are liberated by decomposition (25). The synchronous observation of superposed litter layers offers several advantages over the litter-bag method which has been so widely used in decomposition studies (26). Among others, it does not separate litter components from root systems and their associate microflora. In addition it gives us immediately a wide panorama of most important biological processes taking place during the development of the humus profile (10).

As an example we will describe Scots pine (*Pinus sylvestris*) litter, as it has been studied by Kendrick and Burges (27), and by Ponge (18, 19, 20, 28, 29, 30), using different methods of direct observation. Although this could be considered old-fashioned compared to modern methods of soil organic matter investigations, such as nuclear magnetic resonance (31) or differential thermal analysis (32), there is at present no better mean than microscopy to discern unambiguously the biological signature of litter and humus components.

The site is a 30-yr-old Scots pine stand planted on a sandy soil substrate with moder humus form (24). Soil is an aqualf with a seasonally shallow water table. Ground vegetation is made of a continuous layer of the moss *Scleropodium purum*, together with the bracken fern *Pteridium aquilinum*. Observations to the naked eye of components of the humus profile (28) may already help to discern some discrete changes occurring in the course of time (Table I). These changes do not follow the

***Table I**. Observations in different horizons of a moder humus profile under Scots pine (Orleans forest, France); +++ = dominant in a given horizon; ++ = abundant but not dominant; + = present but not abundant. Modified from Ponge (28). Observations were made within a 5 x 5 cm area. Nomenclature of horizons according to Brêthes et al. (24).*

Horizon	Thickness	Mosses	Needles	Fungi	Mycorrhizae	Faeces	Amorphous org. matter	Sand	Iron oxide
OL1	3 cm	+++ living	+ brown entire						
OL2	2 cm	++ dead	++ black entire						
OF1	1 cm		+++ fragments	++		+			
OF2	1 cm		++ fragments		+	++			
OH1	0.5 cm		+ fragments		+	+++			
OH2	0.5 cm					+	+++	++	
A	1-4 cm						++	++	
E								+++	+

linear pattern still commonly used in theoretical studies on plant liter decomposition (26), and horizons are immediately perceptible to the naked eye. They indicate a discontinuous process. This non-linear pattern is not only due to seasonal cycles of high and low rates of litter input, even perceptible in coniferous stands (33), but also to thresholds in space and time which limit the development of decomposer communities (34) and determine the heterogeneity of the humus profile, as will be seen below.

From these first observations, it appears that pine needles once fallen to the ground take a brown, then black colour (OL horizon), before being broken-up (OF horizon). This fragmentation takes place together with an enrichment in visible fungi (external mycelium) and animal faeces, and the appearance of the mycorrhizal root system of pine. Subsequently the faecal material accumulates without any mixing with mineral matter, thus forming an OH horizon. The appearance of a horizon made of amorphous organic matter (no plant remains or faecal pellets recognizable to the naked eye), partially mixed with sand, indicates seasonal water-logging (see also iron oxide deposits in the E horizon, Table I).

This profile is a moder humus, more particularly a hydro-moder humus.

