Chapter 3

Impact of Microorganisms on Chemical Transformations in Soil

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1. INTRODUCTION

Microorganisms (e.g. bacteria, fungi, actinomycetes, microalgae) play a key role in organic matter decomposition, nutrient cycling and other chemical transformations in soil. In fact general measurements of microbial activity in soil are synonymous with the breakdown of organic matter. Decomposition of organic matter is usually controlled by heterotrophic microorganisms and leads to the release and cycling of nutrients (especially nitrogen (N), sulphur (S) and phosphorus (P)). Microorganisms also immobilise significant amounts of carbon (C) and other nutrients within their cells. The total mass of living microorganisms (the microbial biomass) therefore has a central role as source, sink and regulator of the transformations of energy and nutrients in soil (Table 1). The vast diversity of microbial species, and their ability to break a wide range of chemical bonds, means that they are responsible for many key soil functions including:

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- i) Decomposition of soil organic matter and plant/animal residues with subsequent release of nutrients.
- ii) Transformation of compounds between chemical forms; often leading to the formation of more reactive or gaseous compounds which can be lost from the soil.
- iii) Degradation of synthetic compounds such as pesticides and herbicides.
- iv) Production of antibiotics, which can aid the suppression of soil borne diseases.
- v) Production of soil cementing agents, which may aid aggregation.
- vi) Production and degradation of hydrophobic waxy compounds which can lead to water repellence.
- vii) Plant nutrient acquisition through symbiotic associations (see Chapter 6 on rhizobia and Chapter 7 on mycorrhizas).

Table 1 Key microbial processes mediating chemical transformations associated with nutrient cycling in soil.

Microbial process	Examples of microbial groups involved			
Supply of nutrients				
Mineralisation of organic matter	Heterotrophic microorganisms			
Solubilisation of minerals	Penicillium sp., Pseudomonas sp., Bacillus sp.			
Nutrient transformations				
Methane (CH ₄) oxidation	Methylococcus sp., Methylobacter sp.			
Nitrification				
NH_3 to NO_2^-	Nitrosospira sp. and Nitrosomonas sp.			
NO_2^- to NO_3^-	Nitrobacter sp.			
Non-symbiotic N ₂ fixation	Azospirillum sp., Azotobacter sp.			
Symbiotic N ₂ fixation	Rhizobium sp., Anabeana sp.			
Sulphur oxidation	Thiobacillus sp., Heterotrophic microorganisms			
Loss of nutrients				
CO ₂ production	Heterotrophic microorganisms			
Methane (CH ₄) production	Methanobacterium sp., Methanosarcina sp.			
Denitrification (N_2, N_2O)	Bacillus sp., Pseudomonas sp., Agrobacterium			
	sp.			
Reduction of SO_4^{2-} to H_2S	Desulfovibrio sp., Desulfomonas sp.			

Land management practices have considerable impact on the size and dynamics of microbial populations. Intensification of agriculture has focussed on the use of chemical and mechanical inputs, often at the expense of biologically mediated processes. However, even in fertilised systems, microbial processes can play an important role in nutrient supply to plants (Table 2). Where purchased inputs are either costly or unobtainable, microorganisms have a critical role in maintaining soil fertility and crop health (Giller *et al.* 1997). This chapter therefore examines our fundamental understanding of how agricultural management practices and soil amendments influence soil microbial biomass and its activity, and consequently key chemical transformations in soil.

Table 2 Typical rates $(kg \ ha^{-1} \ year^{-1})$ of soil processes supplying nutrients to crops in temperate agricultural systems and associated typical rates $(kg \ ha^{-1} \ year^{-1})$ of fertiliser application.

Microbially mediated process	Land use	Soil supply	Reference	Fertiliser ¹
N ₂ fixation (white clover)	Grassland	13-280	Ladha et al. 1992	290
N mineralisation	Grassland	65-400	Jarvis <i>et al</i> . 1996	290
S mineralisation	Grassland	18-36	Sakadevan <i>et al.</i> 1993	20-32
P mineralisation	Grassland	23	Brookes et al. 1984	28
N mineralisation	Arable	50-130	Jarvis et al. 1996	200
S mineralisation	Arable	2-6	Kirchmann <i>et al.</i> 1996	10-16
P mineralisation	Arable	5	Brookes et al. 1984	20

¹ Fertiliser recommendation rates derived from Anon. (2000) where: Grassland = Cut and grazed sward of moderate fertility on medium soil, maintenance application of P; Arable = Dominantly cereal based rotation in moderate rainfall areas on medium soils, maintenance application of P.

2. RELEVANCE OF MICROBIAL DIVERSITY

A single gram of soil contains somewhere in the order of 10^{5} - 10^{8} bacteria, 10^{6} - 10^{7} actinomycetes and 10^{5} - 10^{6} fungal and 10^{4} algal colony forming units. Following extraction of soil DNA, Torsvik *et al.* (1994) estimated that one-gram of soil contained several thousand bacterial species. There are probably millions of species of microorganisms within the terrestrial ecosystem but only *ca.* 5% have been identified and/or cultured. With the exception of a few specific populations, our current understanding of microbial functioning has generally been limited to gross estimates of the size and activity of the microbial biomass as a single 'black box' within the soil (see reviews: Jenkinson and Ladd 1981, Wardle 1992, Dalal 1998).

Recent debate in soil research has focused on the importance of microbial diversity in maintaining soil function (Grime 1997, Ritz and Griffiths 2001). Early indications from studies of soil heterotrophic communities across scales of metres to continents showed that despite gross similarities between microbial populations at a coarse scale, at the species to

sub-species level, populations showed strong adaptation/evolution to locality (Fulthorpe *et al.* 1998). However, there is currently little direct evidence that links microbial diversity to soil biochemical transformations (Grime 1997, Ritz and Griffiths 2001).

Even where identifiable components of the soil microbial community have been linked to specific transformation processes, e.g. nitrifying bacteria, denitrifying bacteria, methanotrophs, mycorrhizal fungi and Rhizobium, there is still limited knowledge of the importance of diversity within these groups on the chemical transformations they mediate. The species composition of microbial populations may be of greater direct relevance to the rate of specific ecosystem processes than their diversity per se. Cavigelli and Robertson (2001) found that significantly different N₂O emission rates between soils (differing only in agronomic management) corresponded to differences in denitrifier communities. Less than half of the denitrifying taxa isolated were common to all soils. However, the overall diversity of the denitrifier community in each soil was similar. For processes which are mediated by a range of microbial species, the 'functional diversity' of a microbial population (e.g. the range and complexity of C-substrates that a specific population can decompose) may be of more importance than genetic diversity with respect to ecosystem processes (Zak et al. 1994, Tilman et al. 1997, Hunter-Cevera 1998). Where resilience to environmental change is critical, the different environmental tolerances, physiological requirements and microhabitat preferences of otherwise functionally similar organisms may also be critical (Perry et al. 1989, Yachi and Loreau 1999).

