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Jean-François Ponge, Nicolas Bernier. Changes in humus form and forest dynamics in the French Northern Alps. Bellan-Santini; D., Bonin, G., Emig, C. Functioning and dynamics of natural and perturbed ecosystems, Lavoisier, pp.174-182, 1995. hal-00505507

HAL Id: hal-00505507

<https://hal.science/hal-00505507>

Submitted on 3 Sep 2010

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Changes in humus form and forest dynamics in the French Northern Alps

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RESUME

Deux facteurs de modification de la forme d'humus ont été mis en évidence dans une pessière des Alpes du nord. La dynamique forestière imprime des modifications rapides de la forme d'humus (de l'ordre de la dizaine d'années) résultant d'une constante instabilité des relations entre producteurs primaires et décomposeurs. L'accroissement de cette instabilité, observé avec l'altitude, conduit à un point de rupture qui est matérialisé par la limite supra-forestière.

ABSTRACT

The humus form is governed by at least two factors in spruce forests of the French northern Alps. Forest dynamics induces rapid changes in humus form which result from permanent instability in the functional relationships between primary producers and decomposers. This instability increases with altitude, driving the system up to its breaking-point. This point is the upper limit of the forest.

Keywords: Mountain forests, Humus, Vegetation dynamics, Upper forest limit.

Introduction

Humus takes a prominent place in forest ecosystems: it is the result of the interactions between primary producers (vegetation) and decomposer food webs (soil organisms) (LAVELLE, 1987). When environmental

conditions are changing, it may be thought that these relationships will change in time (PAGE, 1971). Our work hypothesis was that any modification of the relationships between the decomposer food web and primary producers will modify the general equilibrium and the dynamics of the forest ecosystem. For testing this hypothesis we chose the communal spruce [*Picea abies* (L.) Karst.] forest of Macot-La Plagne (Savoy, France), which is extending in altitude from 700 m (where regeneration and maintenance of the forest ecosystem are well managed) up to 2200 m, after which the forest is normally replaced by an ericaceous heath. Between these deadlines, regeneration problems really occur, increasing with altitude: the forest ecosystem is highly sensitive to different kinds of stress conditions that may affect its capabilities for self-renewal (ANDRE et al., 1990). From this observation is issued our second work hypothesis: the upper forest limit does not exist as such but is rather the materialization of the tolerance limit between woodland vegetation (trees comprised) and soil organisms. These relationships are already experienced at low elevation. Our study of humus profiles (BERNIER 1992; BERNIER & PONGE, 1993; BERNIER et al., 1993; PONGE et al., 1993) showed that, whatever the altitude, these interactions never conduct to an equilibrium. All studied profiles exhibited indices of instability, which could be considered as the driving power of ecosystem dynamics. Humus form describes a cycle from mull, which is favourable to the regeneration of spruce, to dysmoder or even mor which are detrimental to young seedlings of this tree species (WEISSEN, 1979). The restricted regeneration niche of spruce results in the mosaic pattern of the forest ecosystem (Fig. 1), its elementary units being small surfaces each having a common history. The forest ecosystem may thus be considered as a patchwork of the different developmental phases of the forest cycle (OLDEMAN, 1990).

Study of a humus profile: dense population of spruce trees about 30 years-old growing at 1550 m elevation

This profile (Fig. 2) was analysed by measuring, layer after layer, the volume ratio of each kind of element that was identifiable under the dissecting or the binocular microscope (PONGE, 1984; BERNIER, 1992; BERNIER et al., 1993). This ratio was quantified by help of a counting point method (BERNIER, 1992). Examination of this profile gave evidence of a succession of litter components that were varying in nature. From 12 to 15 cm depth numerous dead roots of coniferous trees are juxtaposed to dead roots of wood rush [*Luzula sylvatica* (Huds.) Gaud] and hair-grass [*Deschampsia flexuosa* (L.) Trin.]. This root litter layer is immediately topped with a thin layer made of bark pieces. Above that, leaves and leaf bases of wood rush and hair-grass may be found with, above them, numerous moss fragments. At the soil surface, a needle litter of spruce and larch is

only visible. This sequence allows us to have a fairly good knowledge of the recent past of the site: a thick moss layer was present before canopy closure. Before that, an herbaceous vegetation was present, the appearance of which coinciding with an important fall of coniferous bark. These bark pieces testify for repeated fall of trees over a relatively short period of time. The only remains of the past tree stand are bark, root litter and tree stumps that are always visible on the site. This succession of plant deposits is juxtaposed to recent organo-mineral earthworm faeces. Their analysis (Fig. 2) reveals two important organic components: microcristalline fragments (plant cell wall pieces) and amorphous organic matter adsorbed to mineral particles. The former indicates accumulation of mechanically degraded material, the latter is a proof that incorporation of humified organic matter to mineral matter is satisfactory. Humus is always of the mull form despite accumulation of successive litter layers for the last 30 years.

