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Biology and Fertility of Soils

The porosphere as an ecological medium emphasized in Professor Ghilarov's work on soil animal adaptations*

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Summary. The author recalls that the late Professor Mercury S. Ghilarov, from the Institute of Animal Morphology and Ecology in Moscow, was a great pioneer in soil zoology and a far-sighted scientist in the evolution of terrestrial faunas. Professor Ghilarov agreed that during their evolution insects passed through the soil as a transitional medium from aquatic to terrestrial habitats. His theory, which is based on morphological and physiological observations, fits the thermodynamics of soil water the author describes when considering all porous bodies (porosphere), such as soil and other media, permitting a slow and gradual transition from an aquatic towards a xeric aerial system. In conclusion, a general concept of water accessibility for soil animals is formulated.

Key words: Porosphere – Animal adaptations – Water accessibility – Thermodynamics of pores

The late Professor Ghilarov was a great entomologist and an enthusiastic pedozoologist. He was also a far-sighted specialist who studied the evolution of terrestrial faunas. In the course of the VIIIth International Colloquium of Soil Zoology at Louvain-la-Neuve (Belgium), he reviewed the main physiological adaptations which have permitted soil invertebrates to become independent of aquatic conditions and to engage in the conquest of terrestrial environments (Ghilarov 1983). For more than 35 years Ghilarov (1949) advocated a theory on the evolution of insects through the soil as a special medium: *the soil consisting of three phases (solid, liquid and gaseous) has as an environment many peculiar properties. As the air in the soil is almost always saturated with water vapour, and films of water are present around solid particles, the conditions of existence in this medium are a character intermediate between aquatic and epigeion. So for many groups of terrestrial invertebrates the soil was a transitional medium in the course of their evolution from aquatic to terrestrial habitats* (Ghilarov 1959).

Professor Ghilarov based his arguments on the ecophysiological adaptations of soil animals, in particular of insects that were different from those of epigeion forms. These include a high integumental permeability in soil dwellers, skin respiration, in tracheate forms spiracles operating without a closing mechanism, relatively little resistance to cold, little sensitivity to increased CO_2 concentration, saprophagy like aquatic animals (detritophagy), and external insemination (spermatophores). According to Professor Ghilarov, this double nature of soil insects – the combination of properties common to aquatic dwellers and terrestrial forms – is due to remarkable properties of soil as a transitional medium.

Working on the behaviour of microarthropods (Acarina, Collembola) towards soil water (Vannier 1970), I began a study of the principal states of water in the soil. I concluded that soil, like other hygroscopic porous bodies, is a medium intermediate between the hydrosphere and atmosphere. This unique ecological milieu permitted the development of amphibious organisms, and I proposed that the term *porosphere* be used to describe this environment.

*Dedicated to the late Prof. Dr. M.S. Ghilarov

Professor Ghilarov considered soil as the only transitional medium that permitted the conquest of terrestrial biotopes by invertebrates. I extended this idea to all porous bodies having an internal surface which fulfills the same role; even before the formation of modern soils in the Cretaceous era with the first appearance of flowering plants (Angiosperms) I acknowledge that Professor Ghilarov's view based on ecophysiological considerations was of great help in formulating my own view on the evolution of terrestrial faunas through the soil and other solid formations that have in common peculiar properties towards water and respiratory gas.

The thermodynamic laws of water evaporation when applied to a moist soil sample during a funnel extraction (Tullgren type) of microarthropods permit us to describe the gradual succession of hydric states within the soil from a subaquatic system towards a xeric aerial system.

Material and methods

The study of the dynamics of water evaporation is conducted during soil animal extraction with the aid of an experimental model based on the dry funnel technique (Fig. 1). The principle of this model resides in measurement of water loss, using a recording balance, from rectangular slabs of soil (20 × 10 × 2.5 cm) placed in a climatically controlled chamber, and in the periodic collection at 2-h intervals of animals by an automatic fraction collector.

When surrounding conditions are fixed in the climate cabinet, the mode of action of the dry funnel technique is based on the repellent effects of desiccation and temperature. This method is commonly used by soil zoologists to separate arthropods, particularly Acarina and Collembola, from soil and organic material like humus (Vannier 1970).

