CHAPTER II

TREES, SOILS AND SOIL BIOLOGICAL PROCESSES

The title of this book invokes some major questions:

Do trees improve soil fertility? If so, what are the mechanisms involved and how can this knowledge be applied to benefit agricultural systems? Equally, possible deleterious effects of tree species on soil properties require detailed understanding.

This chapter reviews the current understanding of these tree-soil relationships across the spectrum of natural and managed systems. In Section 1, the beneficial and adverse effects of trees on soil are broadly discussed. Practical systems of land use and management by which the said benefits of trees on soils may be implemented are also outlined. These will be detailed further in Chapter V.

It is suggested by J Anderson in section 2 of this Chapter that the development of improved management practices in agriculture using trees should be based on an understanding of the mechanisms by which the productivity of natural forest systems is maintained. In this light, the mechanisms of the efficient nutrient cycles in such natural systems, with particular reference to the effect of disturbance on nutrient retention by the system are outlined. The application of these concepts is then discussed with respect to the significant role of trees in agroforestry systems in improving soil fertility.

In section 3, M J Swift explains that the lack of understanding of the mechanisms described in section 2 precludes the adoption of standard practices by which trees could ameliorate soils. The relationships between the biological processes of litter decomposition, humus synthesis and humus breakdown are reviewed. The influence of trees on these processes should be a basis for soil amelioration.

The need for further investigation concerning the links between plant inputs, soil organic matter status, soil biological processes and soil fertility is emphasised throughout this chapter as an essential prerequisite to efficient management practices.

1. EFFECTS OF TREES ON SOILS

ANTHONY YOUNG

International Council for Research in Agroforestry

SUMMARY

1. Land use systems in which effects of trees on soils play an important part are protective forestry, reclamation forestry (of eroded or salinized land or moving sands), production forestry, agroforestry and applications of these in watershed management.

2. There are some 20 distinct agroforestry practices, defined as arrangements of trees and herbaceous components in time and space.

3. Eleven processes are listed by which trees may improve soils, not all of which are proven.

4. A computerised model, Soil Changes Under Agroforestry (SCUAF), indicates a potential for agroforestry to achieve a steady state of soil fertility under productive use; some critical assumptions in the model require experimental testing.

INTRODUCTION

This book has its origins in the basic concept of the Tropical Soil Biology and Fertility programme (TSBF) : that it is possible to maintain or improve the fertility of tropical soils through the manipulation of soil biological processes. Such a concept can only be achieved through two stages:

i A basic understanding of how soil biological processes operate, and what is their influence on fertility.

ii. The identification of practical management methods by means of which soil biological processes can be manipulated in such a way as to improve fertility.

It was out of discussions of the second stage, the realistic management options, that the present book arose. It was recognized on the one hand, that trees have certain distinctive effects on soils, many of them favourable; and on the other, that there were many circumstances in which land use systems that involve the planting of trees are practicable — not only technically, but also economically and from a social viewpoint. (Swift, 1984; Commonwealth Science Council, 1985; Swift, 1985).

The papers which follow contain discussions of many aspects of the ways in which trees affect soils. The task of this introductory review is to set these detailed aspects into perspective, by an overview of how trees achieve the desired beneficial effects, and what are the practical land use and management systems by which this can be brought about.

The following factors show that trees can be expected to improve soils:

i. The soil that develops under natural woodland or forest, the classic brown earth of temperate regions, red earth of the tropics, is fertile. It is well-structured, has good moisture-holding capacity, is resistant to erosion and possesses a store of fertility in the nutrients bound up in organic molecules. This mature soil is the result of plant succession, with its associated soil changes.

ii. In shifting cultivation, we have a demonstration of the capacity of forest to restore fertility. Nowadays, this practice is often thought of as environmentally undesirable, and certainly this is so once population increase has forced the shortening of the fallows. But formerly, shifting cultivation had something of a good name, as a way of letting the natural ecosystem restore what agriculture in the tropics inevitably (or so it was supposed) removed.

iii. The cycles of carbon and the major nutrients under natural ecocystems have been demonstrated, most notably in rain forest but also in savanna and semi-arid ecosystems. So also has the often substantial nitrogen-fixing power of leguminous trees and certain other species. That is, not only can we observe that trees in fact improve soils, but to some extent, we know the details of how they do it.

iv. Finally, in these background considerations, we have so often observed the adverse effects that follow forest clearance, the almost invariable decline in soil fertility, and sometimes the less easily reversible consequences of erosion.

