15. SOILS AS COMPONENTS AND CONTROLLERS OF ECOSYSTEM PROCESSES

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INTRODUCTION

The recognition of soil as being at once an ecosystem component and a controller of ecosystem processes is based on both its physicochemical and its biological characteristics. Nearly everyone can think of a specific example where parent materials play a major role in ecosystem structure and function. The move from a clay to a sandy substratum, the effect of soil pH and that of drainage and aeration are especially noticeable in plant and soil animal components. The differential distribution of plant species is the characteristic that is most noticeable (Montagnini *et al.* 1986; Inouye *et al.* 1987).

It was long thought that soil characteristics such as the composition of parent materials, particle size, aggregation and bulk density together with chemical attributes such as pH, buffer capacity and the ability to absorb organic and inorganic constitutents were stable attributes. We now realize that all soils are sensitive to both long- and short-term perturbations that can cause major changes in ecosystem processess (Buyanovsky, Kucera & Wagner 1987). Ecosystem–anthropogenic processes have over long periods of time generally (and over very short periods of time in a few cases) completely changed the characteristics of the soil and its ability to support plant growth under either native or agricultural systems. Examples include the extensive areas of the cerrado in Brazil where extensive weathering has caused extreme aluminium toxicity and phosphorus deficiency (Lathwell & Grove 1986). Examples of anthropogenic alterations include erosion and nutrient loss after cultivation or clear-cutting of forest (Vitousek & Matson 1985), the effects of acid rain, contamination with heavy metals, or, in the case of agricultural soils, amelioration with phosphate and lime. Man has an inordinate capability to alter the soil resource, and must realize that changing the steady state that took hundreds and even thousands of years to establish can lead to many unpredictable effects (Waring 1989).

The structure and nature of soil organic matter represents a long-term record of previous ecosystem production, and plant and animal community composition; it is also a continuing controller of the processes occurring within that ecosystem. At least 50% of the carbon dynamics and the vast majority of the other nutrient transformations occur underground (McGill & Cole 1981). The nutrient transformations in turn control plant growth directly, and many interactions between plants and animals and micro-organisms indirectly. Yet the soil was recently described as the only major 'black box' left in ecology (J. E. Cantlon 1988, private communication). There are divergent views concerning the need to unravel the complexities within this box. There is great diversity within the soil populations. Usually more than one type of organism is capable of carrying out a specific reaction. For example, there are many different cellulases. Is it important that we identify each class of enzyme or can we study the overall process? Can we look at the soil as somewhat akin to a complex biochemical entity where the overall processes are most important?

The general relationships governing plant decomposition are known and fairly well described mathematically (Paul & Van Veen 1978; Parton *et al.* 1987). There are a number of major environmental issues that will require a better knowledge of individual-organism controlled processes. These include the following: (i) degradation of pesticides, (ii) controls on organic matter and plant residue mineralization, (iii) nitrification and nitrogen leaching, (iv) a broad range of biological alternatives to the chemicals now used in weed and other pesticide management practices, and (v) the use of genetically engineered organisms in nature. These investigations have become much more feasible with the availability of rapid automated tracer techniques, powerful computers for modelling, high-resolution laser microscopes with image processing, automated organic analyses and molecular genetic techniques such as the gene probe and RNA sequencing.

The micro-organisms as a group dominate the underground biomass both in the size of the nutrient pools held therein and in the range of processes they carry out (Paul & Clark 1988). Feeding on these populations by the soil animals occurs in nearly all ecosystems. However, the significance of the animals varies from system to system. In some systems the mixing effect is extremely important (Coleman, Reid & Cole 1983). In other systems the animals play a major role in decomposition (Clarholm 1985; Hunt *et al.* 1987). In some, though animals are present and can benefit from the organic matter and microbial biomass as a source of food, they may not play a major role in controlling the nutrient cycling.

The products of biological activity are transformed by physical-chemical reactions to form the more stable soil organic matter (SOM) compounds through the processes collectively described as humification (Aiken *et al.* 1985). A better understanding of the SOM dynamics with more exact numbers is required for an improved understanding of past processes, and more importantly for the ability to manage these processes for greater ecosystem productivity and/or stability.

Carbon, nitrogen, phosphorus and sulphur are the major elements in organic matter transformations (McGill & Cole 1981). It has been recognized that the stoichiometry of the C, N and P observed by the Redfield in plankton can be linked to the protoplasmic contents of all life (Reiners 1986). Because soil phosphorus must be supplied by the weathering of minerals, or by its concentration in the surface through root feeding at greater depths, it is said to control the inputs of C and N into soils (Walker & Syers 1976; Tate & Salcedo 1988). The known controls of phosphorus on biological N_2 fixation (Hardy, Lamborg & Paul 1983) further emphasize the significance of this element. In the long term accumulation of bioactive phosphorus may be of the most significance to ecosystem functioning, but in the short term the many and varied transformations of nitrogen show the greatest changes (Parton *et al.* 1987). Accurate measurements of these transformations therefore are most important criteria in the advance toward a more exact ecology.