While little is currently known of the factors that favour the development or maintenance of diversity in microbial populations, it seems logical that agricultural management practices which i) conserve or increase the soil microbial biomass, ii) enable niche environments to develop within the soils physical matrix and iii) provide a range of organic compounds on a regular basis will also tend to maintain a diverse microbial population (see review: Kennedy and Gewin 1997).

3. ENVIRONMENTAL CONTROL

In the soil, microbial communities survive, reproduce and die in a complex 3-dimensional physical framework, which has variable geometry, composition and stability over several orders of magnitude from molecular to field (Foster 1988, Young and Ritz 1998, Ettema and Wardle 2002). Biological activity in soil also changes this framework. The individual effect of environmental and physico-chemical factors on the activity of microorganisms (and hence the breakdown of soil organic matter) has been

widely studied (van Veen and Kuikman 1990, Ladd *et al.* 1993, Strong *et al.* 1998, Strong *et al.* 1999). The diversity of the microbial community in soils and the ubiquity of many processes amongst species usually means that chemical transformations have broad optima in relation to environmental conditions. Microbial communities can also adapt to prevailing soil conditions. For example the optimum pH for amino acid breakdown and uptake by communities of soil bacteria was shown to be very close to the natural pH of the soils from which they were extracted (Bååth 1996).

Soil texture is a primary mediating factor in the operation of external climatic conditions in the soil through its influence on the retention of soil organic matter and development of soil structure and pore size distribution. Good relationships are often found between clay content and microbial biomass (Figure 1), although this is also a result of the relationship between clay content and soil organic matter (Wardle 1992).

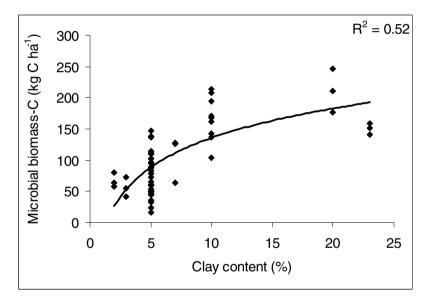


Figure 1 Relationship between clay content and microbial biomass in coarse-texture agricultural soils. Soils (0-5 cm) were collected under winter wheat from a single catchment (10 x 20 km; 450 mm annual precipitation; 0.4 to 2.7 %C). Differences in microbial biomass for a specific clay content reflect the associated range of soil organic C contents resulting from prior differences in crop rotations and farm management practices. D.V. Murphy and N. Milton (unpublished data).

Well-structured finer textured soils also create more niche environments for microbial colonisation. This generally supports greater microbial populations due to protection from desiccation (Bushby and Marshall 1977) and predators (Roper and Marshall 1978) and because of the formation of different oxygen concentrations. For example, Arah and Smith (1989) showed how microbial respiration and soil water interact to create a complex and spatially heterogeneous network of aerobic and anaerobic microsites, resulting in simultaneous nitrification and denitrification.

Microbial activity is often strongly positively related to changes in temperature under field conditions throughout the cropping season when moisture is not limited (Campbell *et al.* 1999). However, external environmental conditions do not apply uniformly throughout the soil and because of the complex dynamics of soil ecosystems, no single parameter is satisfactory as an indicator of microbial activity in soils under different conditions (Dick 1992). Consequently Wardle (1992) showed vastly different responses of the microbial biomass to seasonal climatic variability, even in very similar ecosystems, resulting from the complexity of interactions between soil moisture, temperature and their effects on plant growth.

4. MANAGEMENT PRACTICES

Agricultural management practices ultimately seek to increase or optimise plant and animal productivity. Practices may directly affect microbial activity and soil chemical transformations through modification of the microbial population or a component of it, or indirectly through modification of soil or environmental factors that change microbial habitats. Understanding the interactions between management practices and environmental controls allows estimates of potential impacts on specific processes to be made (Table 3). Many of these practices are typical of modern farming systems (see Chapter 11) and aim to improve the overall biological, chemical and physical fertility of the soil.

4.1 Crop Choice and Rotation

Microbial biomass also appears to be higher in crop rotations than in monocultures (e.g. Anderson and Domsch 1989, Moore *et al.* 2000), which probably reflects the greater niche diversity provided by a wider range of inputs to the soil in crop residues. Not all rotations increase soil organic matter levels and microbial biomass to the same extent. Edwards *et al.* (1990) showed that addition of soybean to a crop rotation did not increase either microbial biomass or activity. However, adapting arable rotations to include green manure, cover crops or short-term pastures will increase the duration of crop cover, and the amount and diversity of crop residues. For example, Campbell *et al.* (1991) showed that changing from a monoculture of spring wheat to a rotation containing a legume or green manure increased

the proportion of the year under plant cover, increased returns of C to the soil and resulted in an increase in microbial biomass. Murphy *et al.* (1998) showed that increasing the proportion of legume in the rotation increased total soil N, microbial biomass N and the seasonal cumulative gross N mineralisation rate (Table 4).

The choice and order of crops within a rotation is made under a number of constraints (e.g. market availability, weed and disease control). It is clear that management of crop choice and rotation has both direct and indirect impacts on the activity and diversity of soil microorganisms (Figure 2). However, how these choices can be practically manipulated to benefit the microbial biomass (or particular components) and microbially mediated chemical transformations, except at the coarsest level, is not yet understood.

Table 3 Likely direct impact of agricultural management practices on the microbial biomass and key C and N chemical transformation processes in an arable cropping system. \uparrow = increase in pool/process, Ψ = decrease in pool/process.

	Microbial biomass	Mineralisation	Nitrification	CO ₂ emissions	Methane production	Denitrification
Crop rotation including grassland or green manures instead of continuous arable cropping.	↑	↑		↑		
Retention of crop residues instead of burning.	↑	↑		↑		
Minimum tillage practices instead of full soil cultivation techniques.	↑	¥		¥	¥	↑
Irrigation of crops in rain-limited cropping environments.	↑	↑	↑	↑		↑
Drainage of agricultural land in high rainfall/waterlogged environments. Application of fungicides to soil.	≁	↑	↑	↑	¥	¥
Application of inorganic N fertilisers to soil.			↑			↑
Application of organic amendments to soil.	↑	↑		↑		↑
Liming of soil to raise pH on acidic soils.	↑	↑	↑	↑		↑

	Continuous wheat	Lupin -wheat rotation	Continuous subterranean clover
Total organic N pool	1008	1002	1463
Microbial biomass N pool	64	68	76
Gross N mineralisation flux	100	120	282
Gross N immobilisation flux	57	61	160
Net N mineralisation flux	43	59	122
N flux through microbial biomass	25	41	49

Table 4 Pools (kg N ha⁻¹) and fluxes (kg N ha⁻¹ cycled during wheat crop) of N in contrasting cropping systems (0-5 cm) in Western Australia (adapted from Murphy *et al.* 1998).

