Organic matter and water-stable aggregates in soils

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Summary

The water-stability of aggregates in many soils is shown to depend on organic materials. The organic binding agents have been classified into (a) *transient,* mainly polysaccharides, (b), *temporary,* roots and fungal hyphae, and (c) *persistent,* resistant aromatic components associated with polyvalent metal cations, and strongly sorbed polymers. The effectiveness of various binding agents at different stages in the structural organization of aggregates is described and forms the basis of a model which illustrates the architecture of an aggregate. Roots and hyphae stabilize macro-aggregates, defined as > 250 μm diameter; consequently, macroaggregation is controlled by soil management (i.e. crop rotations), as management influences the growth of plant roots, and the oxidation of organic carbon. The water-stability of micro-aggregates depends on the persistent organic binding agents and appears to be a characteristic of the soil, independent of management.

Introduction

Good structure for crop growth depends on the presence of aggregates of soil particles 1 to 10 mm diameter which remain stable when wetted. Such water-stable aggregates should be porous (pores > 75 μm diameter) so that they remain aerobic, and yet possess sufficient numbers of pores 30–0.2 μm diameter to retain water for the growth of plants. The pores between the aggregates should be large enough to allow rapid infiltration and drainage.

When an unstable air-dried aggregate is wetted rapidly it slakes into smaller sub-units which may also be aggregates (Emerson, 1977). Slaking is common and occurs in a wide range of soils where the aggregates are not strong enough to withstand the pressures of entrapped air in capillaries or the pressures due to swelling. In the field, slaking of aggregates occurs mainly in surface layers since those below the surface are protected from air-drying and from rapid wetting. Severe slaking with little or no dispersion is serious, particularly where soils are irrigated, because the slaked layers limit infiltration of water and emergence of seedlings.

The sub-units or small aggregates produced by slaking may also be unstable so that individual clay particles may disperse. Spontaneous dispersion occurs if the clay swells to such an extent that the attractive forces between the particles are no longer

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strong enough to hold them together (Emerson, 1977). The particles of clay are released slowly and appear as a spreading cloud around the aggregate (Arnold, 1978). In the field the dispersed clay may block pores which transmit or store water, and slaking and dispersion together produce undesirable structures such as surface crusts. Swelling and dispersion are largely a function of the exchangeable ions associated with the clay, e.g. sodium and magnesium, and electrolyte concentration. However, other materials which influence the surface properties of clay minerals may favour flocculation or dispersion. There is some evidence that organic anions promote dispersion, by blocking positive sites on colloid surfaces, and by complexing polyvalent cations in solution (Bloomfield, 1963; Gillman, 1974). On the other hand, organic polymers may promote flocculation (Greenland, 1965),

While flocculation and dispersion appear to be largely electrostatic phenomena, the stabilizing of larger aggregates involves cementing or binding agents which may be inorganic, organo-mineral associations or organic.

Clay may bind particles into aggregates, but aggregates bound by aluminosilicates only are unlikely to maintain their integrity when wetted. Hydrous oxides of aluminium and iron cement particles together in water-stable aggregates with diameters greater than 100 μm, especially in soils which contain more than 10 per cent sesquioxides. The full extent of cementation by oxides is evident in bauxite and ferricrete (Kroth and Page, 1946; Chesters *et al.*, 1957; Kuznetsova, 1966; Krishna Murti *et al.*,1977). Highly disordered aluminosilicates and calcium carbonate also act as cementing agents. In spite of the generally stable aggregation of calcareous soils, the mechanisms of binding have not been defined. The influence of calcium carbonate may be due, in part, to the concentration of calcium ions in the soil solution which limits dispersion and swelling of the clay (Rimmer and Greenland, 1976).

Organo-mineral associations function as binding agents in aggregates, particularly those less than 250 μm diameter (Edwards and Bremner, 1967; Hamblin, 1977; Turchenek and Oades, 1978).

The inorganic binding agents may be regarded as permanent cements and if they are dominant, the presence of organic glues may be of little extra benefit. Regular cultivation may reduce the content of organic matter and the chemical fertility with little influence on the physical properties of such soils. However, in the surface layers of many agricultural soils, it appears that organic matter plays a major role in binding aggregates to withstand stresses caused by rapid wetting.

Relation of water-stable aggregates to organic carbon content

There have been numerous correlations between the content of organic carbon in soils and water-stable aggregation and some of these are shown in Table 1. The correlations have not always been good for any one or all of the following reasons: (a) only part of the organic matter is responsible for water-stable aggregation, (b) there is a content of organic carbon above which there is no further increase in water-stable aggregation, (c) organic materials are not the major binding agents, (d) it is the disposition rather than the type or amount of organic matter which is important, and (e) some of the water stability in virgin soils is related to physical factors such that the particle reorganization associated with the first disturbance of virgin soil reduces water stability (Heinonen, 1955; Malik *et al.*, 1965, Greenland, 1971*b;* Low, 1972; Tisdall and Oades, 1980*b*). The stability is sometimes related better to free

Table 1
Organic matter and aggregate stability

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46 silt loams (Strickling 1950)
Aggregate stability = 16.9 (org. matter)− 13, $r = 0.87$

519 North American soils (Kemper and Koch, 1966)
Aggregate stability = 40.8 + 17.6 log (org. C)+ 0.73 clay − 0.0045 (clay)^2 + 3.2 Fe_2O_3

189 British soils (Williams 1970)
% water slaking = 2.47 + 0.47 coarse particles (6−0.02 mm)−5.95 (org. C)

28 hard-setting red-brown earths (Grierson 1975)
Aggregate stability = 0.82 + 2.13 (org. C)−(0.6 ESP + 0.3 EMgP)

9 red-brown earths (Tisdall and Oades 1980*b*)
Aggregate stability = 21.5 (org. C)−20.3, $r^2 = 0.93$.

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organic materials than to total organic carbon because this fraction acts as a substrate for microbial production of organic glues (Oades, 1967), and/or because this fraction is a measure of roots and hyphae.

The management of a soil can change the content of organic matter by a factor of two or three and there are sufficient data to show that this change can occur under different climates (Table 2).

Decrease in organic matter

Cultivation is exploitive and causes a decline in the content of organic matter. This decline is aggravated if fallow is included in the rotation where the soil is cultivated to ensure no plant growth, or where crop residues are removed (Ramig and Mazurak, 1964; Ridley and Hedlin, 1968; Emmond, 1971; Martel and Paul, 1974; Juo and Lal, 1977). Where soil is cultivated frequently, aggregates are exposed frequently to physical disruption by rapid wetting and raindrop impact as well as to shearing by implements. The net effect is to expose inaccessible organic matter to micro-organisms and to stimulate oxidation and loss of organic matter (Low, 1954; Rovira and Greacen, 1957; Clement and Williams, 1958; McCalla, 1959; Martel and Paul, 1974; Adu and Oades, 1978). This decline in organic matter is usually accompanied by a decrease in the number of water-stable aggregates.

Increase in organic matter

Organic matter may accumulate under good pastures because the annual addition of phytomass is greater than under crops, e.g. cereals. As well as adding organic residues to soils, growing plants appear to retard the decomposition of organic matter in soils (Führ and Sauerbeck, 1968; Jenkinson, 1977). The number of water-stable aggregates increases under good grass pastures. Because the increase in stable aggregation under pastures is related to the length of root and of vesicular-arbuscular (VA) mycorrhizal hyphae (Barley, 1953; Clement, 1961; Tisdall and Oades, 1980*b*) and because organic residues accumulate at the surface, most of the aggregation is in the top layers of soil (Clement and Williams, 1958).

Table 2

Management and contents or organic matter in soils

Soil	Treatment	% organic matter	Reference
Silt loam	Continuous blue grass	3.36	Johnston *et al.* (1942)
Iowa	Corn oats–clover rotation	3.46	
	Continuous corn	2.86	
Silt loam	Continuous blue grass	3.35	Strickling (1950)
Ohio	Corn–ryegrass rotation	2.17	
	Corn–soybean rotation	1.75	
Rothamsted	Ley 7 years	3.4*	Clement and Williams (1964)
	Arable 7 years	2.2*	
Sod-podzolic	Virgin soil	2.21	Kononova (1966)
Timiryazev	Continuous rye 48 years	1.55	
Chernozem	Virgin soil	4.33	Kononova (1966)
Lenin State	Old arable	4.00	
Silt soil	Grassland 100 years	7.58*	Low (1972)
Lincolnshire	Arable 25 years	2.16*	
Alfisol	Non-tilled	4.52*	Lal (1974)
Nigeria	Tilled	3.38*	
Red-brown earth	Pasture 30 years	5.30*	Turchenek & Oades (1979)
Australia	Wheat fallow rotation	2.08*	
Alfisol	Cover crop	3.14*	Lal *et al.* (1979)
Nigeria	Weed fallow	2.74*	

* Obtained from 2 × % organic carbon.

Aggregate organization

Introduction

There is sufficient information available to indicate that water-stable aggregates with diameters of a few millimetres are not simply a random arrangement of the various particles responsible for the texture of the soil. A prerequisite for water-stable aggregation is flocculation of clay particles—the first stage in the construction of a stable macroaggregate.

