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Interactions between biological processes, cultivation and soil structure

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Summary An inherent (autochthonous) biomass is characteristic of a soil while the input of substrates for plant roots or crop residues promotes the transient (zymogenous) biomass. However successful micro-organisms will show aspects of both types of ecological strategy. The biomass generated from plant residue substrates can include toxin-producing and pathogenic species but also beneficial organisms such as N-fixers and polysaccharide-producers. Rhizosphere activity can, depending on soil, plant and microbial species, stabilize or destabilize soils. Microbial activity should be considered in soil management and it may be possible to manipulate the soil population balance towards beneficial organisms.

Introduction

During the long history of cultivation, a fundamental objective of agricultural science has been to assess the effect on the soil. Evaluations at both the advisory and research level are usually conducted by teams of agronomists, plant physiologists, plant pathologists, soil chemists and soil physicists. It is relatively rare to find soil biologists in such teams and this may be because in the past they have had little to contribute. The science of soil microbiology has tended to be a process-oriented discipline with a strong emphasis on concepts. There has been a tendency to either count the number of viable cells which can be isolated on a selective medium or to isolate individual organisms from the field and demonstrate their biochemical potentials in defined nutrient-rich conditions in the laboratory, without evaluating the potential of the micro-organism back in the agricultural system. To an extent, the biologist can be excused in that suitable techniques were not readily available. However, as we now have a new armoury of methods, for example to determine soil biomass (the total living material in soil excluding roots), the challenge is on.

When evaluating activities in the field, it is vital to consider the underlying fundamental principles and concepts for study. The most obvious but important of these is, perhaps, that there will be no growth

of heterotrophic organisms in soil unless a suitable C and energy substrate is available. Generally, the combined soil organic matter (humus) which usually accounts for by far the greatest fraction of soil C, does not provide a suitable substrate because it has a half-life in excess of 1000 years. However, if the soil is sterilized or air-dried and re-wetted, sufficient C is released from the breakdown of the humus or killed cells to account for the flush in respiration[4] or microbial proliferation[37] that will take place. The principle limitation on growth in soil appears to be substrate availability and not the presence of toxic substances[32,37]. Lack of microbial proliferation in soil is often termed 'microbiostasis' but it seems to me preferable to specify lack of growth or toxicity. The two principle sources of C to the biomass are roots (living or dead) and shoots (falling leaves or crop residues).

The manner in which micro-organisms acquire available substrates in soil was first considered by Winogradsky[61]. The *zymogenous* or fermentative organisms rapidly increase in biomass in response to the input of fresh substrates, but they die out rapidly unless their energy demands are met. By contrast, the soil also supports a relatively constant biomass, which responds little to the input of fresh substrates; this is the *autochthonous* population which needs only a small supply of energy for its survival. In modern ecological terminology, the former group can be considered as r strategists and the latter as K strategists[5]. In practice it is probably unwise to consider these distinctions too rigidly as the completely successful soil organism will certainly exhibit characteristics of both types of ecological adaptation.

The soil biomass and cultivation systems

In the present essay, micro-organisms will receive greatest attention because they usually constitute the major fraction of the soil biomass.

Classical approaches to biomass determination were to assess the biovolume of cells by direct observation. This is both tedious and unreliable, even with modern fluorescent staining techniques[23]. A major breakthrough came when Jenkinson and Powlson[26] showed that by fumigating soil with the chloroform, the rate of mineralization from the dead cells to CO_2 was proportional to the biomass originally present, as assessed by biovolume. However, there may be a fallacy in that the technique can never be regarded as absolute when the calibration method was unreliable. A range of other methods followed, such as a modified fumigation technique where glucose was added to soil and respiration measured over a short (5 h) period[2], P release following fumigation[6], ATP determination[28] and microcalorimetry[57]. In comparative surveys[23,57],

it seemed that the original fumigation method[26] was generally most reliable, although it appeared less useful for acid soils. A problem with all the methods as described is that they depend on the use of sieved soils and such action can be regarded as more stringent than the passage of a plough through the soil. Lynch and Panting[44,47] found for samples taken in winter than sieving resulted in a smaller biomass yield than that obtained in intact cores, possibly because saprophytes dominated and the sieve removed substrates and fungal cells. In summer, the rhizosphere contributed much more to the total soil biomass and the increased biomass, measured on sieving may be the result of activation of the bacterial cells. In spring samples there was no observed effect of sieving so these effects may cancel out[27,47].

