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Aspects of the physical environment of soil organisms

D. E. Smiles

CSIRO, Division of Soils, G.P.O. Box 639, Canberra A.C.T. 2601, Australia

Summary. The physical properties of soil depend upon soil structure which is defined by the size, shape and arrangement of ultimate particles, aggregates of particles, and voids. Properties of the soil change as the amount of water occupying the voids varies, and also because of structural change associated with management and with biological activity. Traditionally, the physical behaviour of this system has been intensively studied in terms of macroscopically measurable properties considered to be "characteristic" of substantial volumes of soil, with the principal aim being the description, prediction, and management at the field scale. In comparison with this effort, study at the scale of the soil pore, or sequence of pores, has been modest. Yet this is the appropriate scale to use when describing the environment of many soil organisms. This paper re-examines basic issues relating to the physical environment affecting soil-borne organisms. It reappraises the relevance of "macroscopic" variables, in relation to experience and behaviour of organisms, comments on methods used to define them, and suggests that important physical variables must be defined at the scale of the particular organism. Within this framework, it is suggested that local "thermodynamic equilibrium" is generally the rule, so that the thermodynamic potential of an entity (such as water), and its measurement, may transcend scale. The distribution of water in soil at a defined water potential is, however, scale-dependent, and at the level of the pore can only be inferred from simple physical models applied to the local geometry of the soil surfaces. This issue is examined in some detail, because the amount and distribution of soil water is important not only in relation to water availability, but also because of the profound effect soil water content has on organism movement, soil strength, thermal properties of soil, and gas transfer.

Key words: Soil organisms – Physical environment – Thermodynamic equilibrium – Pedon – Pore space relationship – Soil moisture – Soil aeration – Mechanical soil properties – Water potential

Ecology is the study of the behaviour of organisms and populations of organisms as a result of interactions with their surroundings. The physical aspects of that environment and, in particular, the soil environment, present such a complicated situation that a practicable resolution to even a precisely defined ecological question may be impossible using scientific methods. One aspect of that complexity is exemplified by the interactions (and their biological consequences) between soil water content and soil suction, soil strength, soil thermal properties and soil ventilation.

Even if this complexity is so great that the ecology of soil organisms lies in "the republic of trans-science" of Weinberg (1972), it is still critically important to study basic processes and interactions in these soil systems, in order to inject rigour into the systems analysis that may be the only practicable alternative to deterministic models.

The following discussion of the physical environment of soil organisms is not definitive, and few of the questions posed are answered. The paper, however, is intended to alert soil biologists to some important soil physical issues that might permit better understanding of the behaviour of soil flora and fauna. Many texts in soil physics (Baver et al. 1972; Marshall and Holmes 1979; Hillel 1980a, b) contain systematic and general discussions of soil physical theory, while Griffin (1972) gives an ecologically oriented presentation.

The present paper introduces the subject as a study of the physics of a porous material, outlining the idea and the importance of soil morphology and structure. Then, because all physical behaviour of the soil is affected by the soil water content, the interaction between water and soil is examined. Finally, some consequences of this interaction are identified in terms of other important soil physical properties.

The paper tends to address the subject from a consideration of organisms within the range of sizes discussed by Vannier (1983), but reference is made to studies of root and seed behaviour because of the general insights these studies reveal.

The issues which emerge are illustrated using data from a soil of contrasting textures (Aeric albaqualf) at Ginninderra, Australian Capital Territory.

Soil morphology and basic definitions

Texts on soil physics are generally introduced by a discussion of the size and properties of the "ultimate" particles in soil. This approach tends to be misleading because of the implication that such knowledge, together with models for packing particles of various sizes and properties, may be used to develop, from first principles, a theory of soil physical behaviour.

In fact, the subject is better introduced as the study of the physical behaviour of relatively large volumes of a structured system comprising a comparatively stable matrix of solid material with individual particles ranging in size from a few nanometres to several millimetres. The particles in this system are clustered in aggregates, and the voids within and between the aggregates contain air and aqueous solution. The water content constantly changes, the total volume of the system may change, and the degree and type of aggregation may change with season and management.

In order to obtain a better understanding of the physical and mechanical environment of soil organisms, it is essential to establish and maintain an image of the real system with all its practical and conceptual difficulties. This does not mean, of course, that the behaviour of organisms cannot be rationally studied by using simple systems, but the ultimate challenge lies in an understanding of their behaviour in the field.

The simplest unit that encompasses the range of structure we must consider is the soil profile.

Soil profile or pedon

These terms are virtually synonymous. The profile is a vertical prism of soil extending from the surface to a depth beyond the influence of present plants or soil animals. It is composed of horizons which may be related genetically, and which are the result of soil-forming processes affected primarily by biological activity and the (predominantly vertical) movement of water. The "pedon" is a sampling unit, defined (U.S.D.A. Soil Survey Staff 1975) as the smallest area necessary to describe the nature, arrangement and local variability of a soil. In Soil Taxonomy (U.S.D.A. Soil Survey Staff 1975), the term "profile" does not appear. It is used here, however, because of its general familiarity.

Fig. 1. Aeric Albaqualf profile illustrating basic physical concepts. The profile contains about 10% clay minerals to a depth of ~0.25 m, where they increase to ~30%. Silt and fine sand decrease correspondingly. The boundary between A1 and A2 horizons appears as colour change at ~0.12 m

Figure 1 shows the soil profile at Ginninderra. Without going into great detail, this profile reveals a significant change in properties at a depth of about 0.25 m. In particular, there is a colour change, a change in the particle-size distribution and a change in the size, shape and arrangement of the soil aggregates and voids, i.e. a structural change. These changes affect the physical behaviour of the soil, and hence its exploration by soil organisms.