In this review I will concentrate on the carbon and nitrogen interactions through the soil organic matter and the microbial biomass. Anthropogenic effects on microbial populations are of great significance to many ecosystems, and the final section is concerned with measuring and understanding these changes.

STORAGE OF CARBON AND NITROGEN

The need for better information relative to the functioning of the global carbon cycle and ecosystem dynamics has lead to a series of intensive studies to establish good base-line data for soil organic matter contents. Information on carbon and nitrogen storage for 3600 profiles has been compiled by Zinke *et al.* (1984). These represent values where carbon and nitrogen contents have been measured to at least one metre depth, and where soil bulk density values are known so that calculations on an area basis can be made (Table 15.1).

It may seem somewhat strange to talk about global measurements in a review designed to lead toward a more exact ecology. I, however, have found that individual scientists are so enamoured by the relative numbers within their own system that they forget to ask the obvious

TABLE 15.1. Estimated amounts of carbon (kg m^{-3}) and nitrogen (g m^{-3}) in the soil profile to 1 m depth in various climatic zones (from Zinke *et al.* 1984)

Climatic zone	C	N	C:N
Dry tundra	3.1	500	6
Moist tundra	10.9	638	17
Wet tundra	21	1250	17
Rain tundra	37	1200	17
Boreal dry bush	10.2	630	16
Boreal wet forest	14.9	980	15
Boreal rain forest	32.0	1500	22
Cool temperate desert	9.9	500	20
Cool temperate steppe	13.3	1030	13
Cool temperate wet forest	12.0	626	19
Cool temperate rain forest	20.3	800	25
Warm temperate desert	1.4	106	13
Warm temperate moist forest	9.3	650	14
Warm temperate wet forest	27.0	1800	14
Subtropical desert bush	5.4	380	14
Subtropical moist bush	9.2	990	9
Tropical desert	1.0	50	20
Tropical dry forest	10.2	885	11
Tropical moist forest	11.4	803	14
Tropical wet forest	15.0	655	23
Tropical rain forest	18.0	600	30

questions, 'Do the numbers make any sense?' and 'What have other people found?' These questions are of most importance when making comparisons on a geographical scale between ecosystems differing in temperature and moisture supply.

The interactive effects of moisture and temperature on primary production and system respiration must be considered together with the effects of different inputs to the substratum, e.g. litter or roots (Aber & Melillo 1980; Berg 1986). The effects of the nature of the substratum on decomposition rates and humification processes, and the role of anaerobiosis, also have to be taken into account (Richards 1987). Table 15.1 shows that increased moisture results in higher carbon accumulation in each of the temperature regimes. It also shows that, although the tropical rain forest does not have the accumulation of C that is found in the temperate forests, there still is a very significant concentration of organic materials potentially available, especially when the deeper soil layers of

these productive forests are taken into account. The N storage levels do not rise as much with moisture as those of C; thus, there is a general tendency for a rise in C : N quotient in more moist conditions. Whether this results from a reduction in decomposition of carbonaceous compounds, from an adaptation by the growing vegetation to lower N contents, from lower rates of N_2-fixation or possibly from higher rates of denitrification in the wetter systems has yet to be determined.

Lavelle (1984) investigated the effect of soil type on organic matter contents. However, organic matter accumulation in soils is so interwoven with moisture, temperature and, to some extent, the parent material that it proved difficult to differentiate the specific profile effects. Nevertheless, the analysis by Zinke *et al.* (1984) of 3600 profiles did show differences due to parent materials. The majority of soils, i.e. those derived from acid intrusive, ultra-basic and metamorphic parent materials, had mean carbon concentrations of 10–12 kg m^{-3}. The soils on basic extrusive materials (volcanic soils) known to contain minerals which have stabilizing effects on soil organic matter as well as having high inherent fertility showed an average of 22 kg m^{-3}. As was the case for all other studies, the diversity in the measurements for the various parent materials was high, showing that a great number of other factors also control soil organic matter content.

THE TURNOVER OF SOIL ORGANIC MATTER

It is now recognized that the majority of soil organic matter exists for extended periods with as much as 50% being at least 1000 years old (Stout, Goh & Rafter 1981; Van Veen & Paul 1981). The concept that a portion of the soil organic matter can be of physical importance in soil structure and erosion resistance, and yet be only very slowly decomposed has led to more exact numbers in nutrient turnover. Carbon dating has defined these old recalcitrant fractions. A second general fraction of organic matter, while not being as chemically resistant, is protected by inclusion within aggregates and by organo-mineral interactions (Jenkinson & Rayner 1977; Anderson & Paul 1984). This fraction persists for decades to as much as centuries. It is often depicted in soil organic matter models as 'protected' or 'stabilized' (Paul & Van Veen 1978; Parton, Stewart & Cole 1988).