The fumigation-respiration technique with intact cores has been particularly suitable for measuring effects of cultivation; it does not depend on an absolute determination but rather a comparison between control and treated soils. This has been useful in demonstrating the seasonal variation in biomass[44,45]. As roots grow, the soil biomass increases by utilizing the C output from the roots so that at the time of maximal root production, biomass is greatest. In direct-drilled crops, root proliferation in the surface layers (5 cm deep) of soil is often greater than that from crops drilled after ploughing; accordingly, biomass is then greater in these soils. When sampling to greater depths (25 cm), the biomass was greater in direct drilled compared with ploughed soils at only one of four sites[53]. This is not particularly surprising because if root production is a major factor determining biomass, the deeper sampling will tend to provide an integrated figure for the biomass down the profile. Thus tillage may not change the overall soil biological activity, but it probably alters its distribution in the profile.

Grassland soils contain a greater root biomass than arable soils by virtue of the perennial nature of the crop. Consequently, the microbial biomass of grassland soils is usually at least double that of arable soils[1,27,45].

Burning of straw residues removes a major portion of the available substrate into microorganisms in soil and thus the biomass can be greater in the surface layer if straw is left on the surface[45]. However, straw is utilized by soil microorganisms more slowly than root exudates for example. Though there may be a transient increase in biomass during the early stages of rapid straw decomposition, subsequent increases are small and difficult to detect[47].

When N fertilizer was applied in spring, the biomass in both March and July increased where the soil had been direct-drilled, but not where

it had been ploughed[47]. The increase in biomass suggests that a fraction of the soil biomass is N-limited, but the precise interpretation is uncertain. The extra biomass following fertilizer additions was on average $100\,kg\,C\,ha^{-1}$ in the surface 5 cm. If the C:N ratio of microbial cells is assumed to be about 5:1, this means that about $20\,kg\,N\,ha^{-1}$ is immobilized in the microbial biomass. This is similar to the extra $25\,kg\,N\,ha^{-1}$ that is often recommended should be added to the seedbed when direct drilling (MAFF 1979)[50]. If that N were in the autochthonous biomass, its release would take much longer than if it were in the zymogenous population. Little is known about the recycling of N from biomass, but such information is desirable from both basic and practical standpoints.

The use of slurries and farmyard manures in agriculture is somewhat similar to the incorporation of straw into soil in that a complex substrate becomes available to microorganisms only relatively slowly. In an experiment initiated in 1893 at the Askov Experimental Station in Denmark, the biomass in unmanured, manured and NPK fertilized plots was recently compared[12]. Microbiological activity was compared by plate counts of bacteria and fungi, ATP content, oxygen uptake, dehydrogenase activity and biomass determined by fumigation. In general the differences were small, these observations being confirmed in a subsequent experiment initiated in 1972[13]. Thus again, variations in the size of the background or autochthonous biomass in the soil appear to be buffered against an agricultural practice which is providing a large substrate input to the soil.

Changing agricultural practices, such as direct drilling have resulted in increased herbicide and pesticide usage. It is critical to assess the effects on the soil biomass of such chemical inputs at rates used in the field. Anderson *et al.*[3] found that at $5\,\mu g\,g^{-1}$ soil the fungicides captan, thiram and verdasan caused transient decreases of 40% in the biomass and a shift in the soil population balance from fungi to bacteria. Long-term decreases were observed when the fungicides were applied at $50\,\mu g\,g^{-1}$. Thus although effective field application rate is difficult to repeat in laboratory experiments biomass determinations are a useful monitor of the environmental input of agrochemicals and it seems pertinent to measure biomass in field plots.