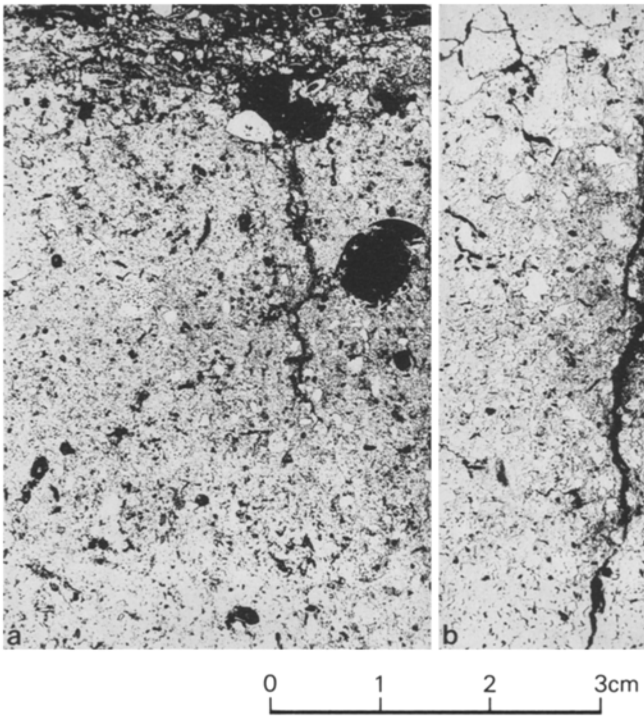

Fig. 2. Soil thin sections of **(a)** A1 horizon (0 – 60 mm), and **(b)** B2 horizon (0.35 – 0.41 m) of profile in Fig. 1, with sections processed (Chartres et al. 1985) so that voids show black. Note structural differences between A1 horizon, which is relatively porous with common, large, irregular-shaped vughs and channels, and B2 horizon, which is more dense and contains predominantly fissures, small vughs and a few channels

Pursuing this issue of variability, Fig. 2a and b show thin sections of the Ginninderra soil profile taken at depths of 0.1 and 0.65 m. These sections illustrate first, the great complexity of soil structure, particularly the arrangements of particles and voids, and second, a qualitative "difference" in structure within the same profile. Taken together, Figs. 1 and 2 indicate the variablity of soil within short distances and the importance of the scale of observation and description.

Bulk density

Because most solid soil constituents have densities of about 2.6 t m^{-3}, while that of the soil solution is very close to 1 t m^{-3}, the mass of a unit volume of soil is a useful gross measure of the amount of solid and liquid it contains. Since soil water content is ephemeral, it is more useful to express soil density as the mass of soil solid per unit volume of soil under field conditions and qualify the bulk density, ϱ, so defined, by the gravimetric water content, θ_g (mass of water per unit mass of soil solid). In general, soil bulk densities tend to lie in the range $1 < \varrho/\mathrm{t\,m^{-3}} < 1.7$, and there are various criteria for soil of different particle-size distributions which define ranges, or upper limits, of bulk density considered acceptable to various organisms. It is important to note that these criteria rarely identify exactly what physcial effect is responsible for the biological response, and that measurements of bulk density rarely give any functional or physiological insights relating biological behaviour to a physical cause. A simple example is provided by beds of uniform glass spheres of diameter 1 and 0.1 mm, respectively. Measurement of a volume of (say) 20 ml of each system will reveal much the same bulk density, but the "pore size" and associated properties will differ greatly (Dallavalle 1948; Griffin 1972).

Figure 3, gives the bulk density profile for the soil shown in Figs. 1 and 2, obtained from ~600-ml cylindrical cores of soil. There is a range of values representing local variability, and bulk density increases with depth from the soil surface, being associated with a decrease in organic matter and the activity of organisms, and an increase in soil self weight. Only in the subsoil do the average values of ϱ appear limiting, but again, the scale of measurement is critical, and at a depth of 0.65 m, soil aggregates have ϱ values as great as 2 t m^{-3}.

Pore-space relations

In general, the reciprocal of bulk density, the specific volume, is a more illuminating idea they is bulk density, particularly when it is shown in diagram relating the components of the specific volume to θ_g. Figure 4 shows this information for the given soil at depths of 0.1 and 0.65 m, indicating the relative amounts of solid, liquid, and gas at any value of θ_g.

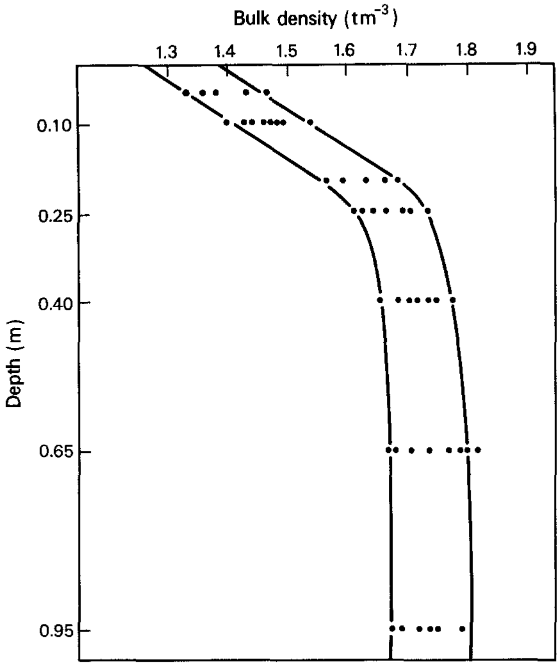

Fig. 3. Bulk density profile measured on 600-ml samples for soil shown in Fig. 1. Note low, but increasing, bulk density in A horizon associated with biological activity, organic matter and overburden and relatively constant density of subsoil. Note also range of values revealed by replication of measurement