Emerson (1959, 1977) suggested that parallel clay crystals (about 5 μm diameter) are grouped together closely enough (about 0.1–1.3 μm apart) to behave in water as a unit called a *domain*. His model, which is not drawn to scale, shows that organic matter stabilizes the aggregate mainly by forming and strengthening bonds between

domains and between quartz particles and domains, though the quartz particles may also be linked directly by organic matter.

Quirk and Aylmore (1971) used the term *quasi-crystals* to describe the regions of parallel alignment of individual lamellae of aluminosilicates in montmorillonite, which exhibit intra-crystalline swelling; they used the term *domain* to describe the regions of parallel alignment of crystals for illite and other clays with fixed lattices, which exhibit inter-crystalline swelling only.

Several models have been proposed to describe the way in which individual mineral particles are held together to form water-stable aggregates of soil. Misuno and Sudo (1958) and Sudo (1962) suggested that particles < 20 μm diameter are bound into water-stable secondary particles 20–60 μm diameter, and that these secondary particles in turn form larger soil aggregates.

Edwards and Bremner (1967) suggested that macroaggregates (> 250 μm diameter) consist of complexes of clay–polyvalent metal–organic matter (C–P–OM) where clay is bonded to humified organic matter through polyvalent metals. Particles of C–P–OM and (C–P–OM)$_x$, both of which are < 2 μm diameter, form micro-aggregates ((C–P–OM)$_x$)$_y$ which are < 250 μm diameter. Bonds of C–P–C and OM–P–OM, and even of aluminium or iron oxide, or H-bonds may occur also. Edwards and Bremner (1967) suggested also that fragments of humified organic matter may be bonded to a single clay particle, and that a single fragment of humified organic matter may be bonded to more than one clay particle.

The interactions between organic polymers and mineral surfaces are complex but the mechanisms are known and have been reviewed by Greenland (1965, 1971a), Mortland (1970) and Theng (1979). The most important mechanism of interaction probably involves bridges of polyvalent cations between the surface of the clay particles or hydroxy polymers and the ligand groups of organic polymers, e.g. carboxyl groups.

Organization of an aggregate from a red-brown earth

The model which we propose is based mainly on information available for red-brown earths and which is taken from the following papers: Burford *et al.* (1964), Turchenek and Oades (1978), Fordham and Norrish (1979), Tisdall and Oades (1979), Tisdall (1980), and Tisdall and Oades (1980b).

In this model there are four stages of aggregation:

$$< 0.2\ \mu m \longrightarrow 0.02\text{--}2\ \mu m \longrightarrow 2\text{--}20\ \mu m \longrightarrow 20\text{--}250\ \mu m \longrightarrow\ > 2000\ \mu m$$

The model may apply generally to soils where organic matter is the main binding agent, but the levels of aggregation may differ. For example, in a black earth, aggregates 1000–2000 μm diameter slaked directly to water-stable particles of about 30 μm diameter (Collis-George and Lal, 1970).

Each stage of aggregation in a red-brown earth is considered in turn.

Aggregates > 2000 μm diameter

In red-brown earths with high contents (> 2 per cent) or organic carbon, water-stable aggregates > 2000 μm diameter consist of aggregates and particles held together mainly by a fine network of roots and hyphae, and in soils which contain low contents (< 1 per cent) of organic carbon, by transient binding agents only. Because

the stability of particles > 2000 μm diameter is related to the growth of roots and hyphae, the stability is controlled by agricultural practices.

Inorganic binding agents including highly disordered aluminosilicates and crystalline iron oxides also stabilize aggregates > 2000 μm diameter but to a lesser extent than organic materials. A cross-section of a water-stable particle > 2000 μm diameter impregnated with white Araldite (Ciba-Geigy, Australia) shows that the particle is porous (Fig. 1a), and consists mainly of particles of about 20–250 μm diameter (Fig. 1b).

Aggregates 20–250 μm diameter

Aggregates 20–250 μm are stable to rapid wetting and are not destroyed by agricultural practices; even in an old arable soil, more than 70 per cent of water-stable particles were 20–250 μm diameter. However, aggregates 20–250 μm diameter can be destroyed by ultrasonic vibration. Aggregates 20–250 μg diameter consist largely of particles 2–20 μm diameter bonded together by various cements including persistent organic materials and crystalline oxides and highly disordered aluminosilicates. The aggregates 20–250 μm diameter are very stable partly because they are small, but also because they contain several types of binding agents whose

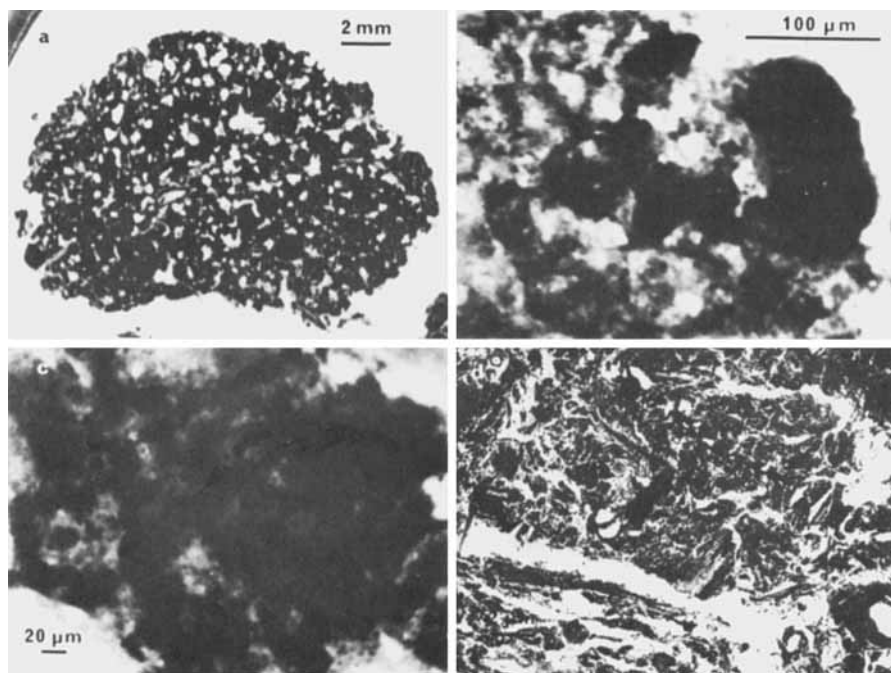
Fig. 1. (a) A cross-section of a water-stable particle > 2000 μm diameter from a red-brown earth, impregnated with white Araldite. (b) & (c) Enlargements of (a). (d) Transmission electron micrograph of an an ultra-thin section of rhizosphere soil. (Micrograph courtesy of Dr R. C. Foster, CSIRO, Division of Soils, Adelaide, South Australia.)

effects are additive. The individual organic bonds must be strong because particles 20–250 μm diameter contained less than one-half as much organic carbon as the much less stable particles > 250 μm diameter. It is not easy to define the site or size of the organic materials within stable particles 20–250 μm diameter because the clay is associated intimately with the organic material. A cross-section (Fig. 1c) and a scanning electron micrograph (Fig. 2) of a water-stable aggregate 20–250 μm diameter show that the aggregate consists dominantly of particles of about 2–20 μm diameter. Particles 20–250 μm diameter would be included in the stable micro-aggregates $((C–P–OM)_x)_y$ described by Edwards and Bremner (1967).

Aggregates 2–20 μm diameter

Water-stable aggregates 2–20 μm diameter consists of particles < 2 μm diameter bonded together so strongly by persistent organic bonds that they are not disrupted by
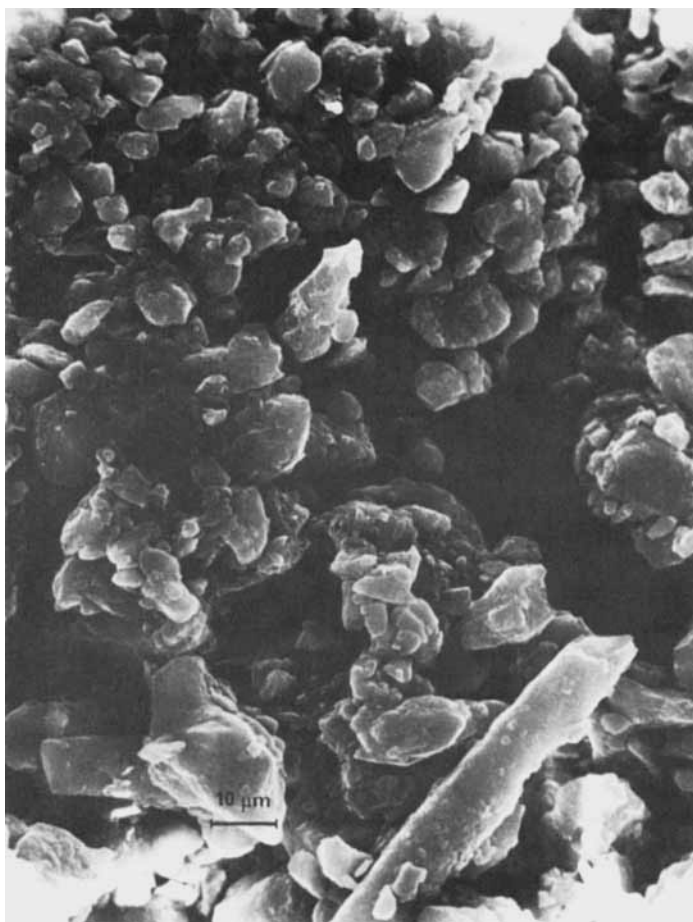

Fig. 2. Scanning electron micrograph of part of a water-stable aggregate 50–250 μm diameter, from the FW rotation of Urrbrae fine sandy loam.

agricultural practices; some particles 2–20 μm diameter from under old pasture resist ultrasonic vibration for 5 min. Particles 2–20 μm diameter, obtained by ultrasonic dispersion or trituration from soils with high contents of clay and high base status, often have high contents of organic materials (Oades and Ladd, 1977; Turchenek and Oades, 1978). This organic-rich fraction (2–20 μm diameter) is often highly water-stable especially in chernozemic soils and in soils under old pasture (Pokotilo, 1967; Turchenek and Oades, 1978).

