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► To cite this version:

| Jean-François Ponge, Augusto Zanella. Humus and time: a love story. 2007. hal-00495381v2

HAL Id: hal-00495381

<https://hal.science/hal-00495381v2>

Preprint submitted on 30 May 2017

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Humus and time: a love story

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Humus, both in the chemical sense (soil organic matter) and in the pedological sense (humus form, humus profile), is known to be slowly built-up through the agency of microbial, faunal and non-biological oxidative processes. Varied processes put the organic matter produced by plants, microbes and animals from the state of dead organs to that of one or several soil horizons where organic matter cannot be longer identified as to its living origin, except at strong magnification (Toutain et al. 1982, Ponge 1991) or by recording biochemical signals (Disnar & Harouna 1994). All these humus-forming processes are time-consuming, but the scale at which they operate may vary from seconds to months and even years if not centuries and millenaries. Given that each humus profile is submitted to environmental influences, any periodical process in its immediate environment will be reflected in the state of change of soil organic matter. The subject of the present paper is to portrait briefly the cycle of change of humus and to discern stable and changing environmental influences.

First, let us imagine what happens during a day-night (circadian) cycle in a forest mull. During the night, some of the decaying leaves still staying on the forest floor have been buried by anecic earthworms in underlying mineral horizons, where they will be submitted to microbial and faunal processing under adequate moisture conditions (Scheu & Wolters 1991). Nutrients liberated by microbial and faunal activity will be taken up by plant roots to be stored in aerial and subterranean organs (Scheu et al. 1999), while soil animals living in the subterranean environment created by soil-dwelling earthworms will benefit from nutrient-rich excreta and microflora (Marinissen & Bok 1988, Salmon 2001). Daily cycles are thus reflected in the state of change of litter, the pulse being the nocturnal foraging behaviour of anecic earthworms (Darwin 1892). The alternation of high (day) and low (night) temperatures and the photoperiod superimpose their own influence on important chemical and biochemical processes which will take place at daily interval. Even in the absence of anecic earthworms, daily temperature and light cycles create a 24-hr clock system, in pace with circadian rhythms of plant physiology (Werner et al. 2006).

At a slower scale of time, yearly cycles are reflected in seasonal changes in litter input and micro-climate. Nutrients accumulated in litter during winter (or summer in Mediterranean regions) are liberated during following seasons under better (milder) temperature and moisture conditions, as far as growing vegetation depletes them in the soil exchangeable system (Mitchell et al. 1992). Losses can occur through leaching (winter) and wind (summer), but the annual cycle of change is the more appropriate way by which humus layers may store and redistribute enough nutrients for sustaining ecosystem requirements in the long-term (Vitousek 1982). All organisms, either of plant, animal or microbial origin, participate to seasonal cycles, to which we may postulate that all of them became adapted in the first early stages of evolution.

Daily and yearly cycles are universal, since they are dictated by the rotation of Earth and its elliptic course around Sun. Other cycles are of a biological origin and thus are subject to less

strict, more chaotic periodicity, and may vary from place to place, but they are still recognizable and may profoundly influence the humus profile.

At a still extended scale of time, the limited duration of life of forest stands imposes its own influence. Although not universal, the alternation of moder and mull humus forms during a forest rotation has been observed several times by synchronic (space-for-time substitution) analysis (Bernier & Ponge 1994, Chauvat et al. 2007). It can be explained by (i) the physiological cycle of nutrient uptake which prevail during the life of a tree (Miller 1984), (ii) the fact that in natural as well as man-made forests trees of the same age are clumped and may thus influence the soil synchronically (Oldeman 1990). Starting with a period (the autotrophic phase) where the trees derive more nutrients for the building of their own biomass than to decomposer activity, the autotrophic phase is followed by the heterotrophic phase where nutritional requirements of the trees are lesser (or nil when cut or thrown by wind) and decomposer communities may recover until a new period of nutritional scarcity is initiated (André 1997, Ponge et al. 1998). Such a cycle is dictated by the events which are at the origin of a clump of trees which underwent a common history and may explain (beside geology and aspect) the mosaic assemblage of humus forms which prevail in most natural or semi-natural forests (Ponge & Patzel 2001, Galvan et al. 2007). Patterns of humus change which are in play in primary or secondary succession participate to the same process, although their cyclic nature can be observed only at the climax (late successional) stage, except if new cycles are initiated by recurrent disturbances (Van Cleve et al. 1993).