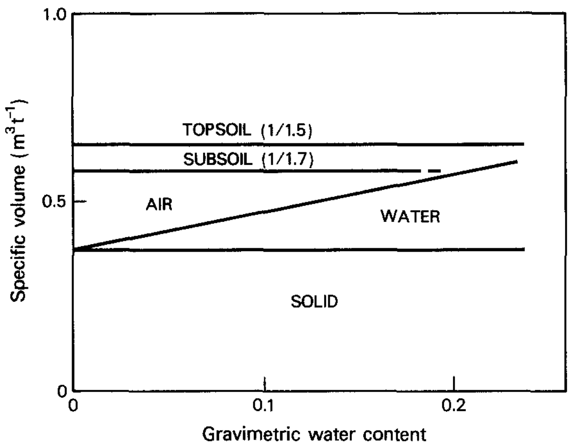

Fig. 4. Pore-space relations of the surface and subsoils shown in Fig. 1. Solid phase represented by labelled rectangle, the water by triangle above, and air-filled void space by top section. The (common) soil solid density is taken as 2.6 t m^{-3}

The specific volume of the coarse-textured surface soil is greater than that of the subsoil clay. The effect reveals the difference in structure between the two materials. However, these differences give no detail of the distribution of the components of the systems, nor do they reveal the distribution of pore sizes shown in Fig. 2a and b.

Volume of soil water

Finally, it is necessary to define θ, the volume of the soil water fraction; θ is related to θ_g and ϱ according to the equation:

$$\theta_g = \theta \varrho_w / \varrho \qquad (1)$$

where ϱ_w is the density of water. In non-swelling soils, θ is the most convenient method of describing water content.

The macroscopic approach

The remainder of this paper explores methods for describing, in an appropriate way, important aspects of the soil physical environment. The approach is basically macroscopic, despite the reservations set out above, but the degree to which macroscopic measurement transcends scale is discussed.

Problems of scale and heterogeneity

Soil physics theory has, in general, been developed assuming that soil may be regarded as a "continuum" with measurable, macroscopic, spatially averaged properties that encompass volumes containing many hundreds of particles and voids. Furthermore, these theories have been tested in effectively homogeneous systems. For these systems, useful predictions about equilibrium and movement of entities such as water, heat or gases are possible. The inhomogeneity revealed by Figs. 1 and 2, however, introduces problems that vitiate a simple application of macroscopic theory.

If, for example, "macroscopic" is defined as an average property measured with a sensory surface of area roughly equal to the area of soil shown in Fig. 2, then there will be problems of heterogeneity at both larger and smaller scales. At a larger scale (the profile, for example), there are systematic change with depth, and random variation as well in these macroscopic properties. A major preoccupation of soil physics is the study of these effects in the hope that, at the scale of the profile, or an agricultural management unit such as a field, reliable predictions can be made. Simplification is possible. For example, it might be possible to describe the gross hydrological behaviour of the Ginninderra soil in terms of average properties that characterize the two identifiable layers of different texture and structure. There would, however, be random variation in the properties of each layer, systematic variations with depth, and systematic and random variation across the field. Despite these difficulties, field behaviour can often be predicted using conventional soil physics theory. Webster (1979) has set out essential aspects of the problem.

If, however, it is a question of describing the environment of a nematode within the soil shown in Fig. 1, then the appropriate scale of measurement is probably that of the void that it occupies. Conventional macroscopic theory has nothing to say, for example, about water flow at this scale. Capillary tube models are available (Dallavalle 1948; Childs and Collis-George 1950; Polubarinova-Kochina 1962), but these models clearly represent gross simplifications of the structure revealed in Fig. 2. Furthermore, the flow within simple pore sequences, only slightly more complicated than that in a capillary tube, is very difficult to describe (Philip 1969a). Indeed, very little research has been directed towards the description or prediction of physical (or other) properties at this scale.

The problem of scale is therefore central to soil biological studies. Furthermore, it is not possible to infer quantitative behaviour at one scale from measurement at another. Philip (1974) examined difficulties with the integration problem (an attempt to predict "macroscopic" behaviour from "microscopic" information). The inference of microscopic detail from integral (macroscopic) information is still more difficult. It appears that the only safe strategy, therefore, is to take measurements at the scale of the organism. In practice, however, this is often very difficult, and Collis-George and Lloyd (1979) argued that there is theoretical, as well as practical, merit in a selective macroscopic measurement.

In thus seeking to explore the opportunities for general or specific applications of macroscopic measurement to soil organism behaviour, and the degree to which some properties transcend scale, this paper first considers the relations between water and soil.

Soil water

Theories of soil physics are generally formulated in terms of the laws of conservation of energy or matter. These equations formally account for the amount of the entity under consideration, by equating the rate of increase of that entity in unit volume (of soil) to the sum of fluxes into and out of the volume.

The flux equation relates the rate of flow per unit area (of soil) to a space gradient of "potential" of the entity. The "potential" may be a concentration or a thermodynamic potential. In either case, it is important that the fluxes and the forces be measurable at the appropriate scale.