Two types of analysis are made concurrently (Vannier 1970): (1) Thermodynamic analysis of the soil. The rate of water evaporation is recorded and the curve recorded indicates the liberation of the principal hydric categories in relation to the energy levels of water retention by solid soil particles. During the same time, temperature is measured with thin probes inside and outside the soil slab and connected to a potentiometric recorder. Air relative humidity is simultaneously deduced from wet and dry bulb temperatures. (2) Stochastic analysis of the procedure of microarthropod fallout: animals are collected at 2-h intervals. The probability that an individual animal leaves its environment is constant during the first period of extraction (casual fallout or natural displacement); then the probability increases abruptly; thus there is a critical point which determines the active or significant fallout during desiccation of the substrate.

Results

On the basis of the crude data curve produced by the apparatus, one can derive an initial diagram representing changes in water content of the soil as a function of time, but the value of this diagram is relatively limited. A more detailed picture of the desiccation process is obtained by following changes in the unidirectional evaporative flux as a function of change in the water content of the soil. It emerges, in fact, that the desiccation of a slab of soil is a polyphasic phenomenon in which three categories of water succeed one another: gravitational water, then capillary water, and finally hygroscopic water (Fig. 2).

The first phase characterizes soils that are soaked with water (Fig. 3). The evaporative flux (g) is

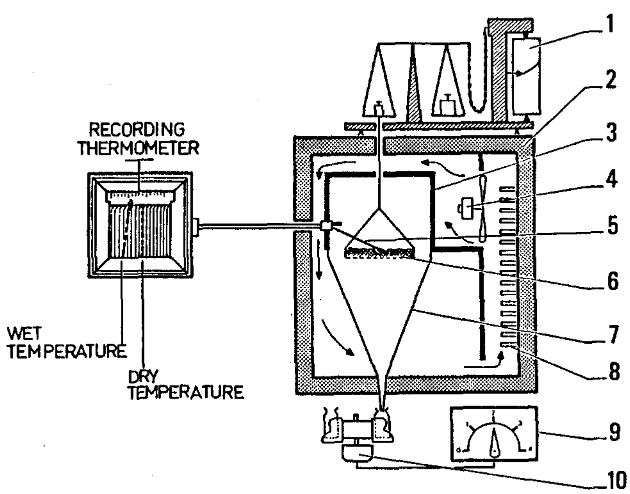

Fig. 1. Schematic diagram of an extraction apparatus for soil microarthropods. *1*, recording balance; *2*, climate chamber; *3*, wind shield; *4*, electric fan; *5*, thermal probe; *6*, sieve with a rectangular slab of soil (20 × 10 × 2.5 cm); *7*, funnel with steep slides; *8*, cooling system; *9*, timer; *10*, automatic fraction collector recovering microarthropod fallout at 2-h intervals

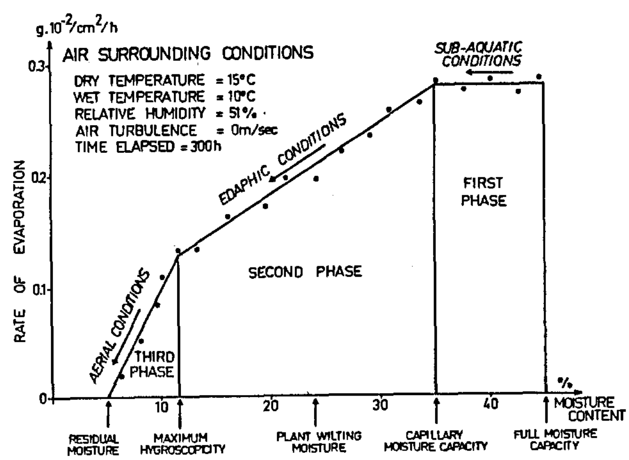

Fig. 2. Curve of unidirectional drying of a moist calcareous soil sample (size, 20 × 10 × 2.5 cm; wet weight, 700 g). The three phases of the evaporation process illustrate the notion of porosphere: the progressive passage from an aquatic system to an aerial system