Problems and benefits of plant residues

In Britain, unlike most countries, straw from one crop is usually burnt prior to drilling a succeeding crop. Although some consider this environmentally unacceptable, there is a clear agronomic advantage

because if a crop is direct drilled beneath unburnt straw in a wet autumn, crop yield is reduced by about 20%[42]. The problems are lessened if the straw is ploughed in[15]. Mechanical difficulties in drilling can be a cause of the problems but even if they are eliminated, biological problems remain[39]. Straw, which is a lignocellulose, provides a potential substrate to pathogenic and other harmful microorganisms. In practice, there is little evidence for a build-up in pathogens under such situations, except one report where *Pythium* infection increased[9]. There is some evidence for apparently benign pseudomonads entering the root cortex as a result of the presence of straw in soil; these can stunt root growth, an effect which depends on the plant cultivar[14]. However, a major interpretation of the adverse effect in that the cellulosic fractions of straw provide a substrate to fermentative bacteria under the wet soil conditions and yield phytotoxic concentrations of acetic and other organic acids[35,58]. This effect has been demonstrated in many laboratory and field investigations and is not restricted to straw. Grass and weed residues can cause similar problems, although in these cases the build-up of pathogenic fungi, particularly *Fusarium culmorum*, is probably relatively more important[21,52].

Straw has a large C:N ratio (*c.* 100:1) whereas the decomposer microorganisms have a much smaller ratio (*c.* 5:1). Thus soil or fertilizer N tends to be immobilized into biomass during the microbial decomposition of straw. Such immobilization is however only temporary. We know too little about the kinetics of recycling of N contained in microbial biomass although the question has been addressed by Ladd[31]. My studies with S H T Harper[38] indicates that the N can be released from biomass during the spring, when the crop is most in need of it. The immobilization would in that case be advantageous because it would tend to prevent winter leaching. There is clearly a need for ^{15}N studies to evaluate such potentials.

Whereas C inputs can increase denitrification in soil, particularly under wet conditions, there is also potential for N-fixing populations to be stimulated. Studies with mixed populations of cellulolytic and N-fixing organisms utilizing cellulosic substrates have shown N gains of 6–14 mg/g substrate consumed[29,43,56]. The fixed N appears to be available to plants[25] at about the same rate as fertilizer N. A cereal crop yielding 7 t straw ha^{-1} treated in this way to provide 5 mg N/g straw, if scaled-up to a simple farm-scale operation, would provide the equivalent of 35 kg N ha^{-1}. As the straw already contains about 3 mg N g^{-1}, the total N content of the straw would amount to 57 kg N ha^{-1}, or about half of the annual fertilizer application to arable crops.

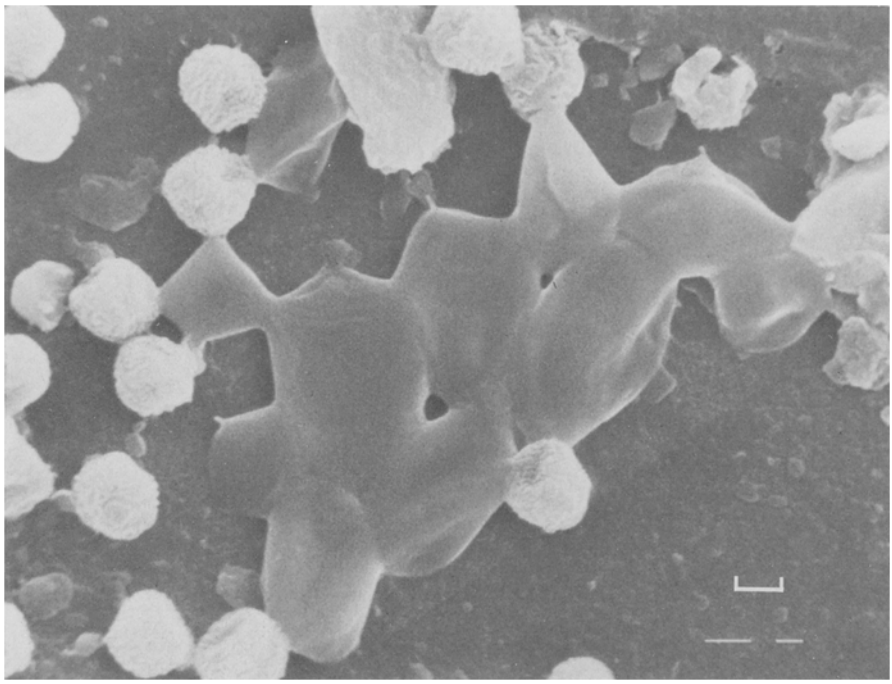

Fig. 1. Bacteria on the surface of straw producing a gum which stabilizes soil aggregates. Bar marker 1 μm. (From collaborative work with Dr L F Elliott, USDA, Washington State University.)