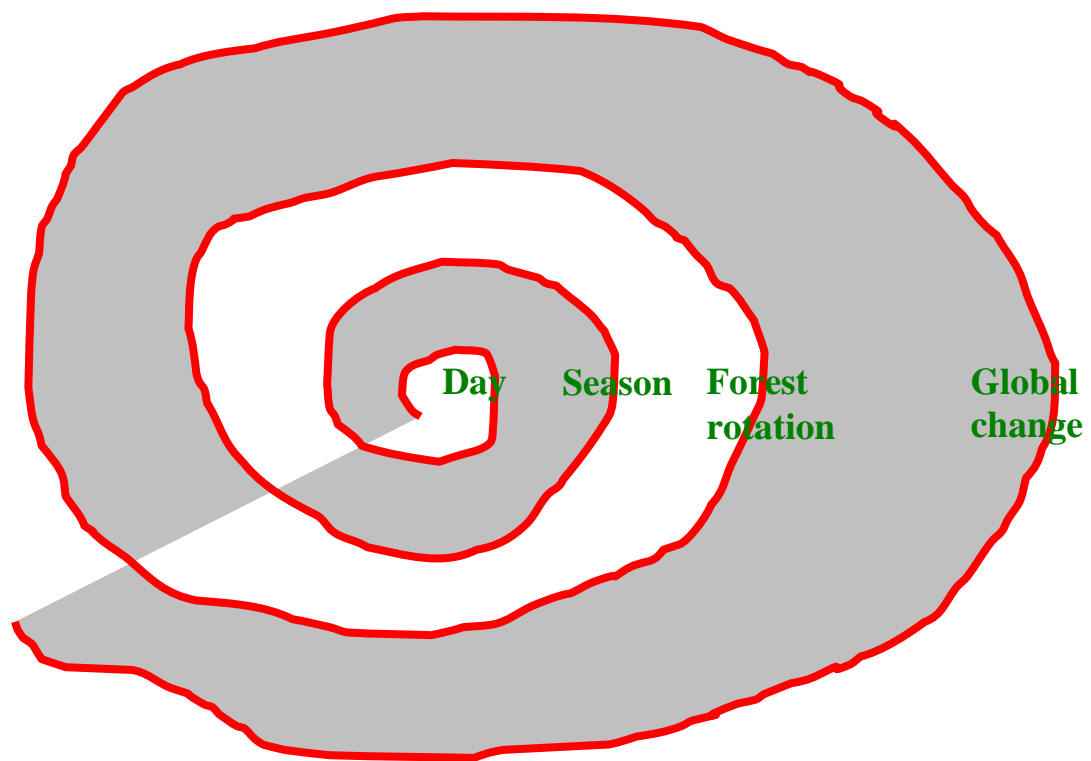
Other processes may combine with the abovementioned cycles of change to shape humus forms, among which global changes take a prominent place. Changes in humus forms occurring under the influence of atmospheric pollution and global warming belong to this type (Belotti & Babel 1993). They impose to organisms constraints to which most of them (except less specialized forms) cannot adapt easily, given that unpredictable events are not included in their phenotypic or ancestor memory. In the same manner as when trees change their physiology with age or are replaced by other species, thresholds of tolerance exist among soil communities, which decide whether some functions cannot be longer realized (for instance the disappearance of litter burial following acidification) or, on the contrary, become possible if organisms can colonize from surrounding refuges (as in a forest patchwork).

All abovementioned environmental forces which drive biological and chemical processes occurring in humus profiles act as synchronizers in an otherwise chaotic assemblage of more or less independent micro-sites (Beare et al. 1995). This synchronization of minute events allows emergent properties (Ponge 2005) to appear in the topsoil, for instance it may help to explain the formation of horizons. Suppose that a pine needle is transformed by a fungus (or even a microbial community) into a black amorphous mass of humified organic matter. This will not form a horizon. Suppose now that thousands of needles not far from each other follow the same transformation during the same lapse of time (unity of time and space is a rule), then a new horizon will appear. This is only possible if synchronic events act upon organisms or chemical reactions.

At last, it has been hypothesized that humus forms have been selected, in the course of geological times, as ecosystem strategies by which plants, microbes and animals associated to form stable, mutualistic assemblages, taking advantage of different kinds of environments and living forms which appeared in the course of past Earth history (Ponge 2003). Although still conjectural, this theory adds another scale of change to our knowledge of humus and time, that of million years. Considering that MULL, MODER, MOR and now AMPHI are stable

attractors in a changing environment (Graefe & Beylich 2006), it ensures that changes in humus forms more abrupt than expected can be predicted to occur both in time and space. This might open new developments in “humus” science, providing enough data (along time sequences or environmental gradients) could be collected to test this hypothesis.

The following scheme summarizes in a symbolic manner the way by which all abovementioned influences can shape humus profiles in the course of time:



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