This approach formally and systematically identifies the fundamental ecological issues. It is used here first, to establish the basic principles of the interaction of water with soils, and second, to explore various ecological issues.

Potential of soil water

Buckingham (1907) established the basis of soil water physics by introducing the concept of the potential of soil water. This developed from the observation that a vertical, saturated soil drains to produce a characteristic water content profile in static equilibrium with a free water surface at the base. Buckingham suggested that "capillary action" holds the remaining water against gravity, and that the attraction between the water and the soil increases with decreasing water content. He proposed that the forces of attraction are conservative, so that a scalar potential can be defined, which represents the work necessary to remove a unit amount of water from the soil, at water content θ, and at elevation z, to the free-water surface. The principle of virtual work implies that at static equilibrium, the potential of the water at all points in the column and in the free water is the same. Thus, taking the free-water surface as a datum (with elevation $z = 0$ and at atmospheric pressure), the potential, ϕ, of the water can be written as:

$$\phi(z) = \Psi(\theta) + Z = 0\,. \tag{2}$$

In this equation, $\Psi(\theta)$ is the water-content-dependent component of the potential, which arises through local interaction of the water and the soil solid surfaces and their geometry, and Z is the gravitational component. If potential is treated as energy per unit weight of water, then this definition is consistent with that of hydraulic head, H, with dimensions (L) and units m, so that Z becomes equal to z. It is possible, however, to use energy per unit mass, E, with units $\mathrm{J\,kg^{-1}}$ and dimensions $(L^2 T^{-2})$, or energy per unit volume of water, P, with dimensions of pressure $(M L^{-1} T^{-2})$. These issues are set out, for example, by Hillel (1980a). The different methods of expression are related according to the equation:

$$E = P/\varrho_{\mathrm{w}} = gH \tag{3}$$

where g is the acceleration due to gravity.

At equilibrium in the column discussed, because $\phi = 0$, $\Psi(\theta)$ is simply equal to minus the elevation of that point relative to the free-water surface at atmospheric pressure.

Soil moisture characteristics

The relation $\Psi(\theta)$ is called the soil moisture characteristic. It is readily measured, and for the Ginnin-

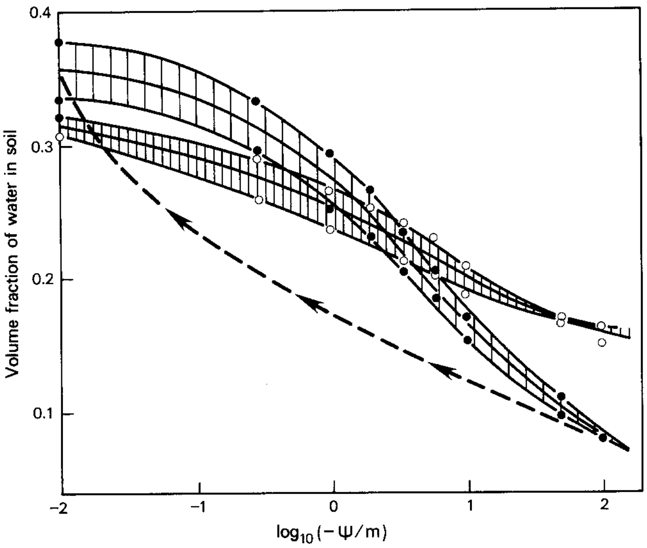

Fig. 5. Draining moisture-characteristic curves of 600-ml samples of soil from depths of 0.1 (●) and 0.65 m (○) of the Fig. 1 profile. At small negative potentials, topsoil is wetter than subsoil because of its greater porosity and "better developed" structure. At potentials more negative than about −2 m, subsoil is wetter because of its greater clay content. *Dashed line* represents a wetting, scanning curve of the surface sample and demonstrates the hysteresis phenomenon. Ψ represents energy that an organism must expend to retain water against the attraction of soil

derra soil it is shown by Fig. 5. For a salt-free soil, Ψ represents the energy that an organism (or any other mechanism) must expend to retain water against the attraction of the soil. An exception to this rule are organisms so small that they are totally immersed in the soil water and do not distort the air water meniscus in their vicinity. Evidently, the smaller the water content, the greater the stress experienced by the organism. The water potential is practically independent of the scale of measurement, and with some reservations for situations involving local disequilibrium during significant flow, it provides a precise definition of a physiologically important environmental property.

It is important to recognize that the moisture characteristic is strongly hysteretic, so the water content at a particular moisture potential during drying is always greater than that observed at the same potential during wetting. The effect is shown in Fig. 5. Any $\Psi(\theta)$ curve should therefore be qualified by information about the previous wetting and draining history of the soil. Much of the basic theory relating to hysteresis derives ultimately from the work of Haines (1930), but Poulovassilis (1962), Topp (1971), and Mualem and Miller (1979) have supplied recent discussions. Hysteresis also provides a biologist with quite subtle methods for experimentally controlling the environment of soil organisms, since, for a particular material, hysteresis permits the imposition of a range of values of θ for a given value of Ψ, and vice versa. As a result, discriminating experiments are possible, using these properties as independent variables.

So far, the discussion has been restricted to salt-free systems. For a soil in which there is a significant salt concentration in solution, there will be an additional component of the water potential, π, which represents the osmotic effect of these solutes. In fact, this effect is only manifest where there are semipermeable barriers that hinder salt movement with the water. In heavy clay soils, electrical double-layer exclusion of anions presents a partial barrier to salt flow, and the effect of π is observed in part. An air gap is effectively a perfect semipermeable membrane. All soil-borne organisms have membranes which, to a greater or lesser degree, are semipermeable, and therefore the total potential of the water must include an appropriately weighted osmotic component when biological responses are being considered.