One of the major reasons for not burning straw in the Pacific Northwest of the United States is that it is retained as part of a conservation tillage system, reducing water and wind erosion[40]. Clearly there is a physical involvement but there is also a biochemical effect where microorganisms produce extracellular polymers, particularly polysaccharides, which provide a cementing action between soil particles, and fungal hyphae bind around the aggregate. This produces aggregates which are stable to the action of water[22,24,49,60]. Plant residues provide energy to 'fuel' the biomass for this function[20,48], which is particularly critical where soils are subject to instability problems. A classical example of unstable soil is volcanic ash. Following the eruption of Mt. St. Helens, Washington State received a covering of ash which had a particle size composition equivalent to the silt loam soil of the region. Laboratory experiments with this 'organic matter-free soil' demonstrated that microbial degradation of straw (Fig. 1) yielded aggregating agents which produced water stable aggregates of the ash and the soil of the region[40]; undegraded straw had no significant effect on stability. Subsequent

experiments (L F Elliott, J M Lynch unpublished) with straw containing various quantities of available C and N showed that straw with the smallest N content (0.25% w/w) resulted in significantly greater aggregation of the soil and ash than the larger N content straws (up to 1.09% w/w).

Water-soluble polysaccharides were extracted from wheat straw composted in glass columns (S J Chapman, J M Lynch unpublished). The neutral sugar content showed the polysaccharide to be of microbial origin but with some hemicellulose-like material when compared with the sugars presented in the fresh straw.

Rhizosphere activities and soil structure

As already indicated, the growth of plant roots in the soil increases the microbial biomass. In general, the stability of soil aggregates increases with biomass (Lynch[36]; E Henness, J M Lynch, M Fletcher unpublished), although the relationship between biomass and stabilizing effect depends on the microbial species (Table 1). However, in an unstable sandy soil, an increase in the biomass of the fungus *Mucor hiemalis* in soil caused a decrease in aggregate stability[36]. It is recognized in practice that the introduction of a grass (or lucerne) ley into arable cropping is a means of improving soil structure but the number of scientific investigations of such effects are small[8,10,33]. The deleterious effect of arable cropping on soil structural condition is also recognized[34,51].

The influence of root growth on soil aggregate stability (measured by turbidimetric and wet sieving procedures) was investigated using five crop species and two soils contained in pots[54]. Aggregate stability of soil contained in pots was improved by the growth in the soil of perennial ryegrass and lucerne for 42 days, whether tested in the fresh or air-dried state. Periodate-sensitive (probably polysaccharides) materials were involved. By contrast, the growth of maize, tomato and wheat for

Table 1. Effect of added bacteria (*Pseudomonas* spp) on the aggregate stability of an irradiated clay loam soil (*Denchworth series*). Data provided by Miss E Henness

Bacterium	Regression line[+]	Correlation coefficient
G1	$y = 0.220x + 0.650$	0.84^{**}
G9	$y = 0.111x + 0.696$	0.79^{*}
G13	$y = 0.026x + 0.632$	0.96^{**}
G15	$y = 0.109x + 0.656$	0.90^{**}

[+] y is the stability index (ratio of transmittance of sample to transmittance of water) as assessed by the turbidimetric assay and x is the dry weight of bacterial cells added (mg g^{-1} soil).

25 days could cause a decrease in the stability of fresh soil aggregates, even though this was not apparent after air-drying when periodate-sensitive materials were released as a consequence of the drying. No attempt was made to distinguish between the effects of the roots *per se* and the associated microbial biomass.

The destabilizing effect of the growth of maize roots in the soil was investigated by treating the soil prior to determining aggregate stability with sodium periodate to assess the importance of polysaccharides, and acetylacetone to assess the importance of organically bound Fe and Al prior to determining aggregate stability[55]. This suggested that the destruction of (organic matter)–(Fe or Al)–(mineral particle) linkages largely accounted for the effect and it seemed that removal of the Fe and Al cations by chelating agents released in the rhizosphere was the most likely mechanism. However, recent studies in my laboratory (E Henness unpublished observations) have indicated that the destabilizing effect of maize root growth is not general.