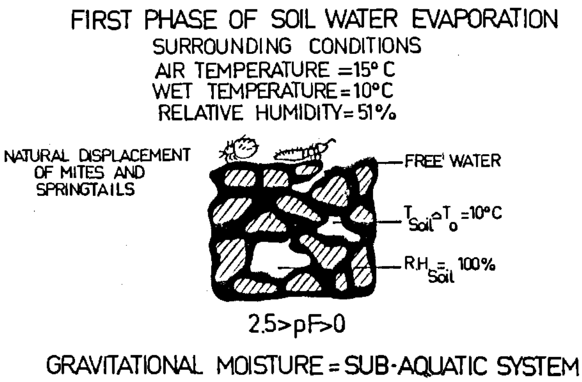

Fig. 3. Diagram of gravitational moisture in the soil framework

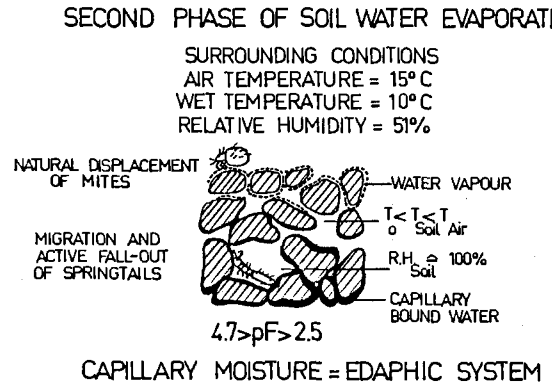

Fig. 4. Diagram of capillary moisture in the soil framework

constant, independent of the nature of the substrate. Elimination of water follows the same laws as those governing evaporation from a free water surface and the desiccation front is located at the surface of the soil sample. The liberation of water molecules is an endothermic phenomenon and the temperature of the substrate (T_{soil}) is constant, equalling the limiting cooling temperature (T_o), the value of which depends on the partial pressure of water vapour in the surrounding air. In other words, it depends upon the relative humidity (RH_{air}) and the ambient temperature (T_{air}). The relative humidity of air in the soil macropores, in contact with the evaporation front (limiting layer), is 100% or at least very close to the saturation point.

At the soil surface, as within open cavities, small animals are in an atmosphere saturated with water vapour. At this stage, the soil favours the development of aquatic and subaquatic species. Extraction of water requires energy to overcome the forces of superficial friction, intermolecular attraction forces, and so on. During the first phase, this energy expenditure is relatively limited. When expressed in the form of suction measured as the height of an equivalent column of water, it corresponds to a range from 1–346 g cm^{-2}, or from 0 to 2.5 in pF units.

The second phase coincides with the decrease in evaporative flux arising when the internal parts of the soil are no longer able to supply the surface with the quantity of water which can be vaporized by the ambient air (Fig. 4). The desiccation front penetrates the interior of the soil sample and, as a result of the decrease in the transfer surface, there is a marked decline in the rate of evaporation, which now shows a linear relationship with the humidity level. The motor forces involved in water transfer at this point are capillary forces for the liquid phase and diffusion forces for the gas phase. The retreat of the desiccation front makes way for a gaseous phase which subsequently occupies the soil interstices. But the internal atmosphere includes the limiting layer, where saturated vapour tension still prevails. The decrease in evaporation rate leads to progressive increase in the internal temperature of the porous mass, to such a degree that T_{soil} has a value between T_o and T_{air}.

The simultaneous presence of air saturated with water vapour and water in the liquid state within the soil creates a new ecological milieu which permits the development of amphibious organisms. Progressive transition to a fully edaphic mode of existence is made possible, requiring animals to develop adaptations to overcome forces binding water to the mineral particles of the soil. These forces are considerable and increase in an exponential fashion with reduction in the relative humidity level of the substrate. Once the capillary spaces have all yielded the water they contained, water retention forces have reached 50 kg cm^{-2} or pF 4.7.