The most important fraction, from a biological viewpoint, is that identified as the active or labile fraction. It is comprised of the microbial biomass itself, microbial detritus (especially cell walls), resistant plant materials and cytoplasmic constituents stabilized by adsorption to

surfaces. Because of their adsorption to surfaces many otherwise decomposable organic compounds persist for periods ranging from years to decades. The chemical diversity of these labile components ensures that no one chemical or physical fractionation can separate them from the rest of the soil milieu. These components can, however, be operationally defined, and can be estimated using long-term incubation or calculations based on isotopic dilution. Isotope dilution experiments with ^{15}N can determine that proportion of soil N that is as equally available as the ^{15}N of constituents that have been allowed to equilibrate in the soil for periods long enough to enter the measurable fractions (Paul & Juma 1981).

The most common method of estimation of the size and mineralization kinetics of the labile pools is to incubate the soil in the laboratory for extended periods (up to 42 weeks) under conditions where moisture and temperature and even aggregate structure have been equalized (Jones, Ratcliff & Dyke 1982). The mineralized N is usually transformed to nitrate, and can be leached from the soil system. The maximum accumulation of mineral N, designated as N_m, is an estimate of the mineralizable N. The decomposition rate constants of individual components of this pool can be determined by computer analysis of the shape of the mineralization curves for either C (Freytag 1986, 1987) or N (Smith *et al.* 1980; Juma, Paul & Mary 1984).

Table 15.2 shows that the spodosols have the highest average organic matter concentration. These soils originated under the moist boreal and subtropical conditions shown by Zinke *et al.* (1984) to be those under which large concentrations of organic matter accumulate. These are followed by the mollisols of the dry temperate and subtropical grasslands, while the aridisols of dry, temperate and subtropical regions have the lowest organic C concentration. These findings are in agreement with those of Zinke *et al.* (1984), reached on the basis of an ecosystem classification. However, the mineral N accumulated under long periods of incubation (N_m) is not a consistent portion of the total N. Twenty-two per cent of the total N of ultisols — the soils from moist, subtropical and tropical regions — is in the labile pool, whereas only 10–11% of the N of mollisols and spodosols representing temperate climates is made available during this incubation period. These differences greatly affect ecosystem functioning.

A more exact ecology requires that a reasonable estimate of the fluxes of soil organic matter on an annual basis be available. The data from Zinke *et al.* (1984) can be utilized to determine the global N content of soils, i.e. 105×10^{15}g (Petagram, Pg). Reasonably good estimates of

TABLE 15.2. Characteristics of different types of cultivated soil, and the mineralization of nitrogen in them (recalculated from Jones, Ratcliff & Dyke 1982)

Soil type/climate	Organic carbon (mg g^{-1})	Total nitrogen (mg g^{-1})	C : N quotient	Mineral nitrogen accumulated ($\mu g\ g^{-1}$)	Mineral nitrogen accumlated as % of total nitrogen
Aridisols (dry, temperate–subtropical)	6.0	0.8	7.5	112	15
Ultisols (moist, subtropical–tropical)	6.7	0.5	13	114	22
Alfisols (moist, temperate–subtropical)	10	1.0	10	171	17
Mollisols (dry, temperate–subtropical)	19	1.7	11	170	10
Spodosols (moist, boreal–subtropical)	33	2.6	13	270	11

global C fluxes now exist (Whittaker & Likens 1973; Bolin *et al.* 1979; King, DeAngelis & Post 1987) and it is known that plant growth is fastest when N is in stoichiometric balance with other elements (Waring 1989). However, as far as I know, there is no published estimate of the global N mineralization capacity of soils. This could theoretically be calculated by summation of individual site data such as those brought together by Smith & Paul (1989), who calculated N mineralization rates on the basis of first-order kinetic analyses and environmental parameters. This approach yielded a range of values from a low of 26 kg ha^{-1} $year^{-1}$ for a eucalypt forest to a high of 1095 kg ha^{-1} $year^{-1}$ in an arable soil. Such incubation data, whether obtained in the laboratory or under field conditions, cannot take into account either the effects of plant uptake or the counteracting fluxes in mineralization-immobilization turnover. The alternative is to relate mineralization of N to uptake of N by plants, which in turn is related to dry matter production by plants.

The series on 'State of the Art Research on Global Carbon Dioxide' (Olson, Watts & Allison 1983; Zinke *et al.* 1984; Farell 1987) has produced a comprehensive compendium on pool sizes and fluxes

involved in the global CO_2 cycles. The authors have developed site-specific as well as global models. Olson, Watts & Allison (1983), on the basis of a comprehensive summary of global primary production, estimated C production by plants to be 60 Pg per annum. This is only slightly higher than the estimates of Whittaker & Likens (1973). The transformation of data on plant primary production to plant N uptake requires a knowledge of plant N contents and of retranslocation of N within the plant. Annual plants such as wheat (Campbell, Nicholachuk & Warder 1977), because of root turnover and plant-N leaching during growth, take up more N than is found at harvest and can require an equivalent of 7% of their net primary C productivity as N uptake. Trees are known to retranslocate a considerable portion of their N content each year (Mellilo 1981) and there is similar evidence for perennial grasses (Clark 1977). While these translocations may lead to an overestimate of uptake by plants, there is a balancing tendency to underestimate uptake as a result of lack of information on rates of fine root turnover. This is known to be high in the few tree species that have been studied critically (Vogt, Grier & Vogt 1986). A stand of Douglas fir (*Pseudotsuga menziesii*) was found by Turner (1977) to redistribute 45% of its N and had a net N uptake requirement equal to 1% of C production.