Thus, in a non-swelling soil, the total potential of the water relative to a reference pool of (pure) water, at atmospheric pressure and elevation $z = 0$, is given by:

$$\theta = \Psi(\theta) - \pi + z \,. \tag{4}$$

The interpretation of Eq. (4), however, must be qualified by the degree to which π is manifest.

Finally, the soil water and its vapour are in equilibrium according to the thermodynamic equation:

$$H(z) = \exp[(\phi - z)g/RT] \tag{5}$$

where H is the relative humidity, g is the acceleration due to gravity (9.81 m s^{-2}), R is the gas constant (for water vapour $R = 461.5\ \mathrm{J\,kg^{-1}\,K^{-1}}$), and T is the absolute temperature (K). Thus, even where there is no contact with liquid water, the continuity of water vapour ensures that thermodynamic equilibrium will be approached at a rate determined by the geometry of the system, the water-vapour transfer properties, and the magnitude of local sinks and sources of water vapour.

In a system without local sinks or sources, equilibration may be quite rapid. For example, a spherical void of diameter 10 mm will reach effective equilibrium, in terms of vapour density, with an equipotential at its perimeter in time $t \sim 0.5$ s, assuming a water-vapour diffusion coefficient of 2.4×10^{-5} m^2 s^{-1} (Carslaw and Jaeger 1973). This "equilibration time" is proportional to the diffusion coefficient, and inversely proportional to the square of the radius (or a characteristic dimension) of the cavity. It is likely that for small organisms totally surrounded by soil, local water-potential equilibrium is generally the case.

Measurement of the soil moisture characteristics

The soil moisture characteristic is routinely determined using a number of complementary methods that have been well described (Black 1965; Rose 1966).

In general, these methods place a sample of soil (disturbed or in a core sampler) in contact with a system, the potential of which is controlled, until static equilibrium is established. The equilibrium water content is then recorded as a function of the imposed water potential.

At potentials in the range $0 > \Psi/\mathrm{m} > -150$, this control is conveniently achieved using tension-plate apparatus (for $0 > \Psi/\mathrm{m} > -7$) and the pressure membrane. In both cases, equilibration takes place through membranes that are relatively permeable (in a molecular sense), and the effect of dissolved salts is not observed.

For $\phi/\mathrm{m} < -100$, the vacuum-desiccator method is available. This method establishes a constant total potential by means of a constant relative humidity controlled by sulphuric acid solutions or saturated salts. The equilibration rate is increased by enclosing soil and solution in an evacuated desiccator. Water transfer to or from the soil takes place in vapour form, so that the method measures the osmotic as well as the matric component of the water potential. Equation (5) is used to relate the relative humidity to ϕ.

These methods are discussed in a mycological setting by Griffin (1972), who also cites other microbiological applications.

The measurement, as opposed to the imposition, of water potential is also well understood, with particular use being made of "null-point" tensiometers in relatively moist soils for $0 > \Psi/\mathrm{m} > -7$, and of psychrometric methods for $\phi/\mathrm{m} < -100$. In the important intermediate potential range, various in-situ methods have been used. These include tensionmeters with semipermeable membranes, containing high-molecular-weight osmotic solutions (Peck and Rabbidge 1969).

Finally, $\Psi(\theta)$ may be measured during flow, and methods for simultaneous and non-destructive measurement of θ and Ψ are available for use in the laboratory or the field (Marshall and Holmes 1979).

Implications of the moisture characteristic

The moisture characteristic also provides information on soil structure (Haines 1927), if $\Psi(\theta)$ is interpreted as a representation of the pore-size distribution of a soil. Haines proposed that each pore could be identified by a characteristic (neck) radius, r_n, and a larger (body) radius, r_b. He then considered filling and emptying of such a pore in terms of the equation:

$$P = 2\sigma/r \tag{6}$$

which relates the pressure drop (P) across an air water meniscus to the surface tension of water, σ, and its effective radius of curvature, r. Filling or emptying of a pore was said to occur when $r = r_b$ or $r = r_n$, respectively (Rose 1966). This approach permits us to infer, from the moisture characteristic, more detailed information on pore sizes and water distribution than is available from the pore-space relations of Fig. 3.

In brief, P of Eq. (6) is related to Ψ by applying Buckingham's arguments about the equilibrium water-content profile, to the rise of water in a capillarly tube of radius r. It then follows (Hillel 1980a) that:

$$\Psi = -2\sigma\cos\alpha/g\varrho_w r\,. \tag{7}$$

In Eq. (7) σ has units N m^{-1}, and α is the contact angle between water and the material of the capillary. When this material is wetted by water, $\alpha = 0$ and Eq. (7) becomes:

$$\Psi/\mathrm{m} = -1.5\times10^{-5}/r\,. \tag{8}$$

The moisture characteristic shown in Fig. 5 may therefore be regraphed with the potential axis converted, using Eq. (8), to a scale of effective pore radius; and hence be interpreted as a volume-based distribution of pore size. This graph is shown as Fig. 6. There are several implications of Figs. 5 and 6. First, because the curves represent drainage from $\Psi = 0$ to increasingly large negative values, it is clear from Eq. (8) that the pores and pore sequences of larger radius must empty before those of a smaller "controlling" radius. The reverse is true of wetting, when the small pores fill first.