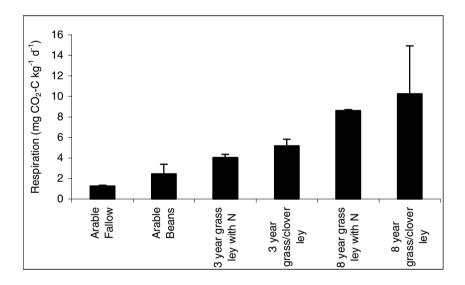


Figure 2 Influence of crop rotation on soil microbial activity (0-23 cm). Data collected in 1996 from the Rothamsted Continuous Ley-Arable experiment UK (est. 1938). Capped bars are standard errors of the mean. D.V. Murphy and P.R. Poulton (unpublished data).

4.2 Crop Residue Management

Microbial activity is generally C-limited in agricultural soils. Retention of crop residues therefore provides a practical means of increasing soil microbial populations without having to import additional organic matter. Management of crop residues changes soil temperature, water and the distribution of plant residues and organic matter which all influence the location and activity of microorganisms (e.g. Hendrix *et al.* 1986; see Chapter 10). Surface mulching of crop residues increased populations of bacteria, actinomycetes and fungi 2-6 times compared to non-mulched treatments (Doran 1980). In contrast, stubble burning reduces inputs of organic matter and increases soil temperature and moisture deficits after harvest and tends to reduce the population and activity of soil microorganisms (e.g. Thompson 1992). For example, Powlson *et al.* (1987) showed that incorporation of straw instead of burning, increase the microbial biomass by 45%, although total C was only 5% higher.

The decomposition of crop residues in soils is largely controlled by their chemical composition, residue management practices (e.g. incorporation method), soil and environmental factors (see review: Kumar and Goh 2000). Residue quality, which controls decomposability and nutrient release (N, P and S), is mainly determined by residue composition i.e. contents of soluble carbohydrates, amino acids, active polyphenols, lignin, nutrients and C:nutrient ratio (Handayanto et al. 1995). The decomposition of crop residues in soils can be partly regulated through the control of the quality of litter inputs. Both crop selection and the mixing of crop residues from separate sources before incorporation have been used to manage nutrient release during microbial decomposition (Palm et al. 1997). It is well known that lignin in plant residues slows microbial decomposition and it is possible to breed plants with higher levels of lignin (Paustian et al. 1995). Developments in plant genetic engineering have resulted in the modification of lignin structure to improve wood quality (in pulp and paper production) and for crop digestibility (Baucher et al. 1998). Manipulation of plant residue quality in this way has significant future implications for controlling soil organic matter formation and subsequent rates of mineralisation.

4.3 Tillage

The greater the intensity of energy input to the soil through tillage the greater the rates of residue decomposition (Watts *et al.* 2000) which regulates the size of the microbial population (Figure 3). Mixing of crop residues and soil also favours the development of bacterial rather than fungal populations and alters both the pathways of decomposition and the network of predators that develop in soil (McGonigle and Miller 1996). Martens (2001) reviewed 21 papers reporting the effects of tillage systems on soil microorganisms and their activity. All tillage systems dramatically reduced the microbial biomass relative to uncultivated native vegetation; the studies reported had high levels of soil organic matter and microbial biomass. However, as tillage intensity decreased, declines in microbial biomass were less (Martens 2001).

In reduced tillage and direct drill systems, microorganisms and their associated processes become concentrated in the surface soil and the proportion of organic carbon immobilised in the microbial biomass is higher than in cultivated soils with similar microbial biomass levels (Wardle 1992). Minimum cultivation practices result in less surface area contact between residues and soil microbial communities reducing decomposition rates; such conditions also favour the development of stable fungal populations during residue decomposition (Martens 2001). In dryland cropping systems, where the soil surface dries out rapidly, colonisation of surface residue by the microbial population may be restricted by water. In such cases, the mulching effect of the residue (i.e. surface area) may be of greater importance to the rate of residue decomposition than its quality/composition (Sparling *et al.* 1995).

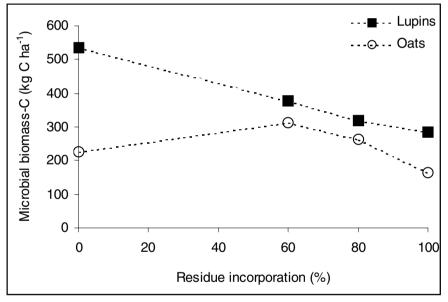


Figure 3 Effect of degree of residue (lupins or oats) incorporation by tillage on the level of microbial biomass in the 0 - 30 cm soil layer of a loamy sand: 0% = brown manure; 60% = offset disc to 10 cm; 80% = disc plough to 15 cm and 100% = molboard plough to 25 cm. Crops were incorporated as a green manure except for the 0% residue incorporation treatment where the crop was killed with chemicals. D.V. Murphy, F. Hoyle and N. Milton (unpublished data).

Minimum tillage and direct drill systems also lead to changes in many of the environmental factors that control microbial activity and residue breakdown. Higher moisture levels, lower O_2 concentrations and reduced soil temperatures result in lower early season microbial activity and lower mineralisation of N in temperate climates despite the higher microbial biomass populations in no till systems (Martens 2001). The altered physical conditions also favour higher losses of N through denitrificatio. Aulakh *et al.* (1984) measured gaseous losses of 12-16 kg N ha⁻¹ year⁻¹ in no till compared to 3-7 kg N ha⁻¹ year⁻¹ in conventionally tilled soils.