A transmission electron micrograph of rhizosphere soil shows a water-stable particle 2–20 μm which consists of particles < 2 μm diameter (Fig. 1d) bound closely together. Fordham and Norrish (1979) also described particles which were bound together by strands of glutinous material, probably organic, to this level of aggregation. However, some particles 2–20 μm diameter are probably simply large floccules (see below).

Development of stable particles 2–20 μm diameter

Electron micrographs of soils or thin sections of soils in the rhizosphere show individual bacteria or colonies of bacteria surrounded by a capsule, composed of carbohydrate, to which particles of fine clay appear firmly attached. The clay particles, which may enclose the bacteria completely, are sometimes oriented tangentially to the bacterial surface to a distance of 0.1 μm from the bacterial surface (Marshall, 1976). The fact that such associations between live bacterial cells and clay particles appear to form aggregates 2–20 μm diameter is supported by the results of Hattori (1973), Ladd et al. (1977) and Ahmed (1981), who found that a large part of the microbial biomass was present in silt-sized fractions. However, since only about 2 per cent of the organic matter in soils consists of biomass (Jenkinson and Rayner, 1977), silt-sized aggregates consisting of living bacteria must be newly formed aggregates. When the bacterial colony has died and its contents have decayed, characteristic fibrous components of the bacterial capsule remain (Foster, 1978), thus leading to an older aggregate; the remains of the colony with its capsule cannot be identified as such, but appears as a matrix of organic matter binding particles of clay. This organic matter can be seen in the transmission electron micrograph of a thin section of soil from the rhizosphere (Foster, 1978, Fig. 2). There is also chemical evidence that aggregates 1–5 μm diameter are old and protect organic matter, which consists mainly of humic acids, within the aggregates (Oades and Ladd, 1977). However, aggregates derived from bacterial colonies may represent only a small number of particles stabilized by microbial debris since fungi contribute more to soil organic matter than do bacteria (Paul and van Veen, 1978). Some fungal hyphae were shown to produce a layer of amorphous material, probably polysaccharide, to which particles of clay were attached firmly (Tisdall and Oades, 1979). Fragmentation of the hyphae could lead to small aggregates stabilized by fungal debris. The hyphal fragments could be derived from VA mycorrhizal fungi which were associated with a living plant, or from saprophytic fungi which grew rapidly in the soil after the addition of readily decomposable material. As with the bacterial colonies, further decay of the hyphal fragment could lead to a matrix of physically protected organic matter within a water-stable aggregate.

Aggregates < 2 μm diameter

Water-stable particles < 2 μm diameter are often floccules where individual clay

plates (which may consist of individual lamellae or groups of lamellae) come together to form a fluffy mass. Initially, the plates are not parallel but are attracted edge-to-edge to form an open card-house structure (Quirk, 1978). However, on drying, the system tends to lower its entropy, so that the plates become parallel and if aligned perfectly will form a crystal 4 nm wide. The crystals may than be joined into larger units with slit-shaped pores 2.5–4.1 nm between the crystals (Murray and Quirk, 1979). In surface soils, perfect alignment of clay plates probably occurs rarely so that the arrangement within particles $< 2 \mu m$ diameter is probably somewhere between that of a card-house structure and that of a crystal. The plates are held together by van der Waal's forces, H-bonding and coulombic attraction. However, the charges of ions associated with the surface of clay are influenced by organic and inorganic materials (Greenland, 1965, 1971a). For example, organic materials may increase or decrease the attraction between the particles.

Some particles $< 2 \mu m$ diameter have been shown to be aggregates of very fine material held together by organic matter and iron oxides. In particles $< 2 \mu m$ diameter, organic material is probably sorbed onto the surface of clays and held firmly by the various bonds described in reviews on organo-mineral interactions.

An idealized model can be drawn to scale showing that an aggregate of soil is built up of structural units of various sizes held together by various binding agents (Fig. 3).

In soil there is considerable overlap between the proposed stages leading to an aggregate several millimetres in diameter, although there appears to be sufficient evidence to warrant the proposed stages, particularly the larger features. The evidence indicates that there is not a smooth continuum of sizes of water-stable particles and that stability of the particles at each stage is associated with a dominant binding agent.

It would be interesting to examine other soils with different textures to determine the size of particle produced by slaking and by physical dispersion.

Nature of organic binding agents

The organic binding agents involved in stabilizing aggregates can be considered in three main groups based on the age and degradation of the organic matter and not on the proportions of chemically defined components. The various binding agents determine the age, size and stability of aggregates. The three groups of organic binding agents considered are transient, temporary and persistent.

Transient binding agents

Transient binding agents are organic materials which are decomposed rapidly by microorganisms. The most important group is the polysaccharides including (i) microbial polysaccharides produced when various organic materials are added to soil, and (ii) some of the polysaccharides associated with roots and the microbial biomass in the rhizosphere (Russell, 1973; Oades, 1978). Polysaccharides are produced rapidly (Harris et al., 1966; Aspiras et al., 1971) but are decomposed rapidly, and are associated with large ($> 250 \mu m$ diameter) transiently stable aggregates (e.g. Guckert et al., 1975).

Based on data from Griffiths and Jones (1965), Harris et al. (1966), Baver et al. (1972), Guckert et al. (1975), Hepper (1975) and others, it is possible to generalize with respect to the dynamics of water-stable aggregates in soil after the addition of
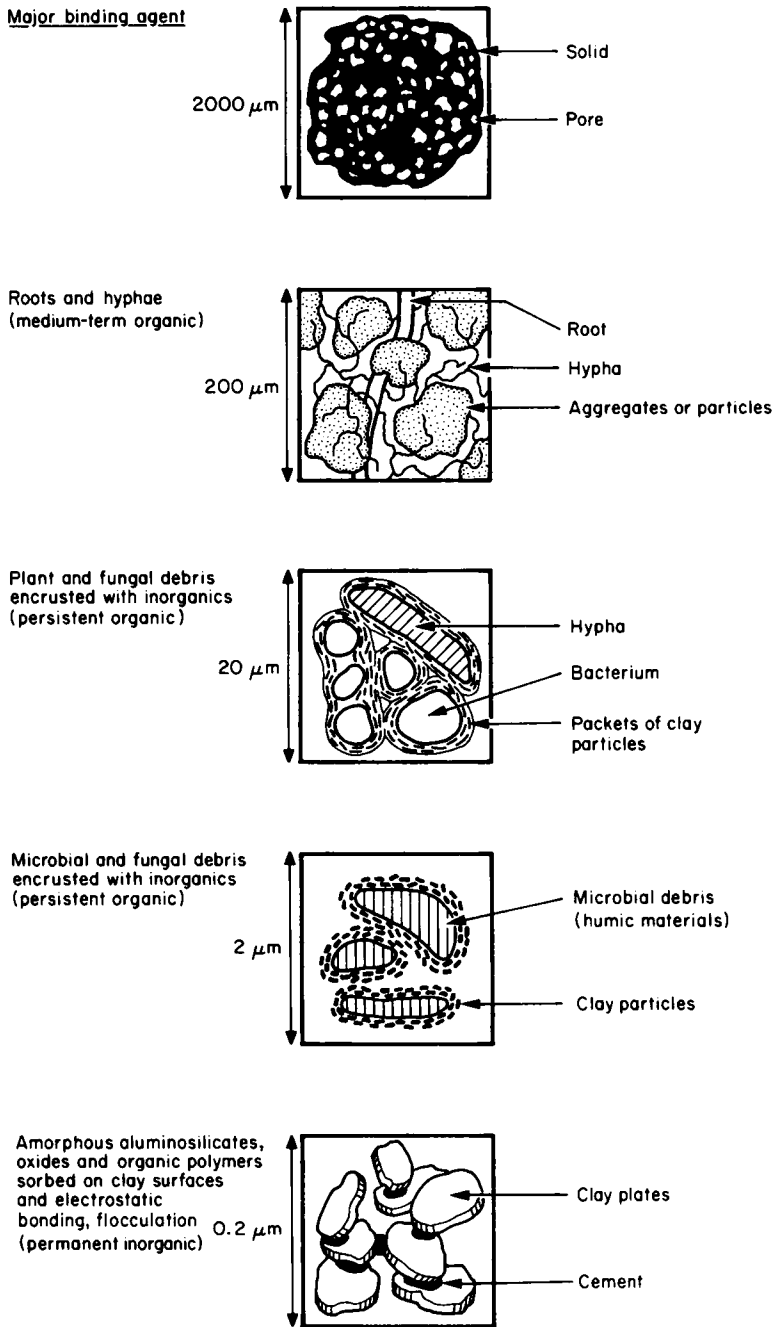
Major binding agent