It is instructive to apply these concepts to the thin sections of soil shown in Fig. 2a and b. The large vertical planar void in Fig. 2b, and the shorter void in Fig. 2a, are approximately 3 mm in width. They would, according to Eq. (8), be empty of water if $\Psi/\mathrm{m} < -1\times10^{-2}$ ($r = 1.5\times10^{-3}$ m), and therefore be filled with water for only a short time after rain. Even the fine, horizontal, planar void that is centre right in Fig. 2b, with a width ~0.1 mm, would be empty of water for $\Psi/\mathrm{m} < -7.5\times10^{-2}$, and hence air-filled at field capacity ($\Psi/\mathrm{m} \sim -2$).

From Fig. 5, it can be seen that in the early stages of drainage ($\Psi/\mathrm{m} > -0.3$) similar volumes of water are released from both topsoil and subsoil, and that the volume of pores of effective radius $r > 0.05$ mm in both samples is about the same. The subsequent, more rapid, drainage of the topsoil indicates a range of pore sizes in the topsoil which do not occur in the subsoil.

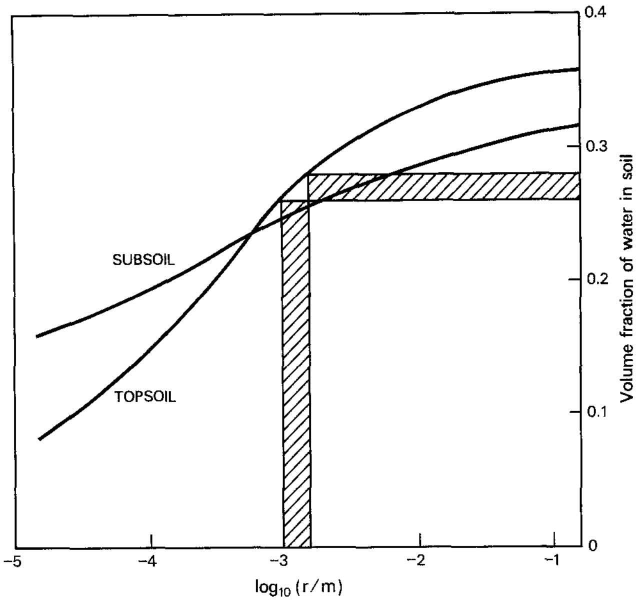

Fig. 6. Graph derived from Fig. 5 and Eq. (8) relating the volumetric water content to "effective" pore radius. Since θ can be interpreted as a fractional area or volume devoted to water in soil, this diagram can be taken as a pore-size distribution. From the hatched area it can be inferred that about 6% of water (at saturation) in the topsoil lies in pores in the range of radius $-3 \leqq \log(r/\mathrm{m}) \leqq -2.8$. Limits to this interpretation are identified in the text

Further, when the volumetric water content has decreased to $\theta = 0.2$, there can be no pores of radius greater than approximately 3×10^{-6} m and 1.5×10^{-6} m in the topsoil and subsoil, respectively, that are filled with water. This statement must be qualified, however. In the first instance, the argument based on Eq. (8) is probably valid only for $\Psi/\mathrm{m} \geqq -2$. At potentials more negative than this, absorption at surfaces is probably more important than "capillarity". In addition, pores will only drain if they retain effective liquid continuity with the water-potential datum. In a soil with a wide range of pore sizes, it is possible for pores to be isolated, in which case there will be local disequilibrium until film and vapour transfer re-establish equilibrium.

At this stage, it is important to recognize that a distribution of pore size can also be derived from micromorphological study of thin sections of the short shown in Fig. 2. It is thus possible to test two independent estimates of the same "property", a test that has been performed with mixed success (Bullock and Thomasson 1979). This outcome is not surprinsing, in view of the difficulties discussed earlier with regard to scale. Both methods, nevertheless, make valid estimates of the space available for movement by organisms, and the moisture characteristic, in particular, permits rational extension of the information contained in the pore-space relation shown by Fig. 4, in order to infer the way the liquid and gas components are distributed in the void space.

Finally, the moisture characteristic, interpreted as revealing a distribution of pore size, can be used to infer particular pore sequences. The theory is set out in detail by Childs and Collis-George (1950), but in essence the likelihood of a two-pore sequence involving pores of defined radius is calculated as twice the product $\delta\theta_1 \times \delta\theta_2$, where $\delta\theta$ is the volume fraction (and hence fractional surface areas) associated with a pore radius. The procedure has been used to calculate soil conductivity and the consequences of drainage on this property. It has also been used to predict the connectivity of air-filled pores, and the way aeration might be affected by changes in water content.

Both properties have important consequences, both for organisms totally confined to the soil water and for those larger organisms that are not restrained by the interfacial tension of the soil solution.

Soil water flow

Macroscopically, soil water flow is described by Darcy's law, which relates the volume flux, v, of water to a space gradient of the potential. For one-dimensional flow, Darcy's law is written:

$$v = -K(\theta)\,\partial\phi/\partial x \tag{9}$$

where x is the space coordinate and $K(\theta)$ is the water-content-dependent hydraulic conductivity. If ϕ is defined with units (m), then K takes dimensions $L\,T^{-1}$ with units m s^{-1} since v has units m s^{-1}. Note that v is not the velocity of the water, and the average pore-water velocity (V) is v/θ. As shown above, however, the wide range of pore sizes and shapes virtually precludes any clear statement about flow at the pore scale, although an order-of-magnitude calculation, using capillary tube models, may be possible (Childs and Collis-George 1950).