It is clear that reducing tillage intensity can increase the size of the microbial biomass population, where crop residues are retained in the system, and lead to a dominance of fungi over bacteria within the microbial biomass (at least in the surface horizons of the soil). Reduced tillage systems therefore have significantly different food webs than conventional intensively tilled systems (Verhoef and Brussaard 1990). However, it is not clear whether changes in community structure or modification in the environmental factors controlling microbial processes has the larger effect on microbially mediated chemical transformations. Where possible. optimisation of tillage systems for soils and rotations should seek to minimise soil disturbance, reduce water and wind erosion, maintain soil organic matter levels and protect soil microbial/faunal populations. However, it is the interactions between tillage and residue management that are critical in the management of microbially mediated chemical transformations in soils

4.4 Irrigation and Drainage

The main effect of irrigation and drainage on the soil microbial biomass is indirect, by regulating the seasonal effects of rainfall and tending to stabilise the soil moisture regime throughout the growing season. Other indirect effects occur as the duration of crop growth and consequent inputs of organic matter through exudates and crop residues tend to increase when irrigation is used. Although these effects have been shown to be important, they are generally smaller than those caused by climate and residue quality (Wilkinson et al. 2002). Irrigation (where practical) is used when crop yields or quality would otherwise be compromised by drought. Soil conditions will therefore be maintained at optimum moisture contents for microbial activity for longer periods of the cropping season. However, this may reduce the turnover of nutrients through the microbial biomass during the growing season, because fewer wet-dry cycles will occur (Wardle 1992). Poorly managed irrigation systems may also lead to increases in soil salinity. This has been shown to reduce microbial enzyme activity and respiration (Garcia and Hernandez 1996). Soil drainage increases soil aeration, reducing losses of N by denitrification, and tends to increase the seasonal duration of microbial activity including nitrification (Table 5). Coupled with increased throughflow of water, this may increase leaching losses of N, as nitrate and hence merely trade one form of N loss for another.

				Gross N fluxes		
	Total C	MB-N	CO ₂ -C	Mineralisation	Nitrification	
	%	mg kg ⁻¹		mg kg ⁻¹ d ⁻¹		
Undrained	7.39*	338	15.9	1.66	0.01	
Drained	6.29	328	18.4*	1.81*	0.32*	

Table 5 Comparison of C and N transformation rates in adjoining undrained and drained grassland soils. * Denotes significant (P<0.10) difference between undrained and drained soils for a given parameter. MB-N = microbial biomass-N. D.V. Murphy (unpublished data).

4.5 Pesticides

Microorganisms play an important role in the biodegradation of pesticides. herbicides and other environmental contaminants. Biodegradation may occur through a series of independent reactions; the direct interaction of a number of microorganisms in a consortium is then required for complete degradation to occur. Enhanced degradation rates (i.e. reduced microbial lag phase) of chemicals can occur after repeated applications to the same soil (Roeth 1986, Smith and Lanford 1990) as a result of preferential selection of the microorganisms/biochemical pathways involved. This adaptation increases the rate of biodegradation and is so effective in some instance that the efficacy of the pesticide (Roeth 1986, Felsot 1989) or herbicide (Audus 1949) is reduced sufficiently to limit plant productivity.

The direct effect of pesticides on soil organisms depends on the type and specificity of the chemical, the susceptibility of target species and the rate of application (van der Werff 1996). Fungicides usually exert predictable negative effects on the fungal component of the soil microbial biomass; nematicides and soil fumigants may also cause a significant temporary reduction in the soil microbial biomass. Herbicides and insecticides tend to have smaller and more variable effects. Hart and Brookes (1996) showed that the continuous use of five pesticides (either singly or in combination) had no measurable long-term harmful effects on the soil microbial biomass or its activity. The addition of aldicarb (2-methyl-2-(methylthio)propionaldehyde O-methylcarbamoyloxime) even increased microbial biomass carbon by 7-16%. The increasing specificity and reduced doses of active ingredients in new pesticide formulations has resulted in negative effects of pesticides on soil microorganisms to be recorded more rarely.

4.6 Inorganic Fertilisers

Mineral fertilisers (usually simply inorganic salts) are primarily used to overcome the nutrient limitations to plant growth, which occur in many farming systems. They may also be used to optimise product quality. The response of the microbial biomass to fertiliser amendments depends critically on whether the nutrient applied is limiting microbial activity or growth. Additionally at high rates of fertiliser addition, osmotic effects may occur, especially in zones close to fertiliser granule or liquid injection points. However, such effects are only temporary and often only at rates of fertiliser addition well in excess of normal farm rates. High concentrations of soluble nutrients in the soil have been shown to discourage the activity of some symbiotic microorganisms. For example, N_2 fixation by rhizobia is significantly reduced in soils with high concentrations of mineral N. Similarly high concentrations of soluble P in soil solution suppress the infectivity of mycorrhizal fungi to their host plants.

Mineral N applications have been shown, depending on the study, to either increase or decrease microbial biomass. However, around half of all studies published show only very slight effects (Wardle 1992). Application of anhydrous ammonia initially kills many soil microorganisms; bacteria and actinomycete populations recover within 1 to 2 weeks. However the fungal population may take as long as 7 weeks to recover (Doran and Werner 1990). Long-term applications of ammonium fertiliser to grassland caused a significant decrease in methane oxidation rates, but the application of nitrate for the same length of time did not (Willison et al. 1995, Table 6). In addition, a negative correlation between short-term methane uptake and the rate of ammonium applied was measured for arable and grassland soils in the laboratory (Tlustos et al. 1998). The use of ammonium fertiliser may also favour the development of a population of soil nitrifiers, which outcompete methanotrophs for niche environments within the soil. While nitrifiers are also able to oxidise methane, their rates of oxidation are significantly slower than those of methanotrophs (Bedard and Knowles 1989).

Targeted chemicals can be used as a fertiliser coating or applied directly to the soil to inhibit nitrification (usually by competition for the active site of the ammonium mono-oxygenase enzyme; McCarty 1999). By maintaining added N in the ammonium form for an extended period, losses can be reduced, plant uptake efficiency increased and microbial immobilisation of applied N may be increased. Use of nitrification inhibitors does not seem to have any long-term negative effect on the population of nitrifying bacteria in soil (apart from reducing N availability). There has been little uptake of such technologies in conventional agricultural practice, however, as the agronomic benefits often do not outweigh their cost. Environmental concerns of nitrate leaching may lead to the use of nitrification inhibitors in specific regions in the future.

