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Ponge Jean-François

► **To cite this version:**

Ponge Jean-François. [What is humus layer, the hotspot of soil biological activities?] (in Japanese, translated from English by Keiko Mori). Milsil, 2015, 8 (5), pp.12-14. hal-01250341

HAL Id: hal-01250341

<https://hal.science/hal-01250341>

Submitted on 5 Jan 2016

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What is humus layer, the hotspot of soil biological activities?

JF PONGE

What can we find under our feet when walking in a forest? Dead leaves or needles, decaying wood and bark, form the litter, OK, but what else? Below the ground, after lifting the superficial litter, an intense activity can be perceived in the humus layer: microbes (fungi, bacteria, algae), plant roots (including the subterranean parts of trees) and fauna abound, making the soil the richest part of the forest ecosystem, both in organisms and functions they achieve. Traces of faunal activity are visible to the naked eye in the form of galleries (earthworms, moles, etc...), deposition of excrements (faecal pellets of varying size and shape), nibbling of litter (skeletonized leaves, tunnelled needles), but many other invisible functions of soil organisms can be observed only with the help of a microscope and laboratory analyses.

As an example, have a look on the humus layer of a pine forest. The humus layer can be treated as a book, flipping its pages allowing us to decipher the story of organic matter. Once dead needles have fallen on the ground, they become rapidly covered with mosses, protruding in the spaces between them (Figure 1). At this stage, faunal activity is feeble but invisible hyphae (cell filaments) of fungi have already invaded the inside of needles in a few weeks, turning their colour to dark brown, as this can be seen in the layer of dead moss just below (Figure 2). Later on, within a year or more, needles are transformed in a mass of humified organic matter in which only small fragments of needles can be seen to the naked eye (Figure 3). Looking with attention will reveal an amorphous dark mass of fine organic matter (**faunal faeces**) with numerous root tips of pine growing upwards through it: these roots are associated with soil fungi in a symbiotic manner, called the **mycorrhiza**. This superficial humus layer, located a few millimetres under the ground surface, is the main seat of tree nutrition and the seat where most soil organisms are living and interact. Hence the need to protect the humus layer for sustaining forest health. Many human activities have endangered and still continue to endanger forests because of misunderstanding the importance of the humus layer.



Figure 1. Pine litter and moss as seen on the ground of a pine forest. Note the black dots on some pale yellow pine needles, testifying for the presence of fungal colonies at the inside.



Figure 2. The layer just under that pictured in Figure 1. Moss is mostly dead. Pine needles are blackened. A twig fragment and some orange-brown bark fragments are visible.



Figure 3. The layer just under that pictured in Figure 2. Needles have been transformed in a dark amorphous mass, through which mycorrhizal root tips of pine are protruding.

Among animals living in this humus layer, enchytraeids take a prominent place. These tiny segmented worms, cousins of earthworms but transparent and of a much smaller size (a few millimetres only), are able to gnaw at pine needles and tolerate the strong acidity of pine humus. Their gut contents can be observed by transparency, revealing their diet and the way they transform it in humus. Under the microscope, the main part of soil organic matter called “humus” reveal tiny plant cell fragments, agglomerated and mashed, without any mixing with mineral particles. This is typical of what is called “**moder**”, the humus form to be found in most coniferous forests and, more generally, forests growing on siliceous rocks in temperate to cold climates.



Figure 4. An enchytraeid, showing its gut contents by transparency. Note the segmentation of the food bolus, giving an indication of the size and shape of its tiny faeces (30-50 micrometres each), which form the main part of pine humus. Photo Cyril Hobbins

How to recognize moder humus? Cut a profile with a sharp knife and look at the superposed organic and mineral-organic layers which are visible to your eyes (Figure 5). Whatever their thickness the following succession is always visible: leaves (or needles) in an incipient stage of decomposition (not nibbled by fauna), then a layer made of fragmented plant remains intermingled with dark fine organic matter (animal faeces of varying size = humus), then a layer made of an amorphous mass of humus. Below these organic layers (horizons) there is a horizon made of a mixture of mineral and humus. Enchytraeids (potworms) are mainly responsible for this mixing process, which only takes place over a few centimetres.