The combination of Darcy's law with the equation of continuity of water results in a non-linear flow equation, the solution of which has provided the basis for substantial industry in soil science over the past half century (Philip 1969b; American Society of Agricultural Engineers 1983). Again, it must be reiterated that the approach is macroscopic and permits no detailed information at a pore level.

In fact, soil fauna and the microbiota are unlikely to be materially affected physiologically by soil water flow as distinct from the soil water potential, since they do not, in general, represent significant sinks for water. In this respect, they will differ from plants, which may experience stress when the flux of water through the soil to the root is substantially less than the evaporative flux into the atmosphere. However, discussion by Currie (1972) and Collis-George and Melville (1975) indicates the importance of water transfer to swelling seeds.

Water movement may, however, affect the distribution of small organisms. Yavuz Corapcioglu and Haridas (1984) and to Roper (1982) have reviewed the effect of water movement on microorganisms in soil, and Wallace (1962) has discussed the mobility of nematodes in relation to water content and water movement.

Other physical issues

The general presentation of the present paper is weighted towards soil water, because the state, amount, and distribution of water in the soil effectively moderates all other physical properties. This section briefly explores other issues of potential significance to a soil organism, in particular, commenting on the consequences of water content.

Soil aeration

The soil atmosphere and its behaviour is not as well understood in detail as are the properties of the liquid phase.

The problem arises, in part, because it is difficult to measure accurate point concentrations and fluxes of gases in the soil. This difficulty is carried over to the biological problems of transfer of water vapour, O_2, and CO_2 to and from organisms.

Keen (1931) appears to be the first to have systematically reviewed the possible processes contributing to soil aeration. He demonstrated that gaseous diffusion can probably account for the rates of transfer of O_2 and CO_2 observed in some field situations. This work appears to have been interpreted to mean that the mass flow of gases arising from barometric pressure change, mass flow of water, or atmospheric turbulence is unimportant. More recently (Fukuda 1955; Farrell et al. 1966; Scotter and Raats 1968, 1969), the effect of periodic pressure changes at the soil surface on gaseous transfer has been examined. It is concluded that within the top 0.1 m of the soil, oscillatory pressure changes may produce considerable transfers of gas. Kimball and Lemon (1971) confirm these conclusions, although they evidently believe that in field soils the effect is two orders of magnitude less than that of molecular diffusion.

If it is assumed that the transfer process is essentially one of diffusion, the flux density ($\mathrm{kg\,m^{-2}\,s^{-1}}$) of the gas may be written as:

$$\bar{v}_g = -D^* \operatorname{grad} \varrho_a \qquad (10)$$

where ϱ_a is the density and D^* the effective diffusion coefficient of the gas in the soil.

D^* depends on the air-filled porosity, ε, of the soil, on the geometry of the system, η, and on D_0, the diffusion coefficient of the gas in air.

This dependency is often written $D^* = \eta \varepsilon D_0$. In many situations, $\eta = 2/3$. A full discussion has been presented by Currie (1970).

The transfer of gas in the soil water can generally be neglected, since the diffusion coefficient in that medium is about four orders of magnitude less than that in air.

The gas laws permit the flux equation to be recast in terms of partial pressure gradients. Then, by considering ϱ_a as a function of both the temperature, T, and the pressure, the consequences of variation in the gradients of each of these factors may be explored.

Substitution of the flux equation into the appropriate continuity equation, which may contain source and sink terms, gives a transient flow equation. Solutions to this equation have been examined by Kirkham and Powers (1972), while Vannier (1983) has reviewed aspects of the chemistry of interaction of O_2 and C in the liquid and gaseous phase in soils, and their biological consequences.

As Kirkham and Powers point out, there is still considerable difficulty in defining the effective diffusivity and also problems with the measurement of gas concentrations. In the case of O_2, which is biologically the most important gas, the use of the platinum-electrode technique promises some hope, although early claims for the bare electrode have not been substantiated. In particular, the measurement of the flux of O_2 to the bare electrode, as an indication of the availability of O_2 in the soil, has been shown to depend on many properties of the soil and on the electrode geometry; McIntyre (1970) has made a full examination of the bare platinum electrode method. In contrast, the membrane-covered electrode does provide a reasonably reliable measurement of O_2 concentration.

Despite these difficulties, the problems of predicting fluxes and concentrations in inert materials with well-defined boundary conditions are not great. Major difficulties arise, however, in describing the geometry of biologically important situations, and the conditions that exist in the immediate environment of a respiring soil organism (Griffin 1972).

Thermal properties of soils

Sensible heat is transferred in soil principally by conduction. This forms a basis of the discussions by Keen

(1931), van Wijk (1963), Rose (1966) and Kirkham and Powers (1972), who rely heavily on heat-conduction theory enunciated, for example, by Carslaw and Jaeger (1973).

The flux of heat $\bar{v}_h$ by conduction is described in a manner analogous of those of water and gas by the equation:

$$\bar{v}_h = -\lambda \operatorname{grad} T \tag{11}$$

where T is temperature and λ thermal conductivity; λ may vary with position, but with a good approximation in field soils, is independent of the temperature.

λ varies principally with the particle-size distribution of a soil, the water content θ, the bulk density ϱ, and the organic-matter content in organic soils. In general, the thermal conductivity is proportional to both water content and bulk density, because an increase in either of these properties will increase the effective interparticle thermal contact within the soil. Typical relations between λ and θ for different soils are given by van Wijk (1963).