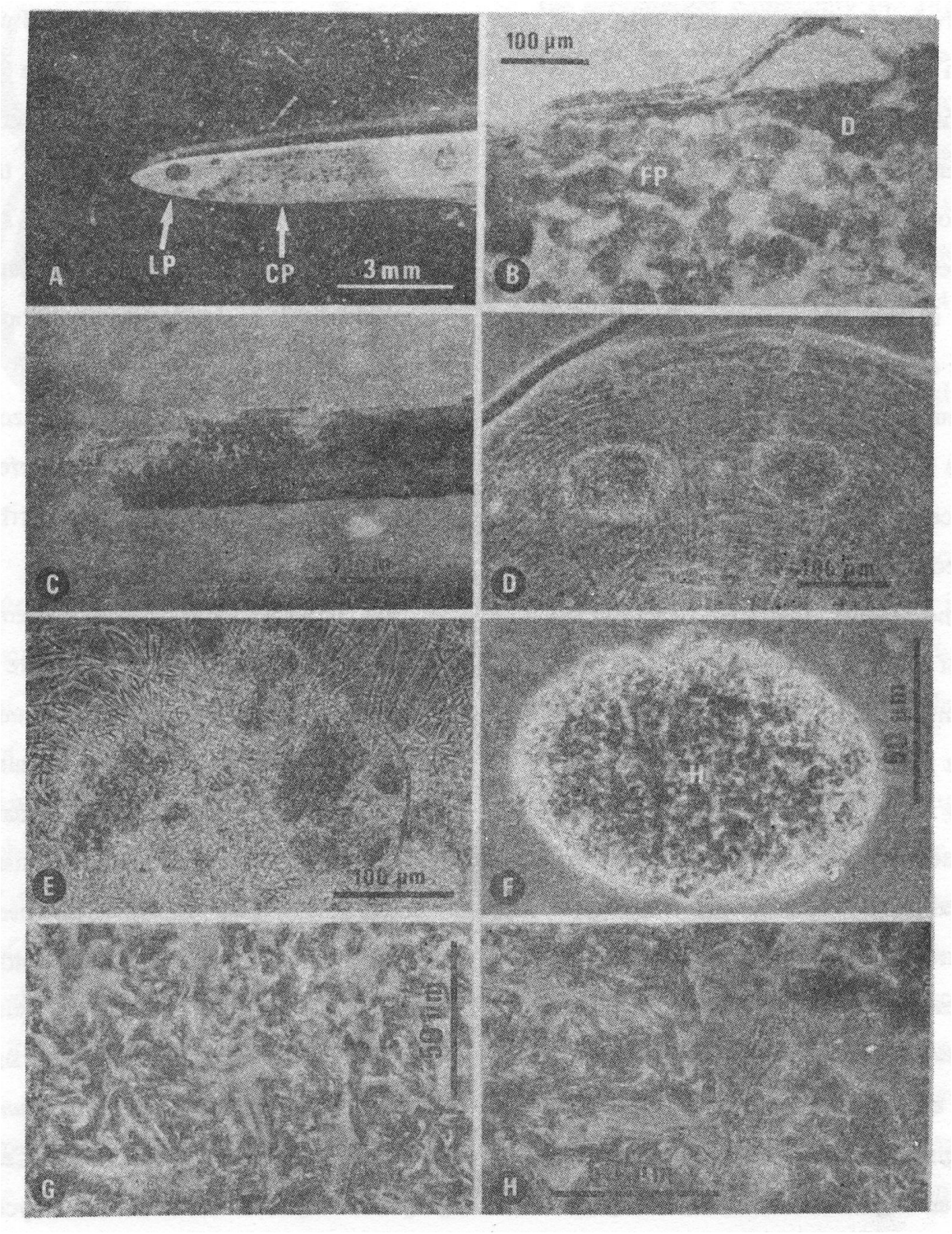
At this stage of the investigations the following succession of living organisms participating in litter decomposition is clearly perceptible. Needles are first invaded by internal fungi (blackening of the needles), then they are consumed by saprophagous epigeic fauna which defecate at the same place where they eat. The development of the mycorrhizal root system of within or around animal faeces is noteworthy.