The fallout of Collembola, mainly atracheate Isotomids, takes place irreversibily as soon as the permanent wilting point for plants (pF 4.2) has been reached in the soil sample. This critical threshold for Collembolans testifies to the force of retention (15.8 kg cm^{-2}) which is exerted by dry matter on capillary water and which the animals are eventually unable to overcome. The low resistance to drought in these Collembola is confirmed by ecophysiological tests measuring their high transpiration rate and integumental permeability (Vannier 1978).

The third phase is heralded by a second point of inflection of the desiccation diagram, reflecting a change in the rate of evaporation (Fig. 2). This situation coincides with the total disappearance of water in the liquid state within the soil sample (Fig. 5). Any water still present is in the form of vapour, and at this particular point the majority of the pores still have a relative humidity close to saturation (pF 4.7 is

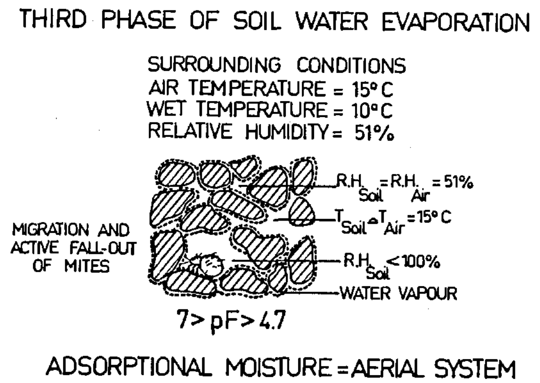

Fig. 5. Diagram of adsorptional moisture in the soil framework

also referred to as the point of maximal hygroscopy). After this point has been passed a saturation deficit is gradually developed in the interstitial atmosphere until the attainment of equilibrium with the ambient air ($RH_{\text{soil}} = RH_{\text{air}}$). Once the evaporation flux has ceased ($g = 0$), the internal temperature will have come to match that of the surrounding air and will subsequently follow its fluctuations closely.

Whilst this hygroscopic equilibrium is being established, the soil animals are forced to combat a severe loss of body water arising from evaporation through their integuments. At the same time, they must perform a considerable amount of work in order to extract the water molecules adsorbed on the linings of the soil cavities (see Vannier 1971). The limit of water availability for certain Acarina, e.g., Oribatid mites, is found in the region of pF 5, when the relative humidity of the air has fallen to 93% and a suction force of 100 kg cm^{-2} must be exerted by the animals to extract water from the substrate. Other Oribatid species are more resistant; their active fall-out appears at pF 6 corresponding to a binding force between water and soil of 1 ton cm^{-2} and a relative humidity of the air in microcavities of 43%. The strong tolerance of mites towards unsaturated air has been investigated by Madge (1964); his findings are in accordance with the slow reaction of these animals in our experiments.

The succession of hydric states described above shows that porous bodies such as the soil permit a slow, gradual transition from an aquatic system towards a xeric aerial system (Fig. 2). From the ecological point of view, the first phase of evaporation corresponds to a period in which aquatic forms can develop without risk. The second phase corresponds to a period of transition during which aerial and aquatic forms can coexist and which characterizes the conditions of life present in an edaphic system. Finally, the third phase is a period which reproduces the conditions of aerial life in which water in the liquid state is no longer available and in which animals must defend themselves against the evaporative power of the air (Fig. 2).

The results of my experiments in this area have allowed the formulation of a general concept of water accessibility for soil animals, just as botanists at the turn of the century had been led to the concept of water availability for plants: *Soil animals are only affected by progressive desiccation of their substrate beyond a critical level of humidity which is constant for each group of species. This critical level is an indicator of the retention forces which dry matter exerts on water and which animals are unable to oppose. As long as the critical threshold of humidity is not attained, individuals of any given species are able to use water to maintain their water balance* (Vannier 1979).