In the absence of sources or sinks for heat, the continuity equation, in terms of temperature, is written:

$$C\frac{\partial T}{\partial t} = -\operatorname{div} \bar{v} \tag{12}$$

in which C, the thermal capacity per unit volume of the soil, is also an increasing function of the water content, θ, and of the bulk density, ϱ.

For one-dimensional flow in a uniform soil, Eq. (12) becomes:

$$\frac{\partial T}{\partial t} = \frac{\lambda}{C}\,\frac{\partial^2 T}{\partial x}\,. \tag{13}$$

Since both λ and C are functions of θ, so also is λ/C (van Wijk 1963).

Any consideration of heat flow in soils has consisted largely of investigations into solutions to this equation, or to its cylindrical or spherical forms, when subject to appropriate boundary conditions.

The varying temperature regime within the soil arises as a consequence of soil surface temperature variations. The basic pattern of these variations is imposed by insolation, and the way in which the net radiation, R_n, at the soil surface is partitioned. The simplest energy-balance equation takes the form:

$$R_n = LE + G + H \tag{14}$$

where E is the evaporation rate of water from the surface, L is the latent heat of evaporation at the soil surface temperature, G is the flux of heat away from the surface into the soil, and H represents the energy loss from the surface in convective exchange with the air. Detailed discussions of the surface energy balance of (bare) soils have been presented by van Wijk (1963), Geiger (1965), and Rose (1966). Well-documented reviews of the problem for vegetated surfaces have been presented by Lemon (1963) and Denmead (1969).

The variation in the surface energy-balance equation over 24 h tends to induce a sinusoidal surface temperature and an attenuated wave that penetrates the soil with a wavelength of the order 0.4 m and a decay to 1% of its surface amplitude at about 0.3 m (when $\lambda/C = 1 \times 10^{-7}\ \mathrm{m^2\,s^{-1}}$). In general, local disequilibrium in temperature is unlikely at the pore scale, so temperature is a well-defined environmental property of soil organisms.

The annual variation is detectable at a depth about 19 times greater, since the "depth of penetration" is proportional to the square root of the period of the wave.

Soil mechanical properties

The effects of soil mechanical properties on the behaviour of soil organisms are ill-defined, although there is a substantial literature on plant root systems and germinating seeds (Barley and Greacen 1967; Collis-George and Williams 1968; Collis-George and Yoganathan 1985a, b; Scott Russell 1977).

The problems are related to scale, and to the need to understand the way the organism interacts mechanically with the soil. For example, to refer briefly to issues raised by the penetration of soil by roots (Barley and Greacen 1967; Greacen et al. 1968), three possible "simple" forms of soil deformation, which might be produced by plants were identified. But more careful analysis (Richards and Greacen 1986) showed that root penetration is a more complicated process, combining knowledge of soil compressibility with that of the mechanics of plant growth. The resultant model is energetically reasonable, both physiologically and in terms of soil mechanics, and it provides a basis for a soil test of mechanical properties appropriate to root penetration. Dexter (1978) used a similar approach to define aspects of earthworm tunnelling, while Lee (1985) presented a summary assembling both mechanical and physiological information on that process. It is interesting that for both root and earthworm penetration of soil, radial expansion of the organism behind the tip/prostomium compresses the soil in its weakest mode, and simultaneously creates axial weakening of the soil ahead of the organism.

Many invertebrates, besides earthworms, may after soil structure substantially. The means they use vary, however, and are often far from clear. Ants and termites, for example, lack the ability to enlarge a cavity by clindrical compression, and presumably act by prising material away, particle by particle. Yet many stages of the Arthropoda are large enough to substantially affect the soil, and some economically important groups are known to be generally soil-condition-specific in their activities (Clark 1974).

Finally, in this section it is important to note that the strength of the soil and the adhesion between particles is both water-content and water-potential dependent (Marshall and Holmes 1979), and soil generally becomes stronger as it dries. At the same time, the ability of an organism, such as the earthworm, to penetrate soil will diminish with increasingly negative water potential, because its turgidity (Lee 1985) (and, by implication, ability to do mechanical work) diminishes with the water potential. The effects of changes in water potential and water content on ants and termites will differ, but certainly the process of tunnelling will become mechanically more difficult with increasing soil desiccation. The effect of water content on ventilation and the energy available to do work will complicate the issue (Barley and Greacen 1967).

Concluding remarks

It is not the purpose of this paper to provide information about the response of soil organisms to their physical environment. Much of that information is available in the literature, although much of it is subject to uncertainty. The intention is rather to describe the physical issues that should be of importance if that environment is to be defined with precision.

The first point made is that the physical behaviour of soil is a fundamental consequence of its structure and water content. Structure in a gross sense varies systematically in space, while water content varies locally, in time.

Within this framework, the precise definition of the environment is complicated, because of the uncertainty about the space and the scale of discourse, appropriate to a particular organism. The difficulty arises because conventional soil physics theory is based in a "continuum" approach with variables averaged by measurement over many hundreds of soil particles and voids. This theory has little to say about physical detail at the scale of a soil pore. Furthermore, present effort is mainly committed to applying theory in the large taking account of field scale and variability, rather than on the smaller scale.

Nevertheless, it is probably appropriate to assume that the "intensity" measures of water potential, temperature and gas partial pressure transcend scale, and expect for cases of local disequilibria, macroscopic measurement of these variables appropriately defines the microenvironment.

The issue is complicated, however, because of the importance of water content on all physical processes, and because the distribution of water, at the microscale, may critically affect the biology without being describable except in an average sense.

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