Microscopic observations may help to get a better insight into these processes (19). Direct observations can be supplemented by isolation techniques (27) but many organisms (both microbial and animal) may be directly identified by their anatomical features. The invasion of needles by fungi begins in the canopy, during senescence of the foliage. Some of these fungi fructify in the superficial litter layers. This is the case for the two common species *Lophodermium pinastri* and *Ceuthospora pinastri*, which can be easily identified by morphological features of their sporocarps. They may appear side by side on the same needle, each confined to its own territory (Figure 1A). At this stage of fungal decomposition (OL1) the action of fauna is scarce, except that some needle parts colonized by *L.pinastri* can be penetrated by enchytraeid worms (the dominant soil fauna). These animals consume internal tissues, leaving their faecal pellets inside the pine needles (Figure 1B). The tough diaphragm formed by the fungus crosses the needle, thus delineating its territory. It acts as a barrier against further tunnelling by the animals. Other needle fungi were observed in the OL horizon, among them the widespread *Verticicladium trifidum*. This fungus, which is easily recognizable by its external ramified conidiophores (28), is chiefly reponsible for the blackening of the needles in the OL2 horizon.

Maximum saprophagous animal activity occurs in the OF1 horizon, where needles are extensively penetrated by enchytraeids, oribatid mites (Figure 1C) and sciarid larvae. Although these animal groups strongly differ from a taxonomical point of view, they form a common decomposer community, which processes the internal tissues of pine needles and transforms them progressively into a faecal mass. This mass, together with recalcitrant plant and fungal remains, constitutes the bulk of the OH horizon, as this has been observed by elsewhere (11). We observed that oribatid faecal pellets present inside the pine needles were consumed by enchytraeids that tunnelled in turn the same needles (Figure 1D). We never observed the opposite successional trend. The dominance of enchytraeid worms in the studied sample suggests that all dead needles are progressively converted into a compact mass of enchytraeid faeces.

In the same horizon (OF1) we observed the development of the fine root system of pine, with its associate mycorrhizal fungi. The latter were already present in the OL2 horizon, but they were less abundant. Masses of enchytraeid faecal

Figure 1. *Direct observation of pine needle decomposition by microscopical methods.* ***A*** *= Two senescence fungi occupying distinct territories on the same needle (OL horizon); LP = Lophodermium pinastri; CP = Ceuthospora pinastri.* ***B*** *= Consumption of internal tissues by an enchytraeid worm (OL horizon); FP = faecal pellets; D = diaphragm of L. pinastri.* ***C*** *= Accumulation of oribatid faecal pellets at the inside of a partly dissected needle (OF horizon).* ***D*** *= Oribatid faecal pellets ingested by an enchytraeid worm (OF horizon).* ***E*** *= Enchytraeid faeces embedded in a mycelial mat formed by a basidiomycetous mycorrhizal fungus (OF horizon).* ***F*** *= Transformation of internal tissues in an oribatid mite intestine (OF horizon); H = humified part.* ***G*** *= Transformation of internal tissues in enchytraeid faeces (OL horizon).* ***H*** *= Bacterial development within internal tissues ingested by enchytraeid worms (OL horizon). Figures 1A, 1B, 1G, 1H, from Ponge (28). Figures 1C, 1D, 1E, 1F, from Ponge (30).*



material are actively penetrated by mycelia of ectomycorrhizal fungi (Figure 1E). In the studied sample the most widespread ectomycorrhizal fungi are the basidiomycete *Hyphodontia sp.* and the ascomycete *Cenococcum geophilum* (17). These fungi are consumed by fungal-feeding animals belonging to a wide range of taxonomical groups (20), among them the same enchytraeid species that consume pine needles.