	No N added	144 kg N ha ⁻¹ y ⁻¹	288 kg N ha ⁻¹ y ⁻¹	Farmyard manure	
	Plot 3	Plot 8	Plot 16	Plot 2.2	
^a Wheat yield	0.93	6.01	8.22	4.93	
(t ha ⁻¹ at 85% dry matter)					
^a Estimated return in stubble	0.6	2.3	3.1	1.9	
and chaff (t ha ⁻¹)					
^a pH (H ₂ O)	8.2	7.3	7.8	7.8	
^a Soil organic C (%)	0.76	1.06	1.16	3.00	
^a Soil organic N (%)	0.09	0.12	0.13	0.31	
^a Olsen P (mg kg ⁻¹)	7	78	75	102	
^b Microbial C (mg kg ⁻¹)	167	259	nd	545	
^c Microbial P (mg kg ⁻¹)	6.0	5.3	nd	28.9	
^d CO ₂ production	7.2	8.5	9.5	13.8	
$(mg CO_2 - C kg^{-1} d^{-1})$					
^d Gross N mineralisation	0.08	0.23	0.39	0.89	
$(mg N kg^{-1} d^{-1})$					
^e Gross nitrification	0.16	0.21	nd	0.76	
$(mg N kg^{-1} d^{-1})$					
^d Methane oxidation	0.50	0.43	0.24	0.53	
$(\mu g CH_4 - C kg^{-1} d^{-1})$					
^e Nitrifier populations gene	$1.3 \ge 10^4$	5 x 10 ⁵	nd	1.2 x 10 ⁵	
copies g ⁻¹					

Table 6 Pools and rates of microbially mediated nutrient transformations in plots of the Broadbalk continuous wheat experiment, Rothamsted Research UK. The soil is a calcareous silty clay loam. Plots 8 and 16 receive maintenance applications of P, K and Mg.

^a P.R. Poulton (unpublished data). Data from 1997 except wheat yield which is the average of 1996-2000. ^b Wu (1991) PhD thesis. ^c Brookes *et al.* (1984). ^d D.V. Murphy (unpublished data). ^e Mendum *et al.* (1999). nd = not determined.

Fertilisers can also have indirect effects on soil microorganisms through effects on plant growth. For example, optimisation of potassium (K) fertilisation can have a stimulatory effect on microbial activity through increases in root exudation, which supply energy to the microbial biomass. The use of fertilisers increase plant yield and thus increases the return of C to soil in above- and below-ground plant residues, which increase soil microbial activity (see review; Dick 1992). On the Broadbalk Continuous Wheat Experiment (started in 1843) long-term inorganic N applications resulted in a small increase in soil organic matter, heterotrophic microbial activity and microbial biomass compared to plots that have never received N fertiliser

(Table 6). However, rates of gross N mineralisation are significantly higher where larger rates of N fertiliser have been applied (Table 6).

4.7 Organic Fertilisers

Many cropping systems use the waste products of livestock enterprises as part of their fertilisation strategy either as solid materials (manure) or in liquid form (slurry). Other organic materials e.g. sewage sludge, food processing wastes and composts of various materials are also applied to soils depending on local availability. The application of organic materials tends to stimulate the microbial biomass directly and substantially, unlike applications of mineral fertilisers (Wardle 1992, Table 6). Organic fertilisers add C, N and other nutrients simultaneously satisfying components of the microbial population which are (usually) otherwise C-limited. Continuing release of nutrients as the materials are slowly decomposed in soils can also sustain the microbial biomass population for longer periods of time compared to the impact of mineral fertilisers e.g. the maintenance of a higher population of nitrifiers where farmyard manure rather than mineral fertilisers were applied in the Broadbalk experiment (Table 6).

Achieving synchrony between crop demand and nutrient supply is very difficult (Myers et al. 1997) particularly where nutrients are supplied solely through microbially mediated chemical transformations and decomposition of a diverse and variable range of organic materials. However, optimum efficiency of nutrient use seems to be achieved in many situations where mineral fertilisers and organic materials are used together in fertilisation strategies for cropping systems (Palm et al. 1997). There is some evidence that the mineral N pool applied in manures is more efficiently used for plant uptake than mineral N fertiliser (Stockdale et al. 1995). Also a large proportionate increase in both microbial P and the conventionally measured forms of available P is measured when farmyard manure is applied over the long-term (Table 6). In soils, which strongly fix inorganic P, combined use of soluble phosphate fertilisers with manure stimulates the uptake of P by the biomass, thus protecting it from immediate fixation and significantly increasing crop yield (Twomlow et al. 1999). Incorporation of the mineral N and P added in manure into the microbial biomass through immobilisation may protect these nutrients from loss before crop roots are fully developed and release of nutrients through microbial biomass turnover and predation may be more closely matched to crop demand.

Application of manures and/or sewage sludge to soils can significantly increase the heavy metal loading of soils. For example, Brookes and McGrath (1984) demonstrated that heavy metals derived from sewage sludge substantially reduced microbial biomass even twenty years after application.

The reduced microbial activity where organic materials are repeatedly applied leads to extreme accumulation of organic matter in the soil (Chander and Brookes 1991). Also, heavy metals decrease microbial diversity as a result of species extinction due to a lack of tolerance to the imposed stress and/or the competitive advantage of certain species who predominate in the presence of the heavy metal stress (Giller *et al.* 1998). Heavy metal content of organic materials therefore has significant implications for the use and management of such materials in agricultural systems.

4.8 Other Soil Amendments

Liming of soils to counteract acidity caused by atmospheric deposition, fertiliser addition or natural mineral weathering is widely practiced to optimise soil pH and other conditions for crop growth. Consequently, liming also increases both microbial biomass and specific populations (e.g. nitrifiers). Liming also creates soil conditions that favour the microbial processes that degrade hydrophobic substances around sand grains and thus reduce the water repellency of sandy soils (Roper 1998) and increase the populations of wax-degrading bacteria (mainly actinomycetes).

Amending clay soils with sand and sandy soils with clay (particularly calcareous clays, i.e. marling) has been practiced for many centuries worldwide to improve crop nutrition and soil structure (e.g. Piggott 1981). Clay amendment still occurs today (e.g. on infertile sandy soils in Australia) and has been shown to increase crop yields and thus plant above- and below-ground returns, which affect the microbial biomass indirectly, as discussed above. Clay amendment also ameliorates the non-wetting characteristics of sandy soils, which is likely to lead to improved water holding capacity and protects microorganisms from desiccation (Bushby and Marshall 1977) thus improving conditions for microbial activity (Marshall 1975).

Applications of glucose and molasses to soil are currently being promoted as a means of 'feeding the microbes' directly and enhancing general soil biological fertility as the additional C is cycled through the soil food web. Daly and Stewart (1999) found that CO_2 evolution increased after addition of molasses to soil but there was no corresponding increase in mineralisation of N, S or P, i.e. the molasses was rapidly broken down without any additional stimulation of microbial decomposition of organic matter in the soil. C addition rates are often low (10-50 kg C ha⁻¹) and given that 40-60% of the organic C is respired during microbial decomposition, little C is directly assimilated by the microorganisms (Wu 1991). As a result, regular applications are likely to be required to enhance microbial activity and cause significant microbial immobilisation of nutrients. Humic acids can also be added to soils where they are degraded and/or transformed by soil microorganisms as a supplemental source of organic carbon (see review; Filip *et al.* 1998).