2000 μm

— Solid

— Pore

Roots and hyphae
(medium-term organic)

200 μm

— Root

— Hypha

— Aggregates or particles

Plant and fungal debris
encrusted with inorganics
(persistent organic)

20 μm

— Hypha

— Bacterium

— Packets of clay
particles

Microbial and fungal debris
encrusted with inorganics
(persistent organic)

2 μm

— Microbial debris
(humic materials)

— Clay particles

Amorphous aluminosilicates,
oxides and organic polymers
sorbed on clay surfaces
and electrostatic
bonding, flocculation
(permanent inorganic)

0.2 μm

— Clay plates

— Cement

Fig. 3. Model of aggregate organization with major binding agents indicated.

organic materials (Fig. 4). Readily available substrates, e.g. glucose, increase water-stable aggregation which is transient (several weeks) because the glues are decomposed readily; treatments with periodate indicate a dominant role for polysaccharides. Less readily available material, such as ryegrass tissue, leads to a gradual increase in water-stable aggregates which persist for several months; polysaccharides are involved to a lesser extent. More recalcitrant substrates, e.g. cellulose, slowly give rise to limited water-stability which persists for months and is not significantly sensitive to periodate.

During the growth of plants, all three mechanisms are involved so there is an increase in water-stable aggregates which persists for months because roots and associated hyphae are decomposed slowly (Tisdall and Oades, 1980*a*). Some of the polysaccharides may be protected from microbial degradation by association with metal ions or tannins or by sorption on the surfaces of clays (Martin, J. P., 1971; Griffiths and Burns, 1972). Such materials and their binding action would then become persistent, even for several years.

The significance of polysaccharides as glues in soil aggregates has been reviewed several times (e.g. Swincer *et al.*, 1968; Martin, J. P. 1971; Cheshire, 1979). Many microorganisms produce exocellular mucilages or gums which are dominantly polysaccharide. Some of these organisms exist in soils, and mixtures of poly-saccharides, with properties which indicate a microbial origin, have been obtained from soils. These preparations, and simpler, better defined polysaccharides from cultured organisms have interacted with clays and have stabilized aggregates. Numerous correlations between carbohydrate or polysaccharide contents of soils and aggregation have been obtained, but in many cases the correlation has been no better than with other organic materials. The most convincing evidence that poly-saccharides function as glues in soil aggregates arose from the use of periodate as a selective oxidant for polysaccharides.

Periodate oxidation led to a decrease in water-stable aggregation of soils, not only
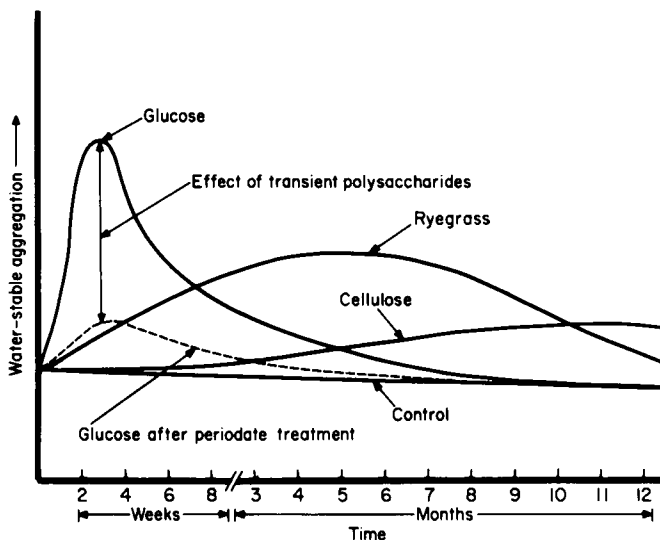

Fig. 4. Changes in water-stable aggregation after the addition of organic materials.

immediately after addition of organic materials to soils, but also on soils which were cultivated frequently and which had low contents of organic matter (Greenland *et al.*, 1962; Stefanson, 1971). However, it is clear that in some soils, other organic binding agents or inorganic cements are present so that removal or destruction of poly-saccharides does not influence aggregation.

The association of polysaccharides (produced by bacteria, fungi and plant roots) with clay particles has been illustrated convincingly by electron microscopy (Jackson *et al.*,1946; Foster and Rovira, 1976; Marshall, 1976; Foster, 1978; Tisdall and Oades, 1979). This work shows clearly the attachment of fine clay particles to capsular or exuded polysaccharides.

It is important to consider the scale at which this association takes place. The polysaccharides bind together clay-sized particles into aggregates which are of the order of 10 μm diameter. It is unlikely that small quantities of polymers with chain lengths of a few hundred ångströms would be important in binding particles into aggregates with diameters of several millimetres.

Inconsistencies in the literature on the role of polysaccharides in binding water-stable aggregates can be explained when one considers the size of aggregates which have been investigated. The methods of assessing aggregation or 'structure' have varied; for example, Greenland *et al.* (1962) determined permeability and Stefanson (1971) used a 10 μm degree of aggregation. (Both these methods assess the effects of the treatment on small aggregates, i.e. those with diameters less than 50 μm. Disintegration of aggregates less than 50 μm, and release of clay and silt-sized material would decrease permeability.)

Tisdall and Oades (1980*b*) assessed the influence of periodate on aggregates with diameters up to 10 mm and found that aggregates with diameters greater than 50 μm were unaffected by treatment with periodate. Mehta *et al.* (1960) examined 2–4 mm aggregates and Webber (1965) > 250 μm aggregates, and both groups of workers found that periodate-sensitive materials were not responsible for stabilizing macroaggregates.

Thus the methods used to study aggregates or the water-stability of soil structure will influence the results obtained when using periodate. The integrity of large aggregates is not affected by treatment with periodate and it seems reasonable to conclude that polysaccharides are not involved in stabilizing aggregates with diameters of several millimetres. However, polysaccharides stabilize aggregates less than 50 μm diameter, and perhaps also floccules of clay. This is in keeping with the molecular size of exocellular polysaccharides and the size of the particles which the polysaccharides glue together. Polysaccharides thus have less relative importance in soils with high organic matter contents, e.g. after many years of pasture growth.

Temporary binding agents

Temporary binding agents are roots and hyphae, particularly vesicular–arbuscular (VA) mycorrhizal hyphae (Hubbell and Chapman, 1946; Bond and Harris, 1964; Tisdall and Oades, 1979). Such binding agents build up in the soil within a few weeks or months as the root systems and associated hyphae grow. They persist for months or perhaps years and are affected by management of the soil (Tisdall and Oades, 1979, 1980*a*, *b*). The temporary binding agents are probably associated with young macroaggregates and can be equated with the organic skeleton grains described by Bal (1973).

Roots. Roots not only supply decomposable organic residues to soil and support a large microbial population in the rhizosphere, but roots of some plants, especially grasses, themselves act as binding agents. They appear to enmesh fine particles of soil into stable macroaggregates, even when the root has died (Fig. 5) (Clarke *et al.*, 1967; Coughlan *et al.*, 1973; Forster, 1979).

Residues released into the soil by roots are in the form of fine lateral roots, root hairs, sloughed-off cells from the root-cap, dead cells, mucilages, lysates and volatile and water-soluble materials (Soper, 1959; Rovira and McDougall, 1967; Shamoot *et al.*, 1968; Martin, J. K., 1971; Dickinson, 1974; Oades, 1978). The amount of organic carbon released by roots is related to the total length of root; Shamoot *et al.* (1968) found that, regardless of species, plants released 20–49 g organic material per 100 g harvested root. The root systems and associated fungal hyphae of pasture plants, especially grasses, are extensive and the upper layer of the soil under pasture is probably all rhizosphere, i.e. the roots are less than 3 mm apart (Thornton, 1958; Barley, 1970).

Part of the effect of plants on water-stable aggregates is also due to localized drying around roots (Allison, 1968). Electron micrographs of the rhizosphere show that particles of clay close to a root tend to be oriented almost parallel to the axis of the root; the percentage of oriented particles increases with the age of the root and with decreasing radial distance from the root (Blevins *et al.*, 1970; Greaves and Darbyshire, 1972; Foster and Rovira, 1976). The particles of clay had probably been reoriented by the expanding roots and by localized drying around the roots, from
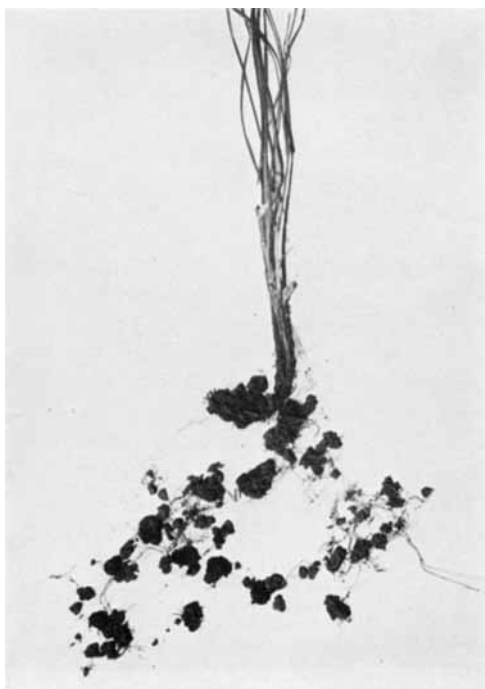

Fig. 5. Particles of soil held together by plant roots.

randomly dispersed positions to positions of minimal energy (Aylmore and Quirk, 1959).