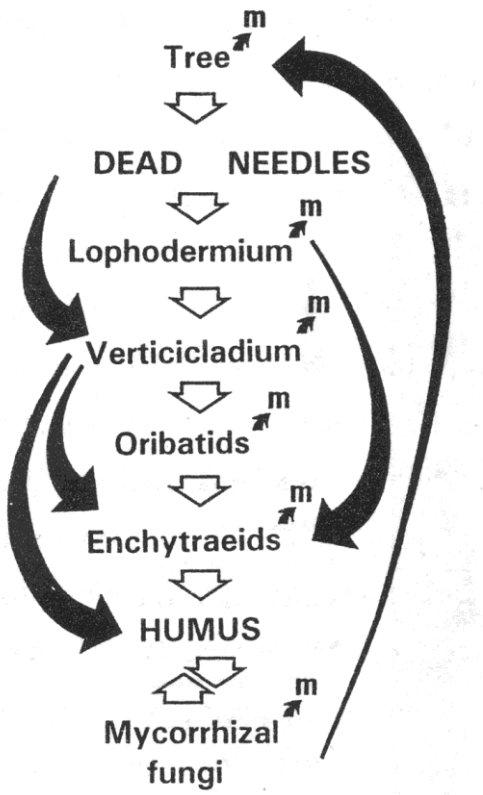
The fate of the internal tissues of a pine needle differs according to the animal group which consumes it. In oribatid intestines we observed, besides a very fine comminution of the ingested material, a distinct browning of pine cell walls at the centre of each preformed pellet. This indicates partial humification before defecation occurs (Figure 1F). In enchytraeid faecal pellets, cell wall fragments are coarse and transparent (Figure 1G). Thus they do not exhibit any sign of humification even after time has elapsed after faecal deposition. A bacterial development was registered inside pine needles which had been penetrated by fauna in the OL horizon (Figure 1H), but this development seemed arrested after colonization of needles by ectomycorrhizal fungi (17).

The so-called humus, from a chemical point of view, is in fact the result of intricate biological processes involving both animals and microbes. A great part of soil organic matter is thus made-up of plant remains (processed by animals, mainly present in their faeces) and microbial tissues (here mainly fungal cell walls). The use of the microscope reveals that the dark colour of the investigated horizons is mainly due to the development of dematiaceous fungi, such as the saprophytic *Verticicladium trifidum* (black needles) and the mycorrhizal *Cenococcum geophilum* (black rootlets and mycelia, with typical anatomical features), and that the bulk of organic matter remains untransformed. Chemical analyses of such soil horizons may reveal the presence of dark humic compounds which are in fact fungal melanins (35).

The abovementioned biological features are typical of the moder system (24), where the nutrition of plants takes place mainly in decaying litter, and where comminuted organic matter is the main site for ion exchange and buffer capacity (36).

The growth of trees is conditioned both by autotrophic processes (photosynthesis) and by heterotrophic processes (litter decomposition). The nature and activity of the decomposer community determines the rate at which and the place where most nutrients are available for tree growth (37). In turn, the quality and quantity of the plant material (litter, root system) determines the decomposer community (4, 38). This means that decomposers (including fauna) and vegetation are involved in feed-back loops such as the one illustrated in figure 2. This implies in turn that links between vegetation and soil organisms are not hierarchical (17), contrary to what has been claimed by several authors (39, 40, 41).

Figure 2. *A feed-back loop involving animals, fungi, humus, dead and living plant material; m = mineralization.*