Discussion

The desiccation process described is characteristic of all hygroscopic materials and of bodies with fine or medium porosity (Krischer 1959). The soil is one member of the group of porous bodies which appeared at the interface between the lithosphere and the hydrosphere, and between the lithosphere and the atmosphere, as a result of the combined physical, chemical and biological mechanisms of erosion. For a physicist, porous bodies are solids with an internal surface which endows them with a remarkable set of hygroscopic properties. For example, a clay such as bentonite has an internal surface in excess of 800 m^2 g^{-1}, and a clay soil containing 72% montmorillonite possesses an internal surface equal to 579 m^2 g^{-1} (Fink et al. 1968). The capacity to condense gases on the free walls of capillary spaces (the phenomenon of adsorption) permits porous bodies to reconstitute water reserves from atmospheric water vapour. In my view, the porous state represents a specific state of matter occupying the same rank as the three other fundamental constituents of our planet (rock, or the lithosphere; water, or the hydrosphere; and air, or the atmosphere). I have proposed the term porosphere as a collective category for all solids with an internal surface (Vannier 1973).

Most orders of the animal kingdom contain representatives which have engaged in the contest for the free aerial environments, but these were only successful after long and slow adaptation in a biotope offering conditions intermediate between those of the hydrosphere and those of the atmosphere. "Terrestrial life is a perpetual conflict between the need for oxygen and the need for water, since the very conditions which favour the entry of oxygen into the organisms also favour water loss" (Maldague 1970). The same view was shared by Professor Ghilarov when he wrote "the soil dwelling permits air respiration with the minimal water loss" (Ghilarov 1959).

Professor Ghilarov's conclusions were more restrictive than mine. His demonstration was based mainly on the adaptative biological features of true soil inhabitants: the intermediate character of the soil as an environment may be proved by the presence in soil insects of many peculiarities characteristic of aquatic invertebrates (permeability of skin, poikilothermism, orientation along gradients of dissolved materials, etc. [Ghilarov 1956]). It works too for all types of porous bodies (porosphere) which can be considered as refuges for many primitives forms. My demonstration is based rather more on the peculiar thermodynamic properties of soil which are the same for all hygroscopic porous bodies. Our two demonstrations are thus complementary to another; therefore one can say the notion of porosphere is highlighted in Professor Ghilarov's work on soil animal adaptations; this idea was surmised 100 years ago, as Professor Ghilarov (1983) quoted in his paper delivered at the former Colloquium of soil zoology: "The great founder of modern soil science Dokoutchaeff (1883) characterized the soil as the "fourth natural body" in addition to the three discriminated by the father of systematics Linnaeus – mineral, plant, and animal".

In setting out the principal stages of the phylogenetic history of respiration (Vannier 1983), I indicated that it was the invertebrates which first undertook and achieved the conquest of aerial conditions at the beginning of the Palaezoic era. It is the invertebrates which today still provide the greatest number of living examples, usually soil-dwelling, the mode of life of which is halfway between aquatic and terrestrial living conditions. A lot of flying insects keep sheltering their larval or nymphal stages in the soil or other porous bodies.

The great transition that took place in the biosphere from the aquatic environment to terrestrial conditions preceded the formation of the soil with which we are nowadays familiar. A large number of these soils developed when the angiosperms made their appearance during the Tertiary era. The term "porosphere" designates the products of disintegration of crystalline or sedimentary rocks, such as muds, silts, volcanic powders, aeolian dusts and sands. These products greatly facilitated the establishment of the first chlorophyll-bearing plants on the surfaces of the continents well before the emergence of the invertebrates; later they were followed by the vertebrates. Aquatic vertebrates like crossopterygian fish or amphibians may have followed the same route as invertebrates, using marine muds and bogginess of the ground to protect themselves from strong water depletion before reaching terrestrial areas.

If the three primary constitutive elements of the Earth (rocks, water and the atmosphere) had exhibited abrupt contact interfaces without any zones of erosion, it would have been likely that faunas and floras would have evolved in directions rather different from those which we can discern around us today. Direct passage, without intermediate stages, from an aquatic environment to the atmosphere was probably achieved for the first time by the Gastropods, a very ancient zoological group. But the acquisition of a shell doubtless represents the most effective solution for living in the atmosphere while making use of the thermodynamic properties of porous bodies. As a general rule, we can assert that all the animal forms which now live in free air at some time or other had close links with the porosphere, either during phylogeny or during ontogeny.

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