This demonstrates that it is possible, from a micromorphological study of an unique humus profile, to understand the past and present functioning of a restricted part of a forest ecosystem. Thus the most controversial point of synchronic analysis, the repetitiveness of the mechanisms by which a site may be time-related to another, may be validated (LEPART et ESCARRE, 1983). The series of humus profiles that were taken in the same site reveals that the renewal of the forest ecosystem is sustained by dynamic processes where primary producers and decomposers play a key role (BERNIER, 1992). These processes take place in the humus profile, with a certain degree of inertia (due to the number of intermediary events necessary), thus explaining the time lags that are at the true origin of ecosystem dynamics. The whole surface of the forest is not at the same phase of this dynamic process, thus the forest cycle is achieved at the inside of small functional units that are relatively independant the one from the other.

Comparative study of the forest cycle along an altitudinal gradient: the problem of the upper forest limit

The study of a whole altitudinal gradient revealed progressive modifications of the processes that allow the forest cover to be self-maintained (BERNIER, 1992; PONGE et al., 1993). At 900 m elevation, changes in humus profiles are weak, the form being always a mull. Nevertheless these shifts are far from neglectable. Acidity fluctuates from pH 5, under spruce-fir thickets 70 years-old, to pH 7 under aged individuals (Fig. 3). Decrease of pH may be registered immediately after the development of coniferous species (overgrowing deciduous shrubs) at the inside of a clearing. At the higher montane level (1500–1700 m) changes in humus

form are more pronounced but acidity remains high whatever the type of humus profile. Optimum for mull formation is in the clearings with herbaceous cover where dense regeneration of spruce takes place. Optimum for moder formation is under spruce trees in full growth, 60 years after. The higher is the elevation, the more important is the moder phase. At the upper forest limit, even the activity of the soil animal groups that are responsible for moder formation decreases. Humus turns to mor, with a dominant fungal activity. Thus, the higher is the elevation, the more the balance between producers and decomposers is impaired, rendering the renewal of the forest cover problematical. This is confirmed by observing the distribution of ericaceous heathlands and associated humus forms. Above the forest limit, the ground is entirely covered by heath. Humus is of the mor type. Nevertheless this level is not the lower limit of the heath. In fact, between 1500 and 2000 m elevation, the two ecosystems (heath and forest) are co-existing without any mixing. At a given elevation, the bilberry (*Vaccinium myrtillus* L.) heath builds a humus profile that anticipates what is observed at a higher elevation in the forest ecosystem. For instance, humus is of the mor form in the heath although of the dysmoder form in the nearby forest islands. At 1550 m elevation, humus is generally of the mull form, except under the heath where it is a dysmoder. Thus when bilberry is present as a dense cover at the montane level, this is not only this subalpine species that arrives at this altitudinal level, but in fact the whole heath ecosystem, with all its components (including soil organisms). Thus it is reasonable to suppose that an antagonism between two co-existing but distinct ecological systems may exist like it may be the case between two distinct species belonging to the same ecosystem (ANDRE and GEN SAC, 1989). This model, if proved to be universal, may be a tool for a better understanding of global changes.

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Legends of figures

Fig. 1. Distribution of individual trees and bilberry cover in the study site S 1550 (Macot forest, altitude 1550 m).

Fig. 2. Analysis of a humus profile. Study site S 1550. Spruce 30 years after canopy closure. Upper left: observation of the whole material under a dissecting microscope (percentages of total material). Upper right: observation of holorganic and organo-mineral fine material under a binocular microscope (percentages of total fine material). These two last categories have been separated by a white hatched line.

Fig. 3. Changes in some features of humus profiles according to vegetation in the study sites S900 and S1550. Acidity (water pH) was measured in the A1 horizon.