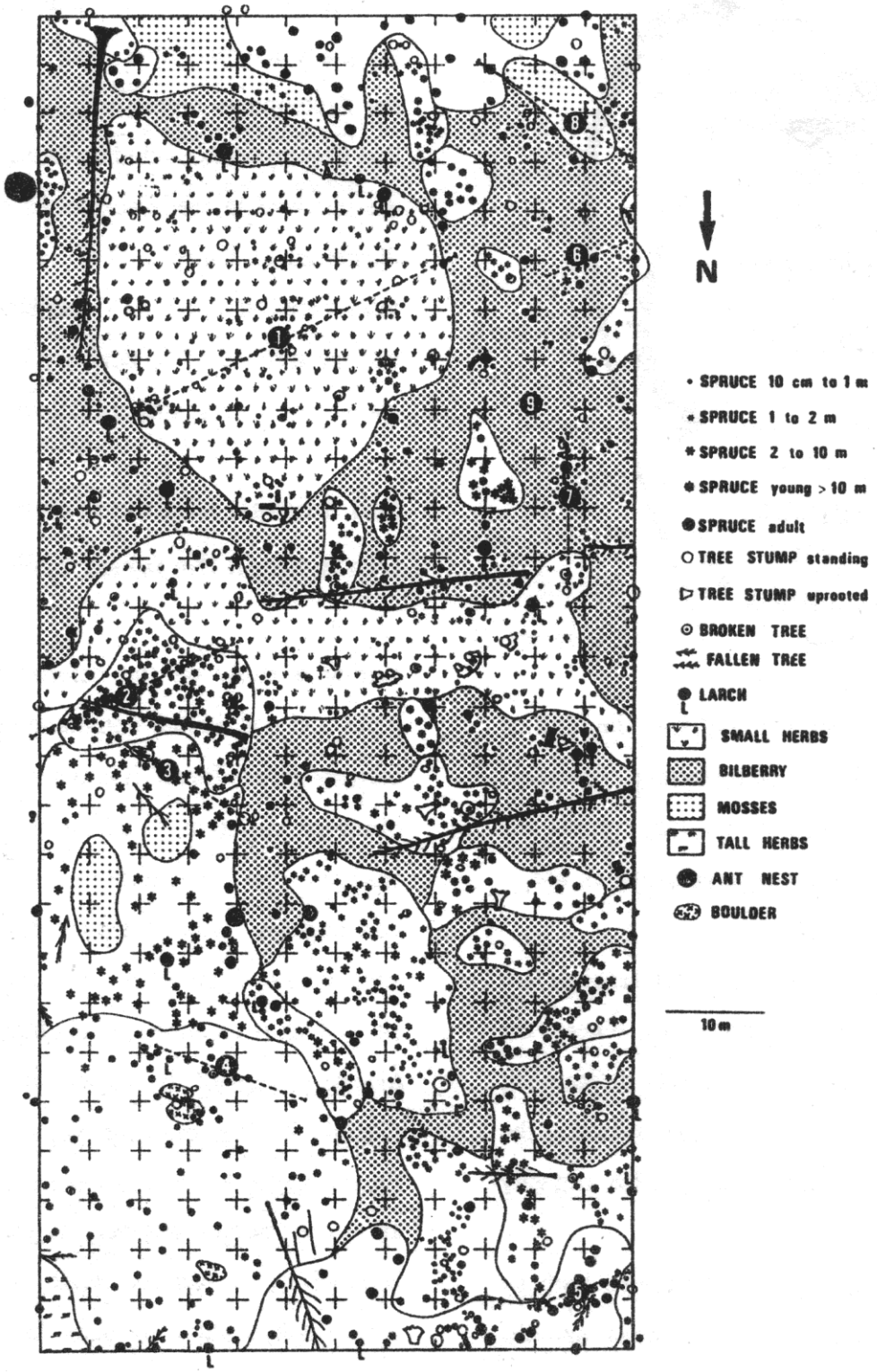


Soil animals and ecosystem dynamics: a trip through the forest cycle

During a study on the heterogeneity of humus types and soil animal communities in a mountain bilberry-spruce forest, it appeared that most of the observed variation could be ascribed to parallel changes in vegetation and decomposer communities which occur during the forest successional cycle (21). On a map of the study site, which is a conservatively managed forest, the mosaic pattern of the vegetation is clearly visible (Figure 3). Successional steps occurring during the development of pure spruce stands are present at a few meters distance, together with zones invaded by a bilberry heath. Regeneration of spruce takes place in gaps in spruce canopy, which have been invaded by a herbaceous ground vegetation. In these locations the humus form is an oligomull with epigeic, endogeic and anecic earthworms, despite a soil water pH around 4 (zone 1). Such gaps in the canopy are currently created by storms, in the present case a clump of around 25 trees (see tree stumps on figure 1) had been storm-felled 20 years before the study. The mull humus form is highly favourable to the regeneration of spruce (17), at least in the absence of tall herb and fern vegetation (42). The mull humus form is present during the first phase of spruce development (zones 2 and 3). In zone 4, where 60-yr-old trees are actively growing in height (about 1m/yr), the humus form is a dysmoder, and the mineral soil shows the clear signs of podzolization which have been commonly attributed to spruce plantations (43). Endogeic and anecic earthworms are absent during this phase, which is coherent with the humus form which we observed.