4.9 Microbial Inoculants

Inoculants have been used successfully to enhance a limited number of microbial populations in soil. Most notably Rhizobium inoculation to legume crops to maximise plant N uptake through symbiotic biological N₂ fixation has proved to be highly successful (see Chapter 6). By 1958, 10⁷ hectares in the former Soviet Union had been treated with various bacterial inocula. increases in yield of 10-20% were reported in 50-70% of trials and similar results have also been obtained elsewhere (Kloepper et al. 1989). Phosphatesolubilising microorganisms (e.g. Aspergillus, Penicillium) have long been promoted to increase P uptake by plants (see review; Whitelaw 2000). Freeliving N₂ fixing microorganisms (e.g. Azotobacter) have also been applied to the soil to increase plant N availability. Soil amendments, with more generalised microbial populations, are still widely used (Daly and Stewart 1999, Kinsey and Walters 1999). However, it is often difficult to determine the causal link between the introduction of beneficial microorganisms and product claims. Increases in plant yield associated with such inoculants have also been partly attributed to the enhancement of root growth by bacterial phytohormone production and/or nutrients supplied by the turnover of the added inoculum itself (Bashan and Holguin 1997, de Freitas et al. 1997).

The performance of microbial inocula in trials is very inconsistent. This is not surprising given the complexity of the relationships between inoculants, indigenous populations, crops, climate and the soil matrix. The major constraint to the successful introduction of microbial inoculants to soil is the ability of an introduced microbial population to exist at levels above indigenous population numbers (Hirsch 1996). In most cases it will be unlikely that introduced microorganisms will be more suited than the indigenous population, which has already co-evolved to cope with localised environmental conditions (e.g. substrate, temperature, prolonged drying, periodic waterlogging, pH) and management pressures (land use, tillage etc.). Greater success is likely with the introduction of endophytes, which have less competition within soil roots. A fundamental understanding of the growth and survival characteristics of the microorganisms along with knowledge of how they are likely to interact with the indigenous microbial population and plant species (i.e. crop rotation) will aid in successful introduction of specific microbial inoculants.

5. CONCLUSION

Many of the chemical transformations, which occur in soil, are mediated Microorganisms therefore have a major by the soil microbial biomass. controlling influence on the cycling and loss of nutrients in soil and the regulation of plant nutrient availability, as well as many other transformation processes. The quantity and quality of organic matter in soil is a major factor in controlling the abundance and activity of microorganisms and therefore underpins many of the microbially mediated chemical transformations in While the direct and indirect effects of common agricultural soil. management practices on the soil microbial biomass are known, it is less clear which combination of locally adapted management practices are able to maintain and increase soil organic matter status and thus likely to optimise the activity of the microbial biomass in soil (see Chapter 11). At the coarsest level it can be readily advised that minimum appropriate soil tillage with regular incorporation of a diverse range of crop residues and other organic materials is the key to supporting enhanced microbial activity and associated chemical transformations in agricultural soils.

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7. **REFERENCES**

- Anderson T H and Domsch K H 1989 Ratios of microbial biomass carbon to total organic carbon in arable soils. Soil Biology and Biochemistry 21: 471-480.
- Anon. 2000 Fertiliser Recommendations for Agricultural and Horticultural Crops. UK Ministry of Agriculture Fisheries and Food Reference Book 209. pp. 177. Stationery Office. London.
- Arah J R M and Smith K A 1989 Steady-state denitrification in aggregated soils a mathematical model. Journal of Soil Science 40: 139-149.
- Audus L J 1949 Biological detoxification of 2,4-D. Plant and Soil 3: 170-192.
- Aulakh M S Rennie D A and Paul E A 1984 Gaseous nitrogen losses from soils under zero till as compared with conventional-till management systems. Journal of Environmental Quality 13: 130-136.
- Bååth E 1996 Adaptation of soil microbial communities to prevailing pH in different soils. FEMS Microbiolgy Ecology 19: 227-237.

- Bashan Y and Holguin G 1997 *Azospirillim*-plant relationships: Environmental and physiological advances. Canadian Journal of Microbiology 43: 103-121.
- Baucher M, Monties B, Van Montagu M and Boerjan W 1998 Biosynthesis and genetic engineering of lignin. Critical Reviews in Plant Sciences 17: 125-197.
- Bedard C and Knowles R 1989 Physiology, biochemistry and specific inhibitors of CH₄, NH₄⁺ and CO oxidation by methanotrophs and nitrifiers. Microbiological Reviews 53: 68-84.
- Brookes P C and McGrath S P 1984 Effects of metal toxicity on the size of the soil microbial biomass. Journal of Soil Science 35: 341-346.
- Brookes P C, Powlson D S and Jenkinson D S 1984 Phosphorus in the soil microbial biomass. Soil Biology and Biochemistry 16: 169-175.
- Bushby H V A and Marshall K C 1977 Some factors affecting the survival of rootnodule bacteria on desiccation. Soil Biology and Biochemistry 9: 143-147
- Campbell C A, Biederbeck V O, Zentner R P and Lafond G P 1991 Effect of crop rotation and cultural practices on soil organic matter, microbial biomass and respiration in a thin black Chernozem. Canadian Journal of Soil Science 71: 363-376.
- Campbell C A, Lafond G P, Biederbeck V O, Wen G, Schoenau J and Hahn D 1999 Seasonal trends in soil biochemical attributes: effects of crop management on a black chernozem. Canadian Journal of Soil Science 79: 85-97.
- Cavigelli M A and Robertson G P 2001 Role of denitrifier diversity in rates of nitrous oxide consumption in a terrestrial ecosystem. Soil Biology and Biochemistry 33: 297-310.
- Chander K and Brookes P C 1991 Effects of heavy metals form past applications of sewage sludge on microbial biomass and organic matter accumulation in a sandy loam and a silty loam UK soil. Soil Biology and Biochemistry 23: 927-932.
- Curl EA and Truelove B 1986 The rhizosphere. Springer-Verlag. Berlin.
- Dalal R C 1998 Soil microbial biomass what do the numbers really mean? Australian Journal of Experimental Agriculture 38: 649-665.
- Daly M J and Stewart D P C 1999 Influence of 'effective microorganisms' (EM) on vegetable production and carbon mineralisation A preliminary investigation. Journal of Sustainable Agriculture 14: 15-25.
- de Freitas J R, Banerjee M R and Germida J J 1997 Phosphate-solubilizing rhizobacteria enhance the growth and yield but not phosphorus uptake of canola (*Brassica napus* L.). Biology and Fertility of Soils 24: 358-364.
- Dick R P 1992 A review long-term effects of agricultural systems on soil biochemical and microbial parameters. Agricultural Ecosystems and Environment 40: 25-36.
- Doran J W and Werner M R 1990 Management and soil biology. *In*: Sustainable Agriculture in Temperate Zones. C A Francis, C B Flora, L D King (eds.) pp. 151-177. Wiley. New York.
- Doran J W 1980 Microbial changes associated with residue management with reduced tillage. Soil Science Society of America Journal 44: 518-524.
- Edwards C A, Lal R, Madden P, Miller R H and House G 1990 Sustainable Agricultural Systems. Soil and Water Conservation Society. Ankeny, Iowa.
- Ettema C H and Wardle D A 2002 Spatial soil ecology. Trends in Ecology and Evolution 17: 177-183.
- Felsot A S 1989 Enhanced biodegradation of insecticides in soil: implications for agroecosystems. Annual Reviews in Entomology 34: 453-476.