In studies of the effects of roots on soil aggregate stability, few attempts have been made to distinguish between the effects of the roots *per se* and that of the associated microbial biomass. Tisdall and Oades[59] suggested that vesicular-arbuscular mycorrhizal fungi (VAM) were responsible for the increase in aggregate stability associated with the root growth of ryegrass. They concluded from direct measurement of hyphal lengths and scanning electron micrograph (SEM) pictures, that the greater stabilizing effect of ryegrass compared to white clover roots was due to the larger population of VAM present in the soil.

Forster[18] provided microscopic evidence that fungi aggregated sand is an embryo dune system and later observations[19] showed that fungi (*Glomus fasciculatus* and *Penicillium* sp) were only really effective in aggregating the sand when roots of the pioneer grass (*Agropyron junceiforme*) were present. Reid and Goss[54] did not find a correlation between the VAM population on roots and soil aggregate stability. It seems likely therefore that in some situations, symbiotic growth of VAM fungi on plant roots will lead to improvements in aggregate stability of soils, and sometimes the growth of saprophytic fungi on root-derived C will be responsible. However neither situation is necessarily the general case and there appears to have been no studies where the relative effect of rhizosphere bacteria has been quantified. Faull and Campbell[16] provided excellent pictorial evidence by transmission electron microscopy (TEM) that a rhizosphere colonist of wheat, *Bacillus cereus* var *mycoides*, was surrounded by an electron transparent region, presumably polysaccharide, to which clay particles

adhered. Subsequently the significance of attachment of clays to bacteria in solution culture was studied in relation to its potential for control of fungal disease[7].

In a simple model of aggregation, Fletcher *et al.*[17] showed that bacteria and clay particles in the fine pores of the aggregate provided a 'cementing' action with the biopolymers produced. Charge interactions were provided by polarization of the net negative charge on the clay and bacterial surfaces or by metal ion bridging between the two. Tisdall and Oades[60] classified aggregate organization according to the size of aggregate: roots and hyphae (200 μm), plant and fungal debris encrusted with inorganics (20 μm), microbial and fungal debris encrusted with inorganics (2 μm) and amorphous aluminosilicates, oxides and organic polymers sorbed on clay surfaces and electrostatic bonding with flocculation (0.2 μm). Such conceptual schemes have been supported to an extent by the excellent TEM pictures of Kilbertus[30]: he was able to quantify the presence of open and closed pores within an aggregate by taking sections across it. Chemically the organic binding agents can be classified as transient (mainly polysaccharides), temporary (roots and fungal hyphae), and persistent (resistant aromatic components associated with polyvalent metal cations, and strongly sorbed polymers)[60].

Conclusion: Soil management

It might be argued that turning the soil with a plough, providing aeration and making otherwise inaccessible substrates available for microbial metabolism would promote degradation of the soil organic matter, including aggregating agents, and therefore result in a decline in soil structure. When sampling to just below plough depth, Powlson and Jenkinson[53] found no change in soil organic matter as a result of cultivation. However, in the surface (2.5 cm deep) aggregates of a range of soils, Douglas and Goss[11] found that both organic matter content and aggregate stability generally decreased with tillage and could be enhanced by direct drilling, an Andover series silt loam being an exception. It is therefore dangerous to generalize on the effects of cultivation on all soils in all horizons. The improvement in stability measured as a result of the introduction of grassland[11] does appear to be a general phenomenon but other crops vary in their effects.

The relative quantitative roles of roots and microorganisms in the processes are still uncertain; very little attention has been addressed to the role of earthworms and their gut microflora in soil aggregate stabilization during the utilization of plant residues. However the question arises as to whether the natural roles of microorganisms may

be manipulated by inoculation of suitable aggregate-forming micro-organisms. Clearly the use of microbial cells *per se* would be inappropriate, except perhaps algae for the soil surface where there might be a continuous source of light and mosture. There would be more scope if the inoculum were produced on plant waste, such as straw, and incorporated into soil after a suitable period of decomposition[40]. However, even with very unstable soils, the procedure might only be economic if the inoculum provided other useful functions such as the minimization of straw toxicity[41] and pathogen colonization, or the provision of plant nutrients, particularly N[43]. Such approaches should be considered as useful targets for soil biotechnology[38].

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