Based on a value for N uptake of 1% of the net primary productivity of C in boreal forests, 2% for tropical forests, 1.5% for temperate forests, and 5% for grasslands, cultivated crops and tundra, one can use data such as those of Whittaker & Likens (1973) to calculate the global plant uptake of N. This is shown in Table 15.3 to be 1.1 Pg. The errors in such an estimate would come from uncertainties in the measurements of plant productivity and from the unknowns in the relative amounts of C and N accumulated. The latter would cause the greater error. While the estimate of 1.1 Pg probably has error levels of 25 to 50%, it provides a meaningful base for comparisons regarding other N fluxes. I hope it will also lead to more exact measurements with the aim of improving these preliminary calculations.

The global soil mineralization values can be estimated from the plant uptake values if the efficiency of soil N uptake is known. This number can be obtained from ^{15}N experiments. Numerous ^{15}N studies have shown that the proportion of added fertilizer N that is taken up by plants ranges from 0.1 to 0.7. The lower values come from forest studies (Heilman *et al.* 1982; Vitousek & Matson 1985) where there is a great deal of N immobilization. The higher values are from very highly fertilized agricultural fields with little N loss and negligible immobilization. The modal value for most field studies approximates 0.44.

TABLE 15.3. Estimates of total soil nitrogen and various fluxes of soil nitrogen for the earth (all in Pg)[a]

Soil N content	105[b]
Internal transformations	
Plant uptake of N	1.1[c]
Soil N mineralized	2.6[c]
Inputs	
Symbiotic fixation	0.12[d]
Asymbiotic fixation	0.060[d]
Fertilizer N applied	0.065[d]
Fertilizer N utilized	0.026[c]
Combustion and atmospheric	0.022[d]
Exports	
Denitrification	0.14[d]
Runoff and erosion	0.025[d]

[a]Pg = petagrams = 10^{15}g = 1 Gt.
[b]Zinke *et al.* (1984).
[c]Based on plant primary production, plant N translocation and efficiency of N uptake (see text).
[d]Knowles (1982).

Dividing the plant N uptake of 1.1 Pg by 0.44 results in an estimation of 2.5 Pg of soil N mineralized on a global basis annually. While the range in estimates has to be extensive for such a diversity of data, the data are very valuable in that they place the amount of soil N mineralization in perspective relative to the amounts of N_2 fixation, denitrification and N losses by erosion.

Biological N_2 fixation at 0.15 to 0.18 Pg (Knowles 1982) is small compared with the 2.6 Pg of soil N mineralized annually. However, the symbiotically fixed N can be assumed to be much more available to the plant, despite the fact that leakage and nodule turnover do occur. The N_2 fixed represents 14–16% of the 1.1 Pg of plant N uptake. The fertilizer N application of 0·065 Pg is subject to the partial uptake limitation discussed above, and, on a global basis, fertilizer accounts for only 2% of the global plant N uptake. Environmentalists who often point to fertilizers as major contributors to atmospheric pollution usually forget that soil N also is subject to low plant uptake, to losses, and to re-immobilization by soil micro-organisms as emphasized by Coleman, Reid & Cole (1983) and Vitousek & Matson (1985).

The values for denitrification and the other losses of N from the soil system have been calculated by techniques different from those used for N_2 fixation, yet the estimate of 0.14 Pg for denitrification is only slightly

lower than that of 0.18 Pg for symbiotic and asymbiotic fixation combined. Runoff and erosion has been estimated to be 0.025 Pg, approximately equal to that of the input of N by combustion and atmospheric precipitation.

MICROBIAL BIOMASS

Reproducible, reasonably rapid techniques for the measurement of the microbial biomass have been available for approximately 10 years, and estimates for microbial biomass in many ecosystems are now available. These allowed Smith & Paul (1989) to relate the size of the microbial biomass and its turnover rate to C inputs (Table 15.4). There is a good relationship between soil C and N content, but none, on a global basis, between litter input and soil organic C or N. Similarly, the size of the microbial biomass depends on many factors and, in the analysis of Smith & Paul (1989), was shown not to be correlated with organic matter content. The scarcity of measurements in some of the major vegetation types precludes accurate comparisons of C to N ratios within the microbial biomass. If the C: N ratios are truly as divergent as the ranges shown in this table, they would be a major factor to be considered in studies on ecosystem functioning.