Plants may also increase water-stable aggregation of soils indirectly by providing food for soil animals, such as earthworms and the mesofauna, enabling large populations to build up. Soil under 3-year-old pasture had few earthworms but after 8 years' pasture there were more than 1.5×10^6 ha^{-1} (Low, 1955). Earthworm casts generally contain more organic matter than the surrounding soil and the casts from soil under pasture were more stable than the surrounding soil (Swaby, 1950). The earthworm may stabilize structure by ingesting soil and mixing it intimately with humified organic materials in its gut (Swaby, 1950; Barley, 1959; Greenland, 1965). In a non-cultivated peach orchard where adequate food and water were present throughout the year, earthworm populations increased in 3 years to 2000 m^{-2}, compared with 150 m^{-2} where food and water were scarce, and infiltration of water was increased over 80-fold (Tisdall, 1978).
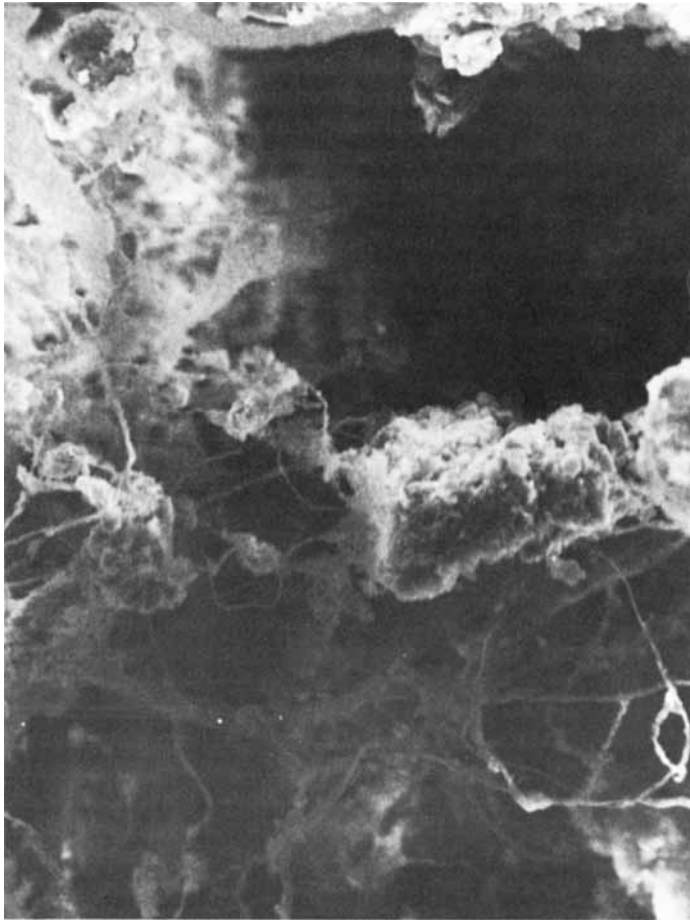

Fig. 6. Scanning electron micrograph of hyphae of VA mycorrhizal fungi binding soil particles into water-stable aggregates.

Hyphae. Hyphae, not necessarily viable, are sticky and encrusted with fine particles of clay and retain their strength when stable, wet aggregates from the field are dissected (Hubbell and Chapman, 1946; Bond and Harris, 1964; Tisdall and Oades, 1979). Water-stable aggregates in sand-dune soils also may be held together by fungal hyphae (Koske *et al.,* 1975; Forster, 1979). Although individual hyphae are not strong, the combined strength of all hyphae and fine roots, especially in a three-dimensional network, holds particles more or less equally in all directions so that aggregates do not slake when wetted rapidly.

Temporary binding agents stabilize macroaggregates, i.e. $> 250\,\mu m$ diameter (Hubbell and Chapman, 1946; Harris *et al.,* 1966; Tisdall and Oades, 1980*b*). This is probably because roots and fungal hyphae are relatively large and because they can grow in large pores in soil (Jackson, 1975; Marshall, 1976) which, in well-drained soils, are likely to contain air even during wet weather. Fungi have been shown to grow mainly in the outer parts of aggregates (Hattori, 1973).

It is believed that stabilization of aggregates by fungi in the field is limited to periods when readily decomposable material has been added to the soil in large amounts leading to a flush of hyphal growth (Martin *et al.,* 1955; McGill *et al.,* 1973; Low and Stuart, 1974). This may be true of the fungal species which most workers have studied. Such species produce characteristic spores, are isolated easily from soil and grow readily on dilution plates. However, fungal hyphae in the field have been shown to be associated with water-stable aggregates of a red-brown earth, with little seasonal variation; unstable aggregates contained few hyphae (Bond and Harris, 1964). Most of the microbial filaments which have been reported to stabilize aggregates in the field in the presence of plants were probably VA mycorrhizal fungi (Mosse, 1959; Koske *et al.,* 1975; Tisdall and Oades, 1979) (Fig. 6). The water-stability of aggregates of a red-brown earth was related directly to the length of external hyphae of these fungi associated with unit weight of aggregates or soil.

Saprophytic fungi. Saprophytic fungi which remain sterile in culture and which are rare or absent from dilution plates may also be included in temporary binding agents, since some of these sterile species could be isolated from soil in the field throughout the year (Warcup, 1967). This group includes dark-coloured fungi which tend to persist in soil for longer periods than hyaline fungi (Martin *et al.,* 1959; Hurst and Wagner, 1969). These melanic fungi occur widely in soils (Warcup, 1967) but tend to be less conspicuous than sporing fungi so that their importance in aggregation may have been overlooked; yet Martin *et al.* (1959) showed that some melanic fungi stabilized aggregates as effectively as did hyaline fungi.

Vesicular–arbuscular mycorrhizal fungi. Vesicular–arbuscular mycorrhizal fungi are widespread in soils, are obligate symbionts, and so far have not been cultured on artificial media (Mosse, 1973, 1975). Only recently have they been implicated in the water-stability of aggregates of soil. It is believed that VA mycorrhizal fungi tend to be most abundant in soils with low or unbalanced levels of nutrients; however, some plants are mycorrhizal even in fertile soils (Mosse, 1973; Sanders *et al.*, 1975). It is not known how long these fungi persist in soil once the host has died, but hyphae were still present in soil several months after the plants were killed although the hyphae may not have been viable (Tisdall and Oades, 1980*a*).

Little is known of the factors which affect the growth of external hyphae in soil, yet the water-stability of macroaggregates depends on hyphal length. However, the fungi produce extensive hyphae in soil and have been reported to extend 10 mm from

the surface of the root (Mosse, 1959; Sanders and Tinker, 1973; Tisdall and Oades, 1979). They extended 30 mm (Hattingh *et al.,* 1973) and 80 mm (Rhodes and Gerdemann, 1975) from the root in soil in modified petri dishes; however, the hyphae may have grown preferentially along the soil plane in the petri dishes so the distances quoted may not represent growth in natural soil.

Other temporary binding agents

Although fungi constitute more than 50 per cent of the microbial biomass in soil and probably contribute more than bacteria to the organic matter in soil (Wagner, 1975; Paul and van Veen, 1978), organic bonds probably develop also from degraded bacterial cells in the rhizosphere or around decaying organic residues (Marshall, 1976; Foster, 1978), i.e. develop from bacterial cells which form transient binding agents.

In desert soils, filaments of blue-green algae formed a solid and mechanically strong net which bound particles of soil or sand into a tough layer on the surface of the soil (Bond and Harris, 1964; Went and Stark, 1968). This layer may become leathery in water and even then may be difficult to break. Algae and lichens or algae and fungal hyphae may also form crusts in desert soils which stabilize the soils against erosion (Fletcher and Martin, 1948; Shields *et al.,* 1957).