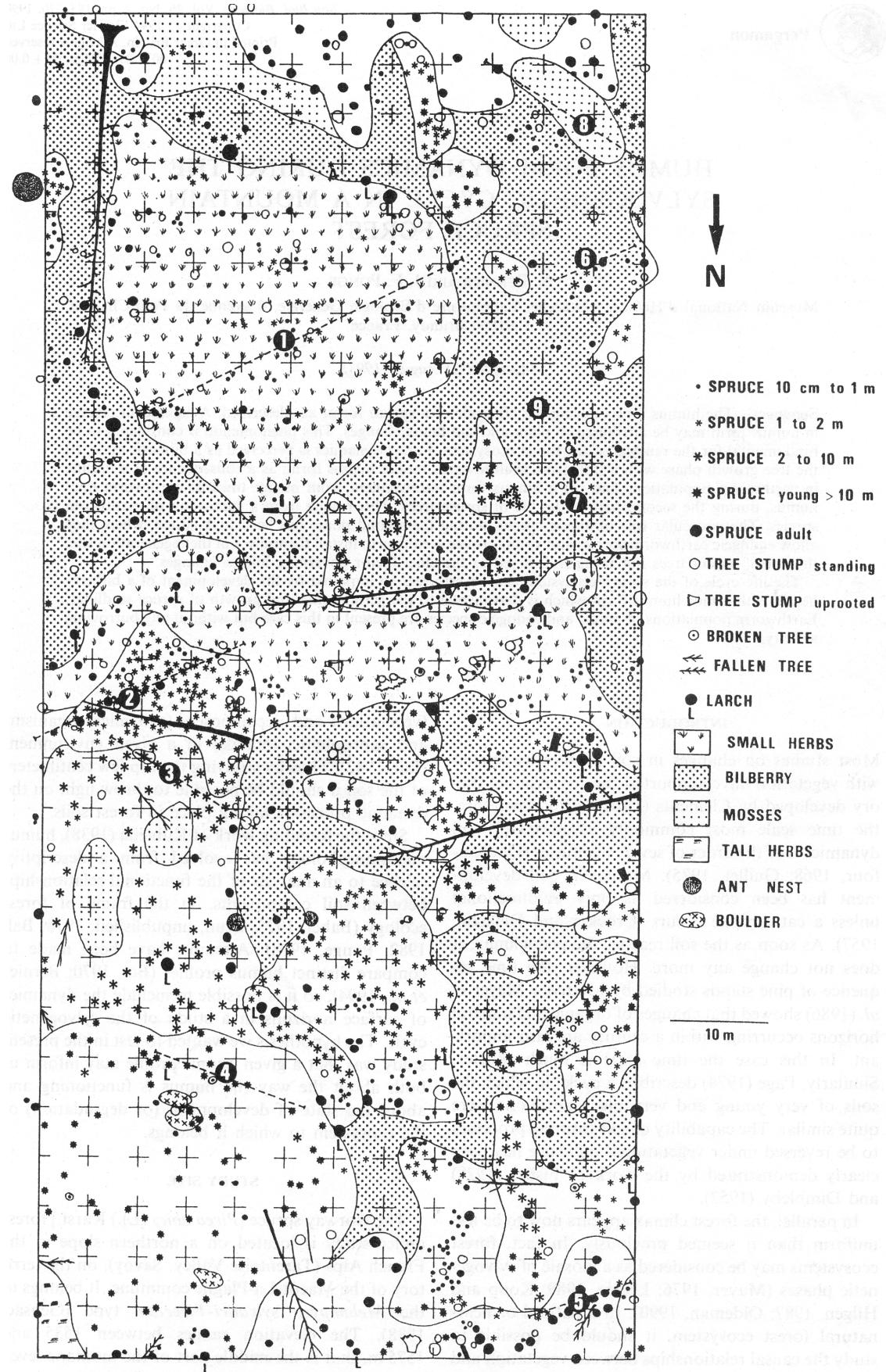
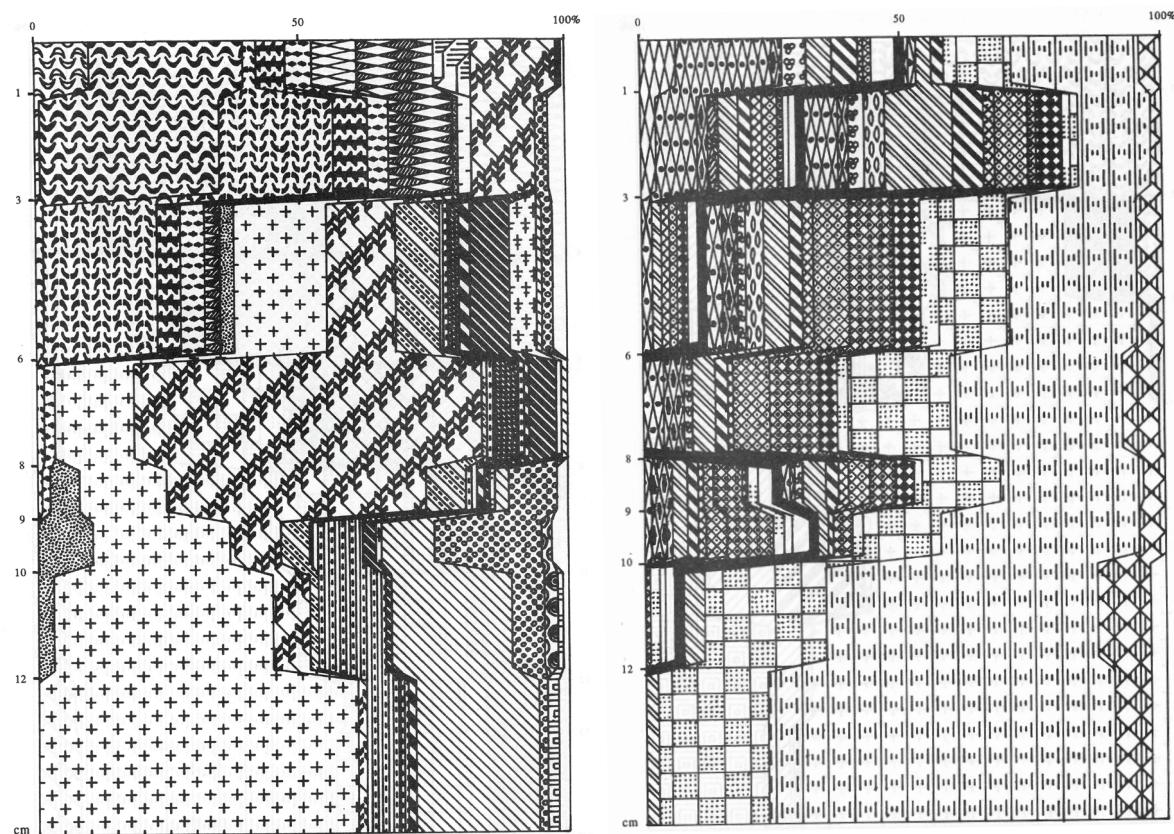