Figure 5. A moder profile in an oak forest. Note from top to bottom the succession of organic layers (intact then fragmented then humified litter) and mineral-organic layers, called horizons.

Moder is a strategy for the forest ecosystem, allowing it to conserve precious nutrients (nitrogen, phosphorus, calcium, etc...) in the organic matter accumulated in the topsoil. This reservoir allows trees (thanks to mycorrhizal fungi) to uptake nutrients when necessary for growth and reproduction (flowering, fruiting). This strategy of nutrient conservation is necessary when nutrients are scarce in the environments or when biological activity is feeble due to harsh climate conditions. Organic horizons are also a tank of water, allowing trees to “drink” even in the dry season.

Many animal organisms are living in moder, from microfauna (nematodes, rotifers, protozoa) to mesofauna (enchytraeids, springtails, mites, insect larvae) but macrofauna (earthworms, centipedes, millipedes, woodlice, snails and slugs) are only poorly represented (although not absent) and play a secondary role in the transformation of litter. Megafauna (moles, voles) are nil.

Mull is another humus form, characterized by a strong burrowing activity of earthworms (replaced by termites or other burrowing animals according to climate context), which is associated with a rapid cycling of nutrients (Figure 6). Mull does not display any layer of humified litter, organic matter

being more or less rapidly mixed with mineral matter, with not enough time to accumulate as pure humus. In mull, humus is only present as mineral-organic assemblages in the form of big excrements (casts) of burrowing fauna. Bacteria, rather than fungi, are the dominant component of microbial communities, because of the important amount of mineral particles, to which most soil bacteria are attached. The root system of trees and forest vegetation explore the mineral-organic horizon where most nutrients are made available by an intense biological activity. In addition to microfauna and mesofauna, macrofauna abound and contribute to the rapid transformation of litter and its incorporation within mineral-organic horizons. Environmental conditions favourable to mull are the richness of the geological substrate (calcareous, dolomitic, volcanic) and a mild climate, both factors maximizing biological activity and allowing a high number of organisms, ensuring a variety of complementary functions, to coexist in harmony. Mull is found in deciduous forests but also in meadows (whether hay meadows or pastures) except at a high level of pesticide or fertilizer use with negative effects on soil fauna.



Figure 6. A mull profile in an oak forest. Note from top to bottom the succession of a thin litter and a thick mineral-organic horizon.

On the opposite side of a gradient of biological activity **mor** is characterized by weak to nil faunal activity, whether in litter comminution and consumption of soil microbes (fungi, bacteria, microalgae). Mor is favoured by cold climate and recalcitrant litter, mostly associated with boreal and high mountain coniferous forests. As a consequence of a decrease in the rate of humification and incorporation of organic matter, undecayed litter accumulates on the ground, permeated by a dense mycelial network, without or very few faecal deposits.



Figure 7. A mor profile in a spruce forest at 2000 m altitude. Note the thick layer (7-8 cm) of compacted spruce needles and two light-coloured areas of fungal development.

Humus forms can be used as a diagnostic tool for the assessment of the good health of forests and other terrestrial ecosystems. Compared to moder, the presence of mull testifies for a rapid cycling of nutrients and good growth conditions for trees and other vegetation. Mull is often associated with multi-layered forests where biodiversity is at an optimum. Moder is an alternative strategy when nutrients are more scarcely distributed in the environment, moder being the extreme when environmental conditions are harsh. This does not mean that moder is “bad”. On the contrary, moder is the best way to keep biodiversity at a reasonable level when the environment is less favourable to biological activity. What is “bad” is when mull shifts to moder, for instance following afforestation by exotic trees (to which native soil organisms are badly adapted) or heavy traffic by engines or badly adapted management practices, such as when immoderate thinning favours the development of ericaceous forest vegetation. However, it must be noticed that an alternation between mull (associated to regeneration and mature stages) and moder (associated to the stage of intense growth, called the pole stage) may occur during the natural development of forests stands, as this has been showed to occur in forests with natural forest cycles (ancient forests, biological reserves).