Persistent binding agents

Persistent binding agents consist of degraded, aromatic humic material associated with amorphous iron, aluminium and aluminosilicates to form the large organo-mineral fraction of soil which constitutes 52–98 per cent of the total organic matter in
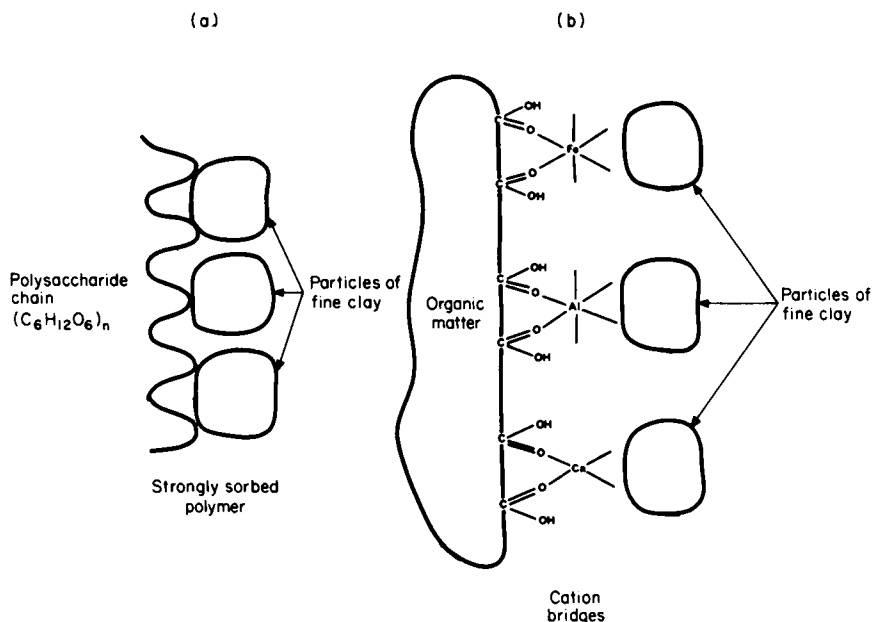

Fig. 7. Interaction of persistent binding agents with the surfaces of clays. (a) Organic polymer sorbed directly to clay surface, (b) humic material associated with clay through di- and trivalent metal cations.

soils (Greenland, 1965; Hamblin, 1977; Tate and Churchman, 1978; Turchenek and Oades, 1978). The persistent binding agents probably include complexes of clay–polyvalent metal–organic matter, C–P–OM and (C–P–OM)$_x$, both of which are < 250 μm diameter, as described by Edwards and Bremner (1967), and are probably included in the skeleton grains described by Bal (1973).

Persistent binding agents are probably derived from the resistant fragments of roots, hyphae, bacterial cells and colonies (i.e. temporary binding agents) developed in the rhizosphere; the organic matter is believed to be the centre of the aggregate with particles of fine clay sorbed onto it (Marshall, 1976; Foster, 1978; Turchenek and Oades, 1978) rather than the organic matter sorbed onto clay surfaces (Emerson, 1959; Greenland, 1965). However, persistent binding agents have not yet been defined chemically. It is likely that a precise chemical formula cannot be defined in the same way that a formula for humic acid cannot be defined. Although some of the binding by persistent materials can be broken with ultrasonic vibration (Edwards and Bremner, 1967), in some soils, especially those with a high percentage of total carbon, organo-mineral complexes within particles 1–20 μm diameter resist limited ultrasonic vibration (Hamblin, 1977; Tate and Churchman, 1978; Turchenek and Oades, 1978).

Also included in this group are strongly sorbed polymers such as some polysaccharides and organic materials stabilized by association with metals (Fig. 7). Multifunctional organic anions associated with di- and trivalent metal cations will act as stabilizing agents, although as mentioned earlier, they may also aid dispersion.

Conclusions

From the pragmatic point of view, it seems reasonable to consider micro- and macroaggregates defined as less than and greater than 250 μm diameter. The microaggregates are stabilized against disruption by rapid wetting and mechanical disturbance, including cultivation, by several mechanisms in which organomineral complexes play a dominant role. Polysaccharides are also involved. The
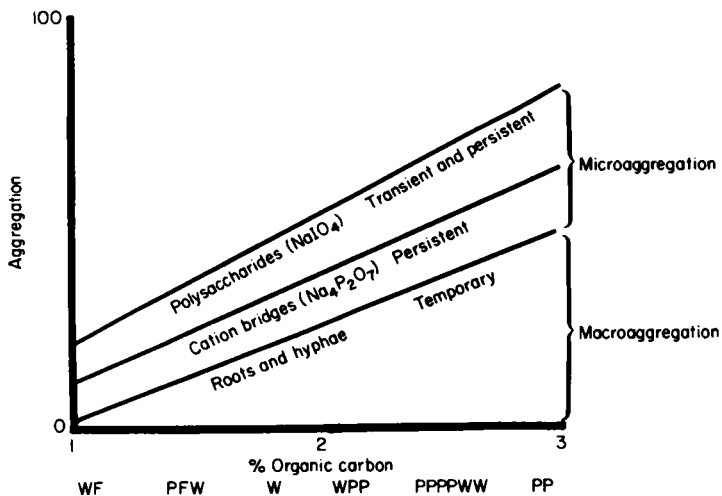
Fig. 8. Effect of crop-rotation on stable macroaggregation. W = wheat, F = fallow, P = pasture.

binding of microaggregates appears to be relatively permanent and is not influenced by changes in the organic matter content of the soil caused by different management, e.g. arable versus ley farming (Fig. 8).

On the other hand, the water-stability of macroaggregates depends largely on roots and hyphae, and thus on growing root systems. Numbers of stable macro-aggregates decline with organic matter content as the roots and hyphae are decomposed and are not replaced. The stabilization of macroaggregates is controlled by management, and is increased under pasture and declines when arable cropping is practised, particularly fallow.

Acknowledgements

REFERENCES

ADU, J.K. and OADES, J.M. 1978. Physical factors influencing decomposition of organic materials in soil aggregates. *Soil Biology and Biochemistry* 10, 109–115.

AHMED, M. 1981. *Microbial biomass in soils.* PhD thesis, University of Adelaide.

ALLISON, F.E. 1968. Soil aggregation—some facts and fallacies as seen by a microbiologist. *Soil Science* 106, 136–143.

ARNOLD, P.W. 1978. Surface-electrolyte interactions. In *The Chemistry of Soil Constituents* (eds D. J. Greenland and M. H. B. Hayes), pp. 355–404. Chichester: Wiley.

ASPIRAS, R.B., ALLEN, O.N., CHESTERS, G. and HARRIS, R.F. 1971. Chemical and physical stability of microbially stabilized aggregates. *Soil Science Society of America Proceedings* 35, 283–286.

AYLMORE, L.A.G. and QUIRK, J.P. 1959. Swelling of clay-water systems. *Nature, London* 183, 1752–1753.

BAL, L. 1973. Internal spatial arrangements of O-matrices. In *Soil Microscopy* (ed. G. K. Rutherford), pp. 260–262. Ontario: Limestone Press.

BARLEY, K.P. 1953. The root growth of irrigated perennial pastures and its effect on soil structure. *Australian Journal of Agricultural Research* 4, 283–291.

BARLEY, K.P. 1959. Earthworms and soil fertility. IV. The influence of earthworms on the physical properties of a red-brown earth. *Australian Journal of Agricultural Research* 10, 371–376.

BARLEY, K.P. 1970. The configuration of the root system in relation to nutrient uptake. *Advances in Agronomy* 22, 159–201.

BAVER, L.D., GARDNER, H. and GARDNER, W. R. 1972. *Soil Physics* 4th edn. New York: Wiley.

BLEVINS, R.L., HOLOWAYCHUK, N. and WILDING, L.P. 1970. Micromorphology of soil fabric at tree root–soil interface. *Soil Science Society of America Proceedings* 34, 460–465.

BLOOMFIELD, C. 1963. *Mobilization phenomena in soils.* Rothamsted Experimental Station Report, pp. 226–239.

BOND, R.D. and HARRIS, J.R. 1964. The influence of the microflora on physical properties of soils. I. Effects associated with filamentous algae and fungi. *Australian Journal of Soil Research* 2, 111–122.

BURFORD, J.R., DESHPANDE, T.L., GREENLAND, D.J. and QUIRK, J.P. 1964. Influence of organic materials on the determination of the specific areas of soils. *Journal of Soil Science* 15, 192–201.

CHESHIRE, M.V. 1979. *Nature and Origin of Carbohydrates in Soils.* London: Academic Press.

CHESTERS, G., ATTOE, O.J. and ALLEN, O.N. 1957. Soil aggregation in relation to various soil constituents. *Soil Science Society of America Proceedings* 21, 272–277.

CLARKE, A.L., GREENLAND, D.J. and QUIRK, J.P. 1967. Changes in some physical properties of the surface of an impoverished red-brown earth under pasture. *Australian Journal of Soil Research* 5, 59–68.

CLEMENT, C.R. 1961. Benefit of leys—structural improvement of nitrogen reserves. *Journal of British Grassland Society* 16, 194–200.

CLEMENT, C.R. and WILLIAMS, T.E. 1958. An examination of the method of aggregate analysis by wet sieving in relation to the influences of diverse leys on arable soils. *Journal of Soil Science* 9, 252–266.

CLEMENT, C.R. and WILLIAMS, T.E. 1964. Leys and soil organic matter. I. The accumulation of organic carbon in soils under different leys. *Journal of Agricultural Science* 63, 377–383.

COLLIS-GEORGE, N. and LAL, R. 1970. Infiltration into columns of swelling soil as studied by high speed photograhy. *Australian Journal of Soil Research* 8, 195–207.

COUGHLAN, K.J., FOX, W.E. and HUGHES, J.D. 1973. A study of the mechanisms of aggregation in a krasnozem soil. *Australian Journal of Soil Research* 11, 65–73.

DICKINSON, C.H. 1974. Decomposition of litter in soil. In *Biology of Plant Litter Decomposition* (eds C. H. Dickinson and G. J. F. Pugh), Vol. 2, pp. 633–658. New York: Academic Press.

EDWARDS, A.P. and BREMNER, J.M. 1967. Microaggregates in soils. *Journal of Soil Science* 18, 64–73.