Field measurements of turnover rates of micro-organisms are not yet available. Microbial turnover therefore has been calculated on the basis of a model that relates microbial growth to available energy supplies (Smith & Paul 1989). The calculated microbial turnover time of 0.07 years in tropical forests shows that a high nutrient input together with optimum growing conditions can result in turnover times faster than have been previously published. However, turnover rates of 14 times per year are still very slow when compared with laboratory growth rates. The similar estimates for turnover time in the microbial biomass of temperate grasslands and forests (0.32 amd 0.30 years) are intriguing. It will be interesting to see whether these estimates continue to be found to be similar as more data become available.

Soils should be the best overall reflection of ecosystem processes. Detailed examination of the 3600 soil profiles in the analyses of Zinke *et al.* (1984) should yield good estimates of variability between and within major life-zones. The variability in samples differed with vegetation type. Forested areas showed the greatest variability, twice that of the mean. Semi-desert and grassland were the least variable.

The most exact numbers, if not always the best interpretations, are obtained from single sites, each with a simple vegetation type on a single soil type. Nevertheless the variability within one agricultural field is often as great as that obtained across a transect of a climatic zone. Differences in slope, aspect and drainage cause differences in major soil type, plant growth and microbial content and activity. Not as easily recognized are the differences found in areas that, although relatively uniform in slope, have differences in parent material and internal drainage.

TABLE 15.4. Plant biomass, input of litter to soil, soil organic matter and microbial biomass of major global vegetation types

	Tropical forest	Temperate forest	Boreal forest	Savannah	Temperate grassland	Tundra
Area (10^{12} m^2)	24.5	12.5	12.0	15	9	8
Carbon in plant biomass (kg m^{-2})	18	14	9	1.8	1.4	0.25
Carbon in above-ground litter fall (kg m^{-2})	1.71	0.37	0.25	0.36	0.67	0.075
Soil carbon (kg m^{-2})	13	9	15	5.4	23	22
Soil nitrogen (kg m^{-2})	0.82	0.64	1.1	0.33	2.1	1.1
Carbon in microbial biomass (g m^{-2})	50	110	35	60	215	20
Nitrogen in microbial biomass (g m^{-2})	2	14	2.5	8.7	51	1
Microbial turnover (years)	0.07	0.30	0.14	0.17	0.32	0.27

Plant biomass and net primary productivity from Whittaker & Likens (1973). Litter from Atjay, Ketney & Duvigneaud (1979). Soil C and N from Zinke *et al.* (1984). Microbial biomass from Smith & Paul (1989).

Geostatistic techniques are making it possible to relate adequately parameters such as plant community structure and nutrient availability to spatial patterns (Montagini *et al.* 1986; Inouye *et al.* 1987). Robertson *et al.* (1988) measured spatial characteristics of N mineralization, nitrification and denitrification at a resolution of 1 m over 0.5 ha of an old field, and showed a high degree of spatial dependence among points sampled within 1 to 40 m of one another. Most of the variation within the sample population was attributed to spatial auto-correlation at a scale > 1 m.

The grassland component of an oak–annual grass savannah on an alfisolic soil in the mediterranean-type climate of central California (Table 15.5) gives an example of the relative sizes of N pools and fluxes found on one site. The site, in the year of analysis, produced 400 g m^{-2} year^{-1} litter C in grasses and 7 g litter N. Although other studies were con-

TABLE 15.5. Carbon and nitrogen transfers in an area occupied by annual grasses within an oak savannah in California; data from Brooks, Jackson & Paul (1986) and Jackson, Strauss & Firestone (1985)

Litter C (g m^{-2} $year^{-1}$)	400 ± 60[a]
Litter N (g m^{-2} $year^{-1}$)	7 ± 1
Microbial biomass C in top 10 cm (g m^{-2})	78 ± 8
Microbial biomass N in top 10 cm (g m^{-2})	19 ± 3
Microbial turnover (years)	0.21
^{15}N uptake	
Plants (%)	29
Soil (%)	45
Unaccounted for (%)	26
Microbial (%)	24
N mineralized in 100 days	3.5
Biomass N/soil N (%)	9.3

[a]SE (n = 5).

ducted on the tree–grass interactions (Jackson, Strauss & Firestone 1985), the data in Table 15.5 are for areas that were not under a tree canopy. The microbial biomass represented 78 g C and 19 g of N. The competitive demand by the microbial biomass is illustrated by the fact that plant uptake accounted for 29% of the added ^{15}N, whereas the microbial biomass accounted for 24% of the N added at a time when the plants were at their most rapid rate of growth. A significant amount of N moved through the microbial biomass into the soil, i.e. 21%, so that the microbial biomass plus soil organic matter constituted the largest pool at 45% of the ^{15}N added. The 24% of the ^{15}N not accounted for was attributed to leaching, denitrification and some herbivory by small animals.

The above figures for a semi-natural system are not greatly different from the averages shown in Table 15.4 for plant and microbial uptake and soil residual N and losses on a much broader geographic basis. However, the uncultivated alfisolic system showed a mineralization rate during a 100-day incubation that accounted for only 3.5% of the total soil N. The cultivated alfisols shown in Table 15.2 mineralized 17% of their N. The microbial biomass of the 0–10 cm depth accounted for 9% of the total N in this fraction, and the turnover time of 0.21 years for the microbial C is supported by the fact that only 25% of the ^{15}N in the microbial biomass accumulated as mineral N in a subsequent 100-day laboratory incubation. Re-immobilization of the N in the presence of available C in this semi-natural system and the great stability of the microbial population are therefore major ecosystem controllers in this savannah.