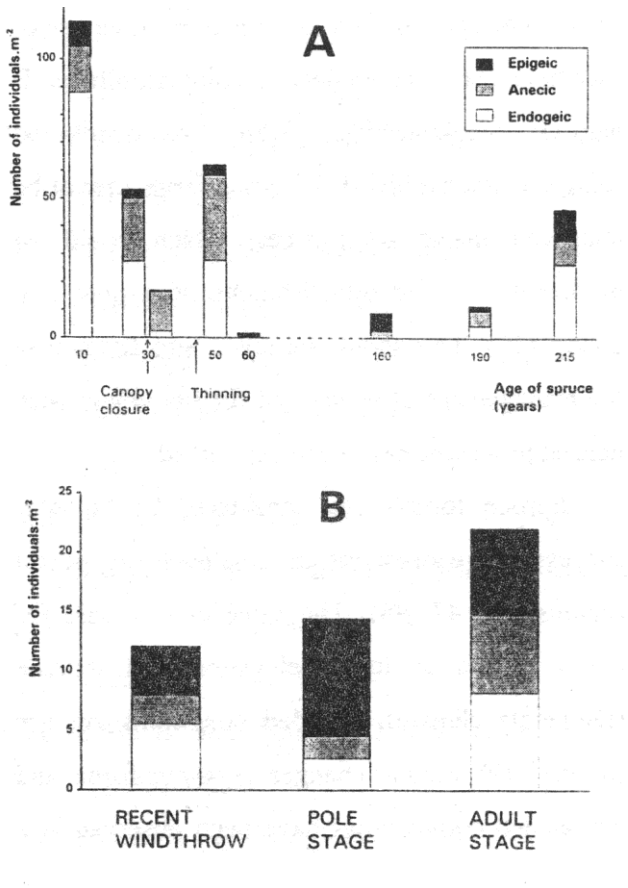
Under adult trees, growing either in groups (zone 5) or isolated within the bilberry heath (zones 6 and 7), we observed a return to the mull humus form. This was not in agreement with the above mentioned concept of podzolization, nor with other studies on the development of humus forms in coniferous plantations (44). When comparing humus profiles along a tree age sequence, it appears that the organic matter accumulated within the OH horizon of the

Figure 3. *The mosaic pattern of vegetation in a mountain bilberry-spruce forest (northern Alps, altitude 1550 m a.s.l.). Sample plots indicated by numbers. 1 = regeneration site (herbaceous vegetation with spruce 0- to 20-yr-old; 2 = spruce 30-yr-old; 3 = spruce 50-yr-old; 4 = spruce 60-yr-old; 5 = spruce 160-yr-old; 6 = spruce 190-yr-old; 7 = spruce 215-yr-old; 8 = moss carpet; 9 = bilberry heath. From Bernier and Ponge (21).*



dysmoder humus form is progressively redistributed and incorporated in the mineral soil under the influence of a burrowing earthworm community (Fig. 4A). The complete earthworm community is progressively built again under adult trees, starting with a small anecic population of *Lumbricus terrestris*, a rather tolerant species (45). Further enrichment of the community takes place with the occurrence of more exacting species such as the endogeic *Aporrectodea*

Figure 4. *Changes in earthworm communities in the course of the forest cycle. A = mountain spruce forest. B = lowland beech forest.*



nocturna. Such parallel changes in earthworm populations, humus forms and vegetation were observed in the same forest at different altitudes (46), and each humus profile revealed traits of its own history, thus argumenting against possible heterogeneity of site conditions. At the montane level the natural regeneration of the spruce ecosystem can be explained by a return to more favourable soil conditions once the period of intense growth of spruce has terminated, i.e. between 100 and 200 years.