- Filip Z, Claus H and Dippell G 1998 Degradation of humic substances by soil microorganisms – a review. Zeitschrift fur Pflanzenernahrung und Bodenkunde 161: 605-612.
- Foster R C 1988 Microenvironments of soil microorganisms. Biology and Fertility of Soils 6: 189-203.
- Foster R C, Rovira A D and Cook T W 1983 Ultrastructure of the root-soil interface. The American Phytopathology Society. St. Paul, Minnesota, USA.
- Fulthorpe R R, Rhodes A N and Tiedje J M 1998 High levels of endemicity of 3chlorobenzoate-degrading soil bacteria. Applied Environmental Microbiology 64: 1620-1627.
- Garcia C and Hernandez T 1996 Influence of salinity on the biological and biochemical activity of a calciorthid soil. Plant and Soil 178: 255-263.
- Giller K E, Beare M H, Lavelle P, Izac A-M N and Swift M J 1997 Agricultural intensification, soil biodiversity and agroecosystem function. Applied Soil Ecology 6: 3-16.
- Giller K E, Witter E and McGrath S P 1998 Toxicity of heavy metals to microorganisms and microbial processes in agricultural soils: a review. Soil Biology and Biochemistry 30: 1389-1414.
- Grayston S J, Vaughan D and Jones D 1996 Rhizosphere carbon flow in trees, in comparison with annual plants: the importance of root exudation and its impact on microbial activity and nutrient availability. Applied Soil Ecology 5: 29-56.
- Grime J P 1997 Biodiversity and ecosystem function: the debate deepens. Science 277: 1260-1261.
- Handayanto E, Cadisch G and Giller K E 1995 Manipulation of quality and mineralisation of tropical legume tree prunings by varying nitrogen supply. Plant and Soil 176: 149-160.
- Hart M R and Brookes P C 1996 Soil microbial biomass and mineralisation of soil organic matter after 19 years of cumulative field applications of pesticides. Soil Biology and Biochemistry 28: 1641-1649.
- Hendrix P E, Parmalee R W, Crossby Jr D A, Coleman D C, Odum E P and Groffman P M 1986 Detritus food webs in conventional and no-tillage agroecosystems. BioScience 36: 374-380.
- Hirsch P R 1996 Population dynamics of indigeneous and genetically modified rhizobia in the field. New Phytologist 133: 159-171.
- Hunter-Cevera J C 1998 The value of microbial diversity. Current Opinion in Microbiology 1: 278-285.
- Jarvis S C, Stockdale E A, Shepherd M A and Powlson D S 1996 Nitrogen mineralisation in temperate agricultural soils: Processes and measurement. Advances in Agronomy 57: 187-234.
- Jenkinson D S and Ladd J N 1981 Microbial biomass in soil: Measurement and turnover. *In*: Soil Biochemistry Volume 5. E A Paul and J N Ladd (eds.) pp. 415-471. Marcel Dekker. New York.
- Kennedy A C and Gewin V L 1997 Soil microbial diversity: Present and future considerations. Soil Science 162: 607-617.
- Kinsey N and Walters C 1999 Neal Kinsey's Hands-on Agronomy. Acres USA.
- Kirchmann H, Pichlmayer F and Gerzabek M H 1996 Sulfur balances and sulfur-34 abundance in a long term fertiliser experiment. Soil Science Society of America Journal 60: 174-178.
- Kloepper J W, Lifshitz R and Zablotowicz R M 1989 Free-living bacterial inocula for enhancing crop productivity. Trends in Biotechnology 7: 39-44.

- Kumar K and Goh K M 2000 Crop residues and management practices: Effects on soil quality, soil nitrogen dynamics, crop yield, and nitrogen recovery. Advances in Agronomy 68: 197-319.
- Ladd J N, Foster R C and Skjemstad J O 1993 Soil structure: carbon and nitrogen metabolism. Geoderma 56: 401-434.
- Ladha J K, George T and Bohlool B B (eds.) 1992 Role of biological nitrogen fixation in sustainable agriculture. Plant and Soil 141: 1-209.
- Marshall K C 1975 Clay mineralogy in relation to survival of soil bacteria. Annual Review of Phytopathology 13: 357-373.
- Martens D A 2001 Nitrogen cycling under different soil management systems. Advances in Agronomy 70: 143-192.
- McCarty G W 1999 Modes of action of nitrification inhibitors. Biology and Fertility of Soils 29: 1-9.
- McGonigle T P and Miller M H 1996 Development of fungi below ground in association with plants growing in disturbed and undisturbed soils. Soil Biology and Biochemistry 3: 263-269.
- Mendum T A, Sockett R E and Hirsch P R 1999 Use of molecular and isotopic techniques to monitor the response of autotrophic ammonia-oxidising populations of the β subdivision of the class *Proteobacteria* in arable soils to nitrogen fertiliser. Applied and Environmental Microbiology 65: 4155-4162.
- Moore J M, Klose S and Tabatabai M A 2000 Soil microbial biomass carbon and nitrogen as affected by cropping systems. Biology and Fertility of Soils 31: 200-210.
- Murphy D V, Fillery I R P and Sparling GP 1998 Seasonal fluctuations in gross N mineralisation, ammonium consumption and microbial biomass in a Western Australian soil under different land uses. Australian Journal of Soil Research 49: 523-535.
- Myers R J K, van Noordwijk M and Vityakon P 1997 Synchrony of nutrient release and plant demand: Plant litter quality, soil environment and farmer management options. *In:* Driven by Nature: Plant litter quality and decomposition. G Cadisch and K E Giller (eds.) pp. 215-229. CAB International. Wallingford, Oxon, UK.
- Neal J L Jr, Larson R I and Atkinson T G 1973 Changes in rhizosphere populations of selected physiological groups of bacteria related to substitution of specific pairs of chromosomes in spring wheat. Plant and Soil 39: 209-212.
- Palm C A, Myers R J K and Nandwa S 1997 Organic-inorganic nutrient interactions in soil fertility replenishment. *In:* Replenishing Soil Fertility in Africa. R J Buresh, P A Sanchez and F G Calhoun (eds.) ASA-SSSA Special Publication 51: 193-218.
- Paustian K, Robertson G P and Elliot E T 1995 Management impacts on carbon storage and gas fluxes (CO₂, CH₄) in mid-latitude cropland. *In:* Soil Management and Greenhouse Effect. R Lal, J Kimble, E Levine and B A Stewart (eds.) pp. 69-83. Advances in Soil Science. Lewis Publishers. Boca Raton, USA.
- Perry D A, Amaranthus M P, Borchers J G, Borchers S L and Brainerd R E 1989 Bootstrapping in ecosystems. Bioscience 39: 230-237.
- Piggott S 1981 The Agrarian History of England and Wales Volume 1. I. Prehistory. pp. 213-214. Cambridge University Press. Cambridge.
- Powlson D S, Brookes P C and Christensen B T 1987 Measurement of microbial biomass provides an early indication of changes in total soil organic matter due to straw incorporation. Soil Biology and Biochemistry 19: 159-164.
- Ritz K and Griffiths B S 2001 Implications of soil biodiversity for sustainable organic matter management. *In:* Sustainable management of soil organic matter. R M Rees,