Table 15.5 shows that the amount of microbial N in the top 10 cm of soil is more than twice the amount in a year's litter fall. The biomass can be either a source or a sink of nutrients. It represents 9% of the N in the surface 10 cm. The range for most values is 5–15% of the total (Smith & Paul 1989). Much of the ^{15}N added to soils remains in the biomass for extended periods after immobilization (Paul & Juma 1981; Schimel, Coleman & Horton 1985). This competition for available N by the microbes and its incorporation into soil organic matter is the reason for the low plant uptake values when ^{15}N is utilized in uptake studies. During immobilization of the ^{15}N there is, however, concurrent release of ^{14}N by microbial turnover. The actual amount of N accumulated by plants comprises both ^{15}N and the released ^{14}N, and thus is greater than that calculated from the ^{15}N per cent excess in the plant. The difference is attributed to the mineralization–immobilization turnover, and further study of this process (Jansson & Persson 1982) will lead to a more exact knowledge of the nutrient dynamics in ecosystems.

THE FORMATION OF SOIL ORGANIC MATTER

A considerable proportion (30–50%) of the organic N of most soils is present in forms which cannot be identified by present-day techniques (Stevenson 1982); these forms are thought to consist of amino N in organo-metal complexes, and N in ring structures as well as in pyrolidines and pyridines (Schnitzer 1982). The latter compounds do not occur to a significant extent in plant residues, but similar forms are found throughout the world on terrestrial sites as well as in sediments. The present theories on the formation of soil organic matter involve the condensation of amino acids, sugars and phenolic substrates to produce dark-coloured, recalcitrant humates high in N (Liu *et al.* 1985; Paul & Clark 1988). The phenolic content can vary with soil type, and NMR studies have shown that the aromatic constituents are not present in as high concentrations as was previously thought (Preston *et al.* 1982; Aiken *et al.* 1985; Wershaw 1985).

The type and extent of decomposition controls both the eventual accumulation and the mineralization of organic matter and nutrients within ecosystems and in different agricultural toposequences (Schimel, Coleman & Horton 1985). People are now asking whether new agricultural managment systems, such as sustainable agriculture, can alter the size of the labile fraction. Continuing research shows that the very large size and diversity of the soil microbial population can supply the needed organisms and enzymes, and that inoculation of foreign organisms into soil seldom has any long-term effect. Development of models that allow

the prediction of litter decay rates and nutrient dynamics have shown that the effects of climate and the chemical composition of macro-litter can be reasonably predicted (Ågren & Bosatta 1987; Parton *et al.* 1987) but internal cycling is still largely looked upon as a 'black box'. The enzyme activity and the ratios of the constituents involved are also being delineated.

Cellulose, a major component of plant litter, disappears more rapidly than lignin during early stages of decay, and overall decay rates are generally higher in litter that has a low initial lignin concentration or a high initial N concentration (Aber & Melillo 1980). Work on kinetics of organic matter has led to a reassessment of the role of lignin in soil organic matter formation. We know that polyphenols, which are degradation products of lignin, can lead to humate formation. Microbial products produced from other substrates can, however, also be of major importance. Voroney, Paul & Anderson (1989), in studying the relative rates of straw and glucose decomposition under field conditions, found that after seven years in the field ^{14}C originally added as glucose was present in higher concentrations and had slower decomposition rates than ^{14}C added as straw. This can be explained by the fact that the addition of the highly available substrate led to the rapid production of a large microbial biomass which on its death and decay resulted in the stabilization of a higher concentration of ^{14}C than did the growth on the straw ^{14}C.

Degradation of lignin ^{14}C by micro-organisms has been found to result in a negligible uptake of the ^{14}C into the microbial bodies themselves (Scott *et al.* 1983). A large proportion of ^{14}C remains in the soil. Whether this remains as humified constituents or as partial degradation products which cannot be separated from the humified constituents by present-day techniques is not known. Other questions concerning the role of lignin in soil organic matter stabilization have come from analyses using ^{18}O (Dunbar & Wilson 1983). The ^{18}O content of lignin is different from that of cellulose. The ^{18}O content of soil humic acids was found to be similar to that of cellulose, but not to that of lignin, indicating that the major source of oxygen in the organic matter may be cellulose rather than lignin.