Fig. 1



| | |
|----------------------------------|----------------------------------|
| 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 |
| HOLLOWGANIC FAECES | COW WHEAT |
| ORGANO-MINERAL | PRENANTHES |
| MOSS <i>Hylocomium splendens</i> | LICHEN |
| Rhytidiodelphus triquetus | 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 |

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

Fig. 2

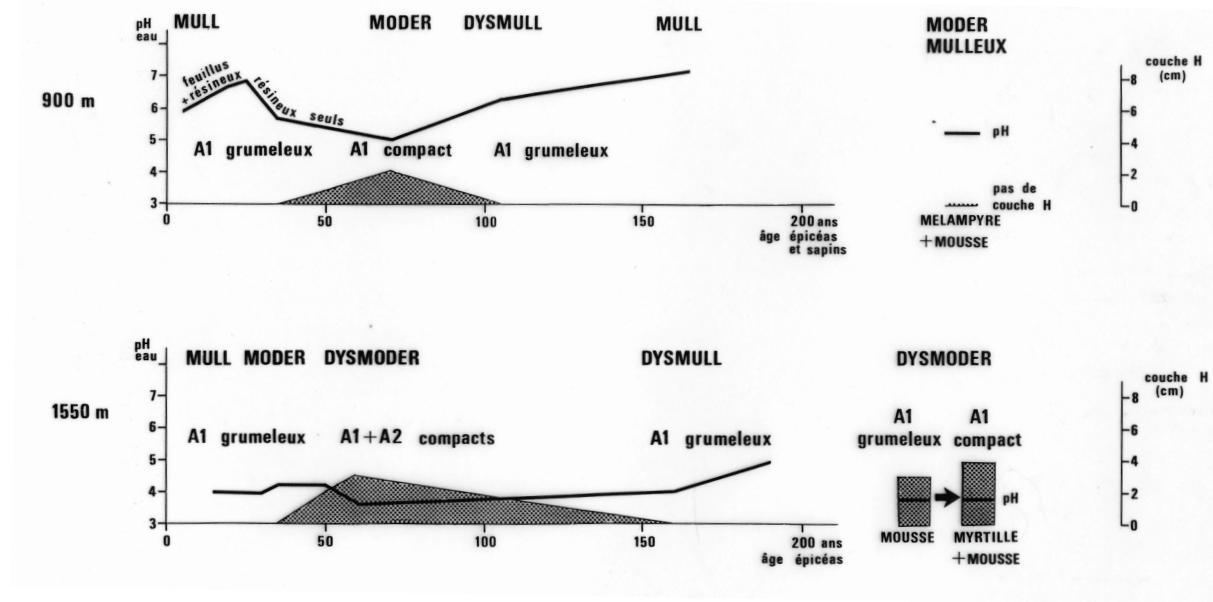


Fig. 3