B C Ball, C D Campbell and C A Watson (eds.) pp. 343-356. CAB International. Wallingford, Oxon, UK.

- Roeth F W 1986 Enhanced herbicide degradation in soil with repeat application. Reviews in Weed Science 2: 45-65.
- Roper M 1998 Sorting out sandy soils. Microbiology Australia 19: 6-7.
- Roper M M and Marshall K C 1978 Effects of a clay mineral on microbial predation and parasitism of *Escherichia coli*. Microbial Ecology 4: 279-289.
- Sakadevan K, MacKay A D and Hedley M J 1993 Sulphur cycling in New Zealand hill country pastures. II. The fate of fertiliser sulphur. Journal of Soil Science 44: 615-624.
- Smith A E and Lanfond G P 1990 Effects of long-term phenoxyalkanoic acid field applications on the rate of microbial degradation. ACS Symposium Series 426: 14-22.
- Sparling G P, Murphy D V, Thompson R D and Fillery I R P 1995 Short-term net N mineralisation from plant residues and gross and net N mineralisation from soil organic N after rewetting of a seasonally dry soil. Australian Journal of Soil Research 33: 961-973.
- Strong D T, Sale P W G and Helyar K R 1998 The influence of the soil matrix on nitrogen mineralisation and nitrification. I. Spatial variation and a hierarchy of soil properties. Australian Journal of Soil Research 36: 429-447.
- Strong D T, Sale P W G and Helyar K R 1999 The influence of the soil matrix on nitrogen mineralisation and nitrification. IV. Texture. Australian Journal of Soil Research 37: 329-344.
- Stockdale E A, Rees R M and Davies M G 1995 Nitrogen supply for organic cereal production in Scotland. *In:* Soil Management in Sustainable Agriculture. H F Cook and H C Lee (eds.) pp. 254-264. Proceeding of third international conference on Sustainable Agriculture. Wye College Press. Ashford, UK.
- Thompson J P 1992 Soil biotic and biochemical factors in a long-term tillage and stubble management experiment on a Vertisol. II. Nitrogen deficiency with zero tillage and stubble retention. Soil and Tillage Research 22: 339-361.
- Tilman D, Knops J, Wedin D, Reich P, Ritchie M and Siemann E 1997 The influence of functional diversity and composition on ecosystem processes. Science 277: 1300-1302.
- Tlustos P, Willison T W, Baker J C, Murphy D V, Pavlikova D, Goulding K W T and Powlson D S 1998 Short-term effects of nitrogen on methane oxidation in soils. Biology and Fertility of Soils 28: 64-70.
- Torsvik V, Goksøyr J, Daae F L, Sørheim R, Michalsen J and Salte K 1994 Use of DNA analysis to determine the diversity of microbial communities. *In:* Beyond the biomass. Compositional and functional analysis of soil microbial communities. K Ritz, J Dighton and K E Giller (eds.) pp. 39-48. Wiley, Chichester, New York.
- Twomlow S, Riches C, O'Neill D, Brookes P and Ellis-Jones J 1999 Sustainable dryland smallholder farming in sub-saharan Africa. Annals of Arid Zone 38: 93-135.
- van der Werff H M G 1996 Assessing the impact of pesticides on the environment. Agriculture Ecosystems and Environment 60: 81-96.
- van Veen J A and Kuikman P J 1990 Soil structural aspects of decomposition of organic matter by micro-organisms. Biogeochemistry 11: 213-233.
- Verhoef H A and Brussaard L 1990 Decomposition and nitrogen mineralisation in natural and agroecosystems: The contribution of soil animals. Biogeochemistry 11: 175-211.

- Wardle D A 1992 A comparative assessment of factors which influence microbial biomass carbon and nitrogen levels in soil. Biological Reviews 67: 321-355.
- Watts C W, Eich S and Dexter A R 2000 Effects of mechanical energy inputs on soil respiration at the aggregate and field scales. Soil and Tillage Research 53: 231-243.
- Whitelaw M A 2000 Growth promotion of plants inoculated with phosphate-solubilising fungi. Advances in Agronomy 69: 99-151.
- Willison T W, Webster C P, Goulding K W T and Powlson D S 1995 Methane oxidation in temperate soils: effects of land use and the chemical form of nitrogen fertiliser. Chemosphere 30: 539-546.
- Wilkinson S C, Anderson J M, Scardelis S P, Tisiafouli M, Taylor A and Wolters V 2002 PLFA profiles of microbial communities in decomposing conifer litters subject to moisture stress. Soil Biology and Biochemistry 34: 189-200.
- Wu J 1991 The turnover of organic C in soil. PhD Thesis. University of Reading. UK.
- Yachi S and Loreau M 1999 Biodiversity and ecosystem productivity in a fluctuating environment. The insurance hypothesis. Proceedings of the National Academy of Sciences of the United States of America 96: 1463-1468.
- Young I M and Ritz K 1998 Can there be a contemporary ecological dimension to soil biology without a habitat? Discussion. Soil Biology and Biochemistry 30: 1229-1232.
- Zak J C, Willig M R, Moorhead D L and Wildman H G 1994 Functional diversity of microbial communities: a quantitative approach. Soil Biology and Biochemistry 26: 1101-1108.