ANTHROPOGENIC EFFECTS ON THE SOIL ENVIRONMENT

Anthropogenic chemicals such as toxic wastes, sewage sludge, acid rain, pesticides and fertilizers have the capacity to influence the soil ecosystem and associated ground waters even at some distance from points of

addition. Specific impurities can be monitored in the soil and in the ground water with great sensitivity. However, we have little knowledge of the effects of long-term exposures of very low concentrations or the interactive effects of different compounds. More exact numbers in this regard are essential. There is a tendency to rely on large safety factors to ensure the protection of both humans and the environment from poorly defined risks, especially where the effects of breakdown products are not known. More measurements as well as mathematical models of the fate and persistence of chemicals are needed to assist in development of monitoring, movement and management strategies. The precision and accuracy of the models describing these reactions need to be defined for a much broader range of ecosystems. We cannot measure these factors empirically in each system, and must be able to rely with confidence on predictive models.

The problems associated with movement and toxicity of chemicals have resulted in an increased interest in the development of biological control agents. The techniques of molecular biology were developed with micro-organisms, and many of the genes to be inserted in plants will come from micro-organisms or will be introduced via microbial vectors (Moses 1987). It is considered that alteration of microbial populations and activities in the rhizosphere can contribute the following: (i) modification of plant growth and development, (ii) control of pathogens, insects, nematodes or weeds, (iii) enhanced nutrient availability, and (iv) degradation of toxic substances. The role of native and of genetically altered organisms, including bacteria, fungi, protozoa and viruses, is now being defined in a number of areas. This work is needed to provide the background information required for further advances in this field.

The release of genetically engineered organisms into the environment will continue to depend upon the decisions of appropriate regulatory agencies and society at large. To realize the potential of biological control mechanisms, and at the same time control the potential risks associated with the introduction of new organisms into nature, much more information is required on the factors that control their population dynamics and their function in the soil and rhizosphere. Specific information is required on the following: (i) development of methodology to measure the potential effects of engineered organisms on other susceptible life, (ii) the ability of genetically altered organisms to grow and survive under field conditions, (iii) the effects of the new organisms on natural environmental processes, and (iv) the ability of introduced organisms to transfer genetic information to native strains in the environment.

Because of the above uncertainties, the modification of plant growth

and development through the use of inserted genes will probably occur earlier than the introduction of genetically engineered micro-organisms. Genes inserted for resistance to specific herbicides are being tested by a number of agencies. A gene for resistance to a herbicide that is reasonably safe environmentally, such as glyphosphate, can now be engineered into crop plants. This could allow the control of all other plants in the field by the application of one, supposedly innocuous, herbicide at very low levels. The possibility of a gene such as this moving from a plant to non-target plant is considered more remote than if a micro-organism had been used as a host. Another example of alteration of plants is the incorporation directly into plants of the broad range of proteinaceous toxins from *Bacillus thuringiensis* (Board on Agriculture 1987). These are activated only after ingestion into insect guts, but questions concerning the safety of the plant for human consumption and the effect on the ecology of non-target crops and soil-associated animals still remain to be answered.

Enhancement of nutrient availability through molecular genetics can readily be imagined in the case of increased symbiotic N_2 fixation or altered phosphatase levels on roots. A less direct approach but one still with great potential impact is the possibility of managing the vast store of nutrients in the microbial biomass. This would require a proper synchronization of microbial growth with plant growth such that nutrients are mineralized during periods of active plant growth and immobilized when plant uptake is not occurring. The active fraction of the soil organic matter (SOM) consists of the microbial biomass and microbial metabolites. These account for the majority of nutrients released and offer some hope for management. Cultivation is one such management tool as it provides new surfaces for microbial activity, and incorporates plant residues. The older fractions of SOM will continue to degrade slowly when abiotic factors make microbial growth feasible. Nutrients released during this time could be taken up by cover crops which would later be incorporated at the time of planting of the major crop. This scenario already occurs to some extent in agro-ecosystems through timing of application of fertilizers and plant residues as well as cultivation. The continued protection of soil by interseeded and cover crops is a major aspect of many of the sustainable agricultural techniques now being tested.

The potential for tinkering with the environment is immense. We, however, do not have the necessary background in basic microbial physiology, plant biology or ecological interactions to be able to predict adequately the outcome of anthropogenic influences. There are also

many ethical, economic and social questions that need to be answered. The basic questions in microbial ecology that need to be answered before widespread introduction of genetically engineered micro-organisms into the environment include the following.

1 What factors control competitiveness in nature? Organisms cannot act in nature unless they find a niche for themselves. It is an axiom of microbial ecology that foreign organisms are very difficult to introduce unless given a special advantage (Paul & Clark 1988). Symbiotic N_2 fixers will establish themselves if the host legume is grown, but many years of inoculation studies have shown the difficulty in trying to introduce more efficient N_2-fixing symbionts if they are not more competitive in the soil itself or in the multifaceted absorption–infection process (Havelka, Boyle & Hardy 1982). Conversely, in genetic engineering for pest or weed control the need for an introduced organism to do its job and then die is a prerequisite, not only from an environmental standpoint but also from an economic one. The company introducing the organism wants to be able to sell the inoculum year after year, thus requiring microbial die-back. Suicidal genes for these organisms are thus being investigated.