Another aspect should not be neglected if we want to understand the mosaic pattern of this forest. A collapse in some important members of the decomposer community, such as burrowing earthworm species, if it occurs over large areas, may have irreversible effects on site conditions. If natural recolonization from well-distributed refuges is impossible, then humus forms cannot be improved under adult trees, which could be detrimental to the establishment of a new tree cohort (17). This should be taken into account in the management of even-aged forests where such natural processes have been eliminated.

Spruce forests are considered to be late-successional ecosystems in subalpine and boreal regions (17, 47, 48). The same can be said for beech forests at lower elevation and latitude (temperate climate) provided conditions are not too dry (49). Similar changes in humus forms and soil animal communities have been observed in a virgin beech forest (22). Earthworm communities, which show a good balance between ecological groups under adult trees, are seriously affected immediately after windthrow (Fig. 4B), although we may suspect that they will partly recover after the development of ground vegetation (the study

was done two years after a violent storm). The pole stage was characterized by the depletion of endogeic and anecic populations, with accompanying accumulation of unincorporated organic matter.

We may wonder whether the improvement in soil conditions observed under adult trees can take place in forests from which key organisms such as burrowing earthworms have been excluded. In such forests with a lower biodiversity, it may be predicted that changes in humus forms occurring in the course of forest succession will reflect only minor changes in epigeic fauna and microflora communities.

Conclusion

Our studies suggest that feed-back loops involving both vegetation, soil animal communities and humus forms are involved in the mosaic pattern of some forest ecosystems. These three components of every terrestrial ecosystem should not be considered separately when studying major processes such as natural regeneration, litter decomposition and nutrient cycling.

Références

1. Bornebusch, C.H. 1930. Forst. Forsogsv. Danmark 11, 1-158.
2. Van der Drift, J. 1962. In: Murphy, P.W. (Editor), Progress in soil zoology. Pages 343-347, Butterworths, London.
3. Schaefer, M. and Schauermann, J. 1990. Pedobiologia 34, 299-314.
4. Ponge, J.F., Arpin, P., Sondag, F. and Delecour, F. 1997. Can. J. For. Res. 27, 2053-2064.
5. David, J.F. 1987. Rev. Ecol. Biol. Sol 24, 515-525.
6. Arpin, P. 1991. Rev. Ecol. Biol. Sol 28, 133-144.
7. Ponge, J.F. 1993. Pedobiologia 37, 223-244.
8. Kubiëna, W.L. 1955. In: McE. Kevan, D.K. (Editor), Soil zoology. Pages 73-82, Butterworths, London.
9. Zachariae, G. 1965. Forstwiss. Forsch. 20, 1-68.
10. Bal, L. 1970. Geoderma 4, 5-36.
11. Rusek, J. 1975. Pedobiologia 15, 299-308.
12. Bal, L. 1982. Zoological ripening of soils. Pudoc, Wageningen.
13. Shaw, C. and Pawluk, S. 1986. Pedobiologia 29, 327-339.
14. Miles, J. 1985. In: Fitter, A.H. (Editor), Ecological interactions in soil. Plants, microbes and animals. Pages 407-427, Blackwell, Oxford.
15. Huhta, V. and Setälä, H. 1990. Biol. Fert. Soils 10, 155-162.
16. Coleman, D.C., Odum, E.P. and Crossley, D.A.Jr. 1992. Biol. Fert. Soils 14, 104-111.
17. Ponge, J.F., André, J., Zackrisson, O., Bernier, N., Nilsson, M.C. and Gallet, C. 1998. BioScience 48, 523-530.