EMERSON, W.W. 1959. The structure of soil crumbs. *Journal of Soil Science* 10, 235–244.

EMERSON, W.W. 1977. Physical properties and structure. In *Soil Factors in Crop Production in a Semi-Arid Environment* (eds J. S. Russell and E. L. Greacen). pp. 78–104. Queensland: University of Queensland Press.

EMMOND, G.S. 1971. Effect of rotations, tillage treatments and fertilizers on the aggregation of a clay soil. *Canadian Journal of Soil Science* 51, 235–241.

FLETCHER, J.E. and MARTIN, W.P. 1948. Some effects of algae and molds in the rain-crust of desert soils. *Ecology* 29, 95–100.

FORDHAM, A.W. and NORRISH, K. 1979. Electron microprobe and electron microscope studies of soil clay particles. *Australian Journal of Soil Research* 17, 537–543.

FORSTER, S.M. 1979. Microbial aggregation of sand in an embryo dune system. *Soil Biology and Biochemistry* 11, 537–543.

FOSTER, R.C. 1978; Ultramicromorphology of some South Australian soils. In *Modification of Soil Structure* (eds W. W. Emerson, R. D. Bond and A. R. Dexter), pp. 103–109. London: Wiley.

FOSTER, R.C. and ROVIRA, A.D. 1976. Ultrastructure of wheat rhizosphere. *New Phytologist* 76, 343–352.

FÜHR, F. and SAUERBECK, D. 1968. Decomposition of wheat straw in the field as influenced by cropping and rotation. In *Isotopes and Radiation in Soil Organic-Matter Studies*, pp. 241–250. Vienna: IAEA.

GILLMAN, G.P. 1974. The influence of net charge on water dispersible clay and sorbed sulphate. *Australian Journal of Soil Research* 12, 173–176.

GREAVES, M.P. and DARBYSHIRE, J.F. 1972. The ultrastructure of the mucilaginous layer on plant roots. *Soil Biology and Biochemistry* 4, 443–449.

GREENLAND, D.J. 1965. Interactions between clays and organic compounds in soils. *Soils and Fertilizers* 28, 415–425; 521–532.

GREENLAND, D.J. 1971a. Interactions between humic and fulvic acids and clays. *Soil Science* 111, 34–41.

GEENLAND, D.J. 1971b. Changes in the nitrogen status and physical conditions of soils under pastures, with special reference to the maintenance of the fertility of Australian soils used for growing wheat. *Soils and Fertilizers* 34, 237–251.

GREENLAND, D.J., LINDSTROM, G.R. and QUIRK, J.P. 1962. Organic materials which stabilize natural soil aggregates. *Soil Science Society of America Proceedings* 26, 366–371.

GRIERSON, I.T. 1975. *The effect of gypsum on the chemical and physical properties of a range of red-brown earths.* M.Ag.Sc. thesis, University of Adelaide.

GRIFFITHS, E. and BURNS, R.G. 1972. Interaction between phenolic substances and microbial polysaccharides in soil aggregation. *Plant and Soil* **36**, 599–612.

GRIFFITHS, E. and JONES, D. 1965. Microbiological aspects of soil structure. I. Relationships between organic amendments, microbial colonization, and changes in aggregate stability. *Plant and Soil* **23**, 17–33.

GUCKERT, A., CHONE, T. and JACQUIN, F. 1975. Microflore et stabilité structurale des sols. *Revue d'Ecologie et de Biologie du Sol* **12**, 211–223.

HAMBLIN, A.P. 1977. Structural features of aggregates in some East Anglian silt soils. *Journal of Soil Science* **28**, 23–28.

HARRIS, R.F., CHESTER, G. and ALLEN, O.N. 1966. Dynamics of soil aggregation. *Advances in Agronomy* **18**, 107–169.

HATTINGH, L., GRAY, L.E. and GERDEMANN, J.W. 1973. Uptake and translocation of ^{32}P-labelled phosphate to onion roots by endomycorrhizal fungi. *Soil Science* **116**, 383–387.

HATTORI, T. 1973. *Microbial Life in the Soil.* New York: Marcel Dekker.

HEINONEN, R. 1955. Soil aggregation in relation to texture and organic matter. *Agrogeologisia Julkaisuja* **64**, 17. (Abstract in *Soils and Fertilizers* 1956, **19**, 43).

HEPPER, C.M. 1975. Extracellular polysaccharides of soil bacteria. In *Soil Microbiology* (ed. N. Walker), pp 93–100. London: Butterworths.

HUBBELL, D.S. and CHAPMAN, J.E. 1946. The genesis of structure in two calcareous soils. *Soil Science* **62**, 271–281.

HURST, H.M. and WAGNER, G.H. 1969. Decomposition of ^{14}C-labelled cell wall and cytoplasmic fractions from hyaline and melanic fungi. *Soil Science Society of America Proceedings* **33**, 707–711.

JACKSON, M.L., MACKIE, W.Z. and PENNINGTON, R.P. 1946. Electron microscope applications in soils research. *Soil Science Society of America Proceedings* **11**, 57–63.

JACKSON, R.M., 1975. Soil fungi. In *Soil Microbiology* (ed. N. Walker), pp. 165–180. London: Butterworths.

JENKINSON, D.S. 1977. Studies on the decomposition of plant material in soil. V. The effects of plant cover and soil type on the loss of carbon from ^{14}C labelled ryegrass decomposing under field conditions. *Journal of Soil Science* **28**, 424–434.

JENKINSON, D.S. and RAYNER, J.H. 1977. The turnover of soil organic matter in some of the Rothamsted classical experiments. *Soil Science* **123**, 298–305.

JOHNSTON, J.R., BROWNING, G.M. and RUSSELL, M.B. 1942. The effect of cropping practices on aggregation, organic matter content, and loss of soil and water in the Marshall silt loam. *Soil Science Society of America Proceedings* **7**, 105–107.

JUO, A.S.R. and LAL, R. 1977. The effect of fallow and continuous cultivation on the chemical and physical properties of an alfisol in Western Nigeria. *Plant and Soil* **47**, 567–584.

KEMPER, W.D. and KOCH, E.J. 1966. *Aggregate stability of soils from Western United States and Canada.* United States Department of Agriculture Technical Bulletin No. 1355.

KONONOVA, M.M. 1966. *Soil Organic Matter* 3rd edn. Oxford: Pergamon Press.

KOSKE, R.E., SUTTON, J.C. and SHEPPARD, B.R. 1975. Ecology of *Endogone* in Lake Huron and dunes. *Canadian Journal of Botany* **53**, 87–93.

KRISHNA MURTI, G.S.R., SINGH, G. and RENGASAMY, P. 1977. The nature of soil clays and the stability of microaggregates. *Australian Journal of Soil Research* **15**, 115–119.

KROTH, E.M. and PAGE, J.B. 1946. Aggregate formation in soils with special reference to cementing substances. *Soil Science Society of America Proceedings* **11**, 27–34.

KUZNETSOVA, V.V. 1966. Evaluation of the role of different soil constituents in creating water-stable soil structure. *Soviet Soil Science* 1966, 1030–1037.

LADD, J.N., AMATO, M. and PARSONS, J.W. 1977. Studies of nitrogen immobilization and mineralization in calcareous soil. III. Concentration and distribution of nitrogen derived from the soil biomass. In *Soil Organic Matter Studies,* Vol. 1, pp. 301–312. Vienna: IAEA.

LAL, R. 1974. No-tillage effects on soil properties and maize (*Zea mays* L.) production in Western Nigeria. *Plant and Soil* **40**, 321–331.

LAL, R., WILSON, G.F. and OKIGBO, B.N. 1979. Changes in properties of an alfisol produced by various crop covers. *Soil Science* **127**, 377–382.

Low, A.J. 1954. The study of soil structure in the field and the laboratory. *Journal of Soil Science* **5**, 57–74.

Low, A.J. 1955. Improvements in the structural state of soils under leys. *Journal of Soil Science* **6**, 179–199.

Low, A.J. 1972. The effect of cultivation on the structure and other physical characteristics of grassland and arable soils (1945–1970). *Journal of Soil Science* **23**, 363–380.

Low, A.J. and STUART, P.R. 1974. Micro-structural differences between arable and old grassland soils as shown in the scanning electron microscope. *Journal of Soil Science* **25**, 135–137.

McCALLA, T.M. 1959. *Microorganisms and their activity with crop residues.* Nebraska Agricultural Experimental Station Bulletin No. 453.

McGILL, W. B., PAUL, E.A., SHIELDS, J.A. and LOWE, W.E. 1973. Turnover of microbial populations and their metabolites in soil. *Bulletins from the Ecological Research Committee–NFR (Statens Naturvetensk apliga Forshningstad) (Stockholm)* **17**, 292–301.

MALIK, M.N., STEVENSON, D.S. and RUSSELL, G.C. 1965. Water-stable aggregation in relation to various cropping rotations and soil constituents. *Canadian Journal of Soil Science* **45**, 189–197.

MARSHALL, K.C. 1976. *Interfaces in Microbial Ecology.* Cambridge, Mass.: Harvard University Press.

MARTEL, Y.A. and PAUL, E.A. 1974. Effects of cultivation on the organic matter of grassland soils as determined by fractionation and radiocarbon dating. *Canadian Journal of Soil Science* **54**, 419–426.