2 What is the diversity of the soil microbial community? Only a very small percentage (0.1–10%) of the microbial populations identified in soils and sediments can be grown on laboratory media (Klug & Reddy 1984). Does this mean that there is a great deal of untapped diversity in the soil population that may be easier to address for scientific purposes than new organisms that must be produced by modifying known ones? Novel organisms isolated from one environment to be used in another would probably pass regulatory examinations more easily than genetically engineered organisms. It is, however, possible that we already know much of the diversity in soil organisms but that the environmental 'stress' under which soil organisms normally grow keeps them from developing under laboratory conditions.

Techniques of molecular genetics have made available to us the analytical methodology required to answer the diversity question. The use of gene probe methodology (Holben & Tiedje 1988) and the analysis of the higher-order structure of ribosomal RNA sequences make it possible to analyse phylogenetic and quantitative aspects of naturally occurring mixed microbial populations (Pace *et al.* 1986). The need to understand the microbial ecology, diversity and functioning of organisms in nature before genetically engineered organisms are introduced into the environment will also provide some of the funds necessary for the basic studies, now that tools for these studies are available.

3 What is the effect of the physico-chemical environment on function?

The effects of 'stress' on microbial activity and morphology is starting to be understood (Atlas 1984). Other relevant effects include the known controls played by interaction with the extensive organic and inorganic surfaces in nature (Fletcher & McEldowney 1984). The inability to isolate vesicular-arbuscular mycorrhiza, the study of the role of fungistasis in plant diseases, and the role of anaerobiosis in decomposition are examples of problems where biochemical activity cannot be studied until we obtain a more quantitative understanding of the interaction of genetic and environmental controls on microbial activity such that we can grow the organisms adequately in the laboratory.

4 What is the accessibility of the gene pool of soil organisms? What we know about gene exchange has come from laboratory studies with a restricted list of bacteria such as *Agrobacterium*, *Pseudomonas* and, to some extent, *Rhizobium* and *Bradyrhizobium*. Bacteriophages are known to be able to transfer genetic information, but their mechanism of crossing barriers between bacterial species is not known. The ability of bacteria to overcome substances such as antibiotics, heavy metals, pesticides and anthropogenic wastes is often carried on plasmid genes (Barkay & Olson 1986). The movement of these genes in nature and the effects of the extra plasmids on the host micro-organisms in the competitive natural environment must be studied. Most of the genes controlling the bacterial contribution to symbiotic N_2 fixation are also plasmid-borne. The fates of plasmids in natural ecosystems, therefore, are of great importance to the ecology of both managed and native systems.

It is of paramount importance that the basic questions in microbial ecology be answered before there is a widespread introduction of new microbial genetic material into nature. The analytical power associated with genetic research makes much of this research feasible (Berger & Kimmel 1987). The recognition that research centres, such as one in microbial ecology, are required to develop the background knowledge required before genes are introduced into nature now makes exact knowledge in this field of ecology possible.

Microbial ecology and 'macro-ecology' have tended to operate in separate fields, and the concepts developed for 'macro-ecology' have not played a major role in microbial ecology (Check 1988). At the same time the huge population sizes, and now the funding in microbial ecology, should make it possible to utilize this field to answer many questions in 'macro-ecology'. This can come about only through the application of a more exact biology, using the power of the new analytical techniques and the capabilities of mathematical analyses available to us now and in the near future.

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VII. APPLIED ECOLOGY

Long before the Society launched its *Journal of Applied Ecology* in 1963, there was a strong tradition of papers with an overt or implied practical application amongst the work of ecologists in many fields. These were, however, often the work of individual scientists who could see how the results of their fundamental studies might be applied. Just as the last 20 years have seen an increasing tendency for ecologists to work in interdisciplinary groups, it has become apparent that if some of the major ecological problems of the world in the late twentieth century are to be solved, there is a need for collaborative efforts by many kinds of scientists. There are many such problems, but we have chosen three to illustrate the theme.

Krause reviews that most complex intertwining of biological and environmental changes which have become known in continental Europe as 'forest decline', but are in reality the latest and potentially most damaging stage in man's centuries-old destruction of forests. Understanding the multiple causes of the decline, and their interactions, can be achieved only by the co-operation of scientists with as varied backgrounds as meteorology, microbiology, soil chemistry, plant physiology and biochemistry, and entomology as well as forestry. Integrating and synthesizing the information gathered so far is the classic role of the ecologist.

On a more intimate scale is the study of the management problems of parts of the Norfolk Broads in eastern England, reported and discussed by Moss. It is a fascinating account, not viewed through the rosy glass of hindsight, but presented rather as an evolving approach to an interdisciplinary project destined to force the author into unexpected channels of enquiry. It illustrates most clearly our intention of looking at exactness in ecology in a much more flexible way than the reductionism which has characterized exactness in so many other sciences. It is a very human study in its honest illustration of how progress in science is strongly dependent upon the idiosyncracies of its practitioners. At the same time it reveals much about the ways in which human endeavours have created the problem in the first place.

Ecology as a whole, and applied in particular, cannot be divorced from human and social elements of the real world. The truth of this is