18. Ponge, J.F. 1990. Eur. J. For. Pathol. 20, 290-303.
19. Ponge, J.F. 1991. Plant Soil 138, 99-113.
20. Ponge, J.F. 1991. Geoderma 49, 33-62.
21. Bernier, N. and Ponge, J.F. 1994. Soil. Biol. Biochem. 26, 183-220.
22. Ponge, J.F. and Delhaye, L. 1995. Biol. Fertil. Soils 20, 24-32.
23. Oldeman, R.A.A. 1990. Forests: elements of silvology. Springer-Verlag, Berlin.
24. Brêthes, A., Brun, J.J., Jabiol, B., Ponge, J.F. and Toutain, F. 1995. Ann. Sci. For. 52, 535-546.
25. Meyer, F.H. and Göttsche, G. 1971. In: Ellenberg, H. (Editor), Ecological studies. Analysis and synthesis. Vol. 2. Pages 47-52, Springer-Verlag, Berlin.
26. Berg, B. and Ågren, G.I. 1984. Can. J. Bot. 62, 2880-2888.
27. Kendrick, W.B. and Burges, A. 1962. Nova Hedw. 4, 313-344.
28. Ponge, J.F. 1984. Rev. Ecol. Biol. Sol 21, 161-187.
29. Ponge, J.F. 1985. Pedobiologia 28, 73-114.
30. Ponge, J.F. 1988. Pedobiologia 31, 1-64.
31. Hempfling, R., Ziegler, F., Zech, W. and Schulten, H.R. 1987. Z. Pflanzenernähr. Bodenk. 150, 179-186.
32. Saiz-Jimenez, C. and De Leeuw, J.W. 1987. Sci. Tot. Environ. 62, 115-119.
33. Van Lear, D.H. and Goebel, N.B. 1976. Soil Sci. Soc. Am. J. 40, 116-119.
34. Burges, A. 1960. J. Ecol. 48, 273-285.
35. Paim, S., Linhares, L.F., Mangrich, A.S. and Martin, J.P. 1990. Biol. Fertil. Soils 10, 72-76.
36. Federer, C.A. and Hornbeck, J.W. 1985. Water, Air, and Soil Pollut. 26, 163-173.
37. Delecour, F. 1978. Pédologie 28, 271-284.
38. David, J.F., Ponge, J.F., Arpin, P. and Vannier, G. 1991. Oikos 61, 316-326.
39. Lavelle, P., Blanchart, E., Martin, A., Martin, S., Spain, A., Toutain, F., Barois, I. and Schaefer, R. 1993. Biotropica 25, 130-150.
40. Beare, M.H., Coleman, D.C., Crossley, D.A.Jr, Hendrix, P.F. and Odum, E.P. 1995. In: Collins, H.P., Robertson, G.P. and Klug, M.J. (Editors), The significance and regulation of soil biodiversity. Pages 5-22, Kluwer, Dordrecht.
41. Coûteaux, M.M., Bottner, P. and Berg, B. 1995. TREE 10, 63-66.
42. Weissen, F. 1979. Bull. Soc. Roy. For. Belgique 86, 115-123.
43. Nihlgård, B. 1971. Oikos 22, 302-314.
44. Van Berghem, J.W., Mettivier Meyer, H.J.B., Sevink, J. and Verstraten, J.M. 1986. In: Fanta, J. (Editor), Forest dynamics research in Western and Central Europe. Pages 85-93, Pudoc, Wageningen.
45. Satchell, J.E. 1967. In: Burges, A. and Raw, F. (Editors), Soil biology. Page 259-322, Academic Press, London.
46. Bernier, N. 1996. Plant Soil 178, 1-28.
47. Zackrisson, O. 1977. Oikos 29, 22-32.
48. Gensac, P. 1988. Rev. For. Fr. 40, 285-296.

49. Teissier du Cros, E., Le Tacon, F., Nepveu, G., Pardé, J., Perrin, R. and Timbal, J. 1981. Le hêtre. INRA, Paris.