MARTIN, J.K. 1971. Labelled material leached from the rhizosphere of plants supplied with $^{14}CO_2$. *Australian Journal of Biological Sciences* **24**, 1131–1142.

MARTIN, J.P. 1971. Decomposition and binding action of polysaccharides in soil. *Soil Biology and Biochemistry* **3**, 33–41.

MARTIN, J.P., ERVIN, J.O. and SHEPHERD, R.A. 1959. Decomposition and aggregating effect of fungus cell material in soil. *Soil Science Society of America Proceedings* **23**, 217–230.

MARTIN, J.P. MARTIN, W.P., PAGE, J.B. RANEY, W.A. and DE MENT, J.D. 1955. Soil aggregation. *Advances in Agronomy* **7**, 1–37.

MEHTA, N.C., STREULI, H., MULLER, M. and DEUEL, H. 1960. Role of polysaccharides in soil aggregation. *Journal of the Science of Food and Agriculture* **11**, 40–47.

MISONO, S. and SUDO, S. 1958. *Bulletin of the National Institute of Agricultural Science (Tokyo) Ser. B.* 213. Cited in Hattori (1973).

MORTLAND, M.M. 1970. Clay-organic complexes and interactions. *Advances in Agronomy* **22**, 75–117.

MOSSE, B. 1959. Observations on the extra-matrical mycelium of a vesicular–arbuscular endophyte. *Transactions of the British Mycological Society* **42**, 439–448.

MOSSE, B. 1973. Advances in the study of vesicular–arbuscular mycorrhiza. *Annual Review of Phytopathology* **11**, 171–196.

MOSSE, B. 1975. Specificity in VA mycorrhizas. In *Endomycorrhizas* (eds F. E. Sanders, B. Mosse and P. B. Tinkler), pp. 469–484. London: Academic Press.

MURRAY, R.S. and QUIRK, J.P. 1979. Clay–water interactions and the mechanism of soil swelling. *Colloids and Surfaces* **1**, 17–32.

OADES, J.M. 1967. Carbohydrates in some Australian soils. *Australian Journal of Soil Research* **5**, 103–115.

OADES, J.M. 1978. Mucilages at the root surface. *Journal of Soil Science* **29**, 1–16.

OADES, J.M. and LADD, J.N. 1977. Biochemical properties: carbon and nitrogen metabolism. In *Soil Factors in Crop Production in a Semi-Arid Environment* (eds J. S. Russell and E. L. Greacen), pp. 127–160. Queensland: University of Queensland Press.

PAUL, E.A. and VAN VEEN, J.A. 1978. The use of tracers to determine the dynamic nature of organic matter. *Transactions of the 11th International Soil Science Society Congress* **3**, 61–102.

POKOTILO, A.S. 1967. Chemical composition of the separates of ordinary and southern chernozems. *Soviet Soil Science* 1854–1862.

QUIRK, J.P. 1978. Some physico-chemical aspects of soil structural stability—a review. In *Modifications of Soil Structure* (eds W. W. Emerson, R. D. Bond and A. R. Dexter), pp. 3–16. London: Wiley.

QUIRK, J.P. and AYLMORE, L.A.G. 1971. Domains and quasi-crystalline regions in clay systems. *Soil Science Society of America Proceedings* **35**, 652–654.

RAMIG, R.E. and MAZURAK, A.P. 1964. Wheat stubble management. I. Influence on some physical properties of a chernozem soil. *Soil Science Society of America Proceedings* **28**, 554–557.

RHODES, L.H. and GERDEMANN, J.W. 1975. Phosphate uptake zones of mycorrhizal and non-mycorrhizal onions. *New Phytologist* **75**, 555–561.

RIDLEY, A.O. and HEDLIN, A.O. 1968. Soil organic matter and crop yields as influenced by the frequency of summer fallowing. *Canadian Journal of Soil Science* **48**, 315–322.

RIMMER, D. and GREENLAND, D.J. 1976. Effects of calcium carbonate on the swelling behaviour of a soil clay. *Journal of Soil Science* **27**, 129–139.

ROVIRA, A.D. and GREACEN, E.L. 1957. The effect of aggregate disruption on the activity of microorganisms in the soil. *Australian Journal of Agricultural Research* **8**, 659–673.

ROVIRA, A.D. and MCDOUGALL, B.M. 1967. Microbiological and biochemical aspects of the rhizosphere. In *Soil Biochemistry* (eds A. D. McLaren and G. H. Peterson), Vol. 1, pp. 417–463. New York: Marcel Dekker.

RUSSELL, E.W. 1973. *Soil Conditions and Plant Growth* 10th edn. London: Longmans.

SANDERS, F.E., MOSSE, B. and TINKER, P.B. (Eds.) 1975 *Endomycorrhizas*. New York: Academic Press.

SANDERS, F.E. and TINKER, P.B. 1973. Phosphate flow into mycorrhizal roots. *Pesticide Science* **4**, 385–395.

SHAMOOT, S., MCDONALD, L. and BARTHOLOMEW, W.V. 1968. Rhizo-deposition of organic debris in soil. *Soil Science Society of America Proceedings* **32**, 817–820.

SHIELDS, L.M., MITCHELL, C. and DROUET, F. 1957. Algae- and lichen-stabilized surface crusts as soil nitrogen sources. *American Journal of Botany* **41**, 489–498.

SOPER, K. 1959. Root anatomy of grasses and clovers. *New Zealand Journal of Agricultural Research* **2**, 329–341.

STEFANSON, R.C. 1971. Effect of periodate and pyrophosphate on the seasonal changes in aggregate stabilization. *Australian Journal of Soil Research* **9**, 33–41.

STRICKLING, E. 1950. The effect of soy beans on volume weight and water stability of soil aggregates, soil organic matter content, and crop yield. *Soil Science Society of America Proceedings.* **15**, 30–34.

SUDO, S. 1962. *Bulletin of the National Institute of Agriculture (Tokyo) Ser.* B. **12**, 255. Cited in Hattori (1973).

SWABY, R.J. 1950. The influence of earthworms on soil aggregation. *Journal of Soil Science* **1**, 195–197.

SWINCER, G.D., OADES, J.M. and GREENLAND, D.J 1968. Studies on soil polysaccharides. II. The composition and properties of polysaccharides in soils under pasture and under a fallow–wheat rotation. *Australian Journal of Soil Research* **6**, 225–235.

TATE, K.R. and CHURCHMAN, G.J. 1978. Organo-mineral fractions of a climosequence of soils in New Zealand tussock grasslands. *Journals of Soil Science* **29**, 331–339.

THENG, B.K.G. 1979. *Formation of Properties of Clay–Polymer Complexes.* Amsterdam: Elsevier.

THORNTON, R.H. 1958. Biological studies of some tussock-grassland soils. II. Fungi. *New Zealand Journal of Agricultural Research* **1**, 922–938.

TISDALL, J.M. 1978. Ecology of earthworms in irrigated orchards. In *Modification of Soil Structure* (eds W. W. Emerson, R. D. Bond and A. R. Dexter), pp. 297–303. London: Wiley.

TISDALL, J.M. 1980. *Stabilization of soil aggregates by plant roots.* Ph.D. thesis, University of Adelaide.

TISDALL, J.M., COCKROFT, B. and UREN, N.C. 1978. The stability of soil aggregates as affected by organic materials, microbial activity and physical disruption. *Australian Journal of Soil Research* **16**, 9–17.

TISDALL, J.M. and OADES, J.M. 1979. Stabilization of soil aggregates by the root systems of ryegrass. *Australian Journal of Soil Research* **17**, 429–441.

TISDALL, J.M. and OADES, J.M. 1980a. The management of ryegrass to stabilize aggregates of a red-brown earth. *Australian Journal of Soil Research* **18**, 415–422.

TISDALL, J.M. and OADES, J.M. 1980b. The effect of crop rotation on aggregation in a red-brown earth. *Australian Journal of Soil Research* **18**, 423–434.

TURCHENEK, L.W. and OADES, J.M. 1978. Organo-mineral particles in soils. In *Modification of Soil Structure* (eds W. W. Emerson, R. D. Bond and A. R. Dexter), pp. 137–144. London: Wiley.

TURCHENEK, L.W. and OADES, J.M. 1979. Fractionation of organo-mineral complexes by sedimentation and density techniques. *Geoderma* **21**, 311–343.

WAGNER, G.H. 1975. Microbial growth and carbon turnover. In *Soil Biochemistry* (eds E. A. Paul and A. D. McLaren), Vol. 3, pp. 269–305. New York: Marcel Dekker.

WARCUP, J.H. 1967. Fungi in soil. In *Soil Biology* (eds A. Burgess and F. Raw), pp. 51–110 London: Academic Press.

WEBBER, L.R. 1965. Soil polysaccharides and aggregation in crop sequences. *Soil Science Society of America Proceedings* **29**, 39–42.

WENT, F.W. and STARK, N. 1968. The biological and mechanical role of soil fungi.*Proceedings National Academy of Science* **60**, 497–504.

WILLIAMS, R.J.B. 1970. *Relationships between the composition of soils and physical measurements made on them.* Rothamsted Experimental Station Report for 1970, Part 2, 5035.