SYSTEMS OF LAND USE AND MANAGEMENT

What are the practical systems of land use and management in which the planting and tending of trees, at least in part with a view to their effects on soils, play a part? These include the following:

i. Protective forestry: the protection of sloping or other environmentally sensitive land by peservation of its natural forest cover, or upgrading of such cover where it is partially degraded. There may be multiple outputs - water, wildlife conservation and recreation.

ii. Reclamation forestry: the reclamation of eroded, salinized or other degraded land by afforestation. The reclamation process can be followed by agroforestry, through a combination of productive use with maintenance of the improved soil conditions.

iii. Production forestry: forestry, of which the primary aim is timber or fuel wood production, but in which soil amelioration is either an explicit secondary aim or at least a management requirement.

iv. Agroforestry. This refers to a range of land use practices in which trees are grown in association with agricultural crops or pastures, and in which there is both an economic and an ecological interaction between the tree and non-tree components. A critical part of this definition, and that which distinguishes it from social forestry, is the existence of ecological interactions between the trees and other components, interactions which take place through the medium of microclimate or, our present concern, soils. Most agroforestry is social forestry, that is, forestry carried out the village or farm woodlots which, if they are managed only with the aim of maximizing wood production, is not agroforestry. Agroforestry is not one kind of land use but a collective name of a wide range of practices.

v. *Watershed management:* *land use planning which takes the watershed as the spatial unit, and which is particularly concerned with soil and water conservation.* This is of a different nature, since it frequently involves any or all of the land use practices i-iv above. It is mentioned as a type of planning framework which makes much use of the effects of trees on soils.

THE RANGE OF AGROFORESTRY PRACTICES

Agroforestry is not one kind of land use by a collective name for a wide range of practices. Three terms may be defined.

Agroforestry components consist of trees (including shrubs), agricultural crops, pastures, livestock and occasionally other components. To qualify as agroforestry, the tree component must always be present.

Agroforestry practices consist of arrangements of agroforestry components in space and/or time.

Agroforestry systems are specific examples of agroforestry practices, as found in a particular area. They are defined by such details as the tree and non-tree species, management practices, outputs (production and service), and the social and economic functions of the systems.

POSSIBLE ADVERSE EFFECTS

It would be a biased unscientific view if the possible adverse effects of trees on soil were to be ignored. Some possible effects of this kind are as follows:

i. Nutrient loss, resulting from whole-tree harvesting, with possible adverse effects on second-cycle plantation forestry. This is a matter of concern to foresters, and raises the question of forest fertilization. The better the management, the greater the problem becomes at first sight, since with a faster annual increment, a greater volume of nutrients is removed at harvest. Litter fall and root growth may compensate.

ii. Moisture depletion. Some species of eucalypts have been blamed for dessicating the soil; and, an earlier point of debate, afforestation of reservoir catchments can in some circumstances reduce total water yield, despite regularizing flow. These are controversies on which firm views are held, and I shall refrain from comment.

iii. Soil erosion. A badly-managed forest can lead to accelerated erosion, as in the case of some teak plantations on sloping land. It should also be made clear that agroforestry does not necessarily conserve the soil; wrongly sited or poorly managed, it can be just as destructive as other land use systems.

iv. Adverse chemical and biological effects. Under this heading are grouped together such aspects as acidification by pine litter, or allelopathic effects of substances from litter or roots.

HOW DOES THE TREE DO IT?

What are the mechanisms by which the generally favourable effects of trees upon soils are achieved? Some are well proven, some reasonable supposition; and among the latter are numbered some of the hypotheses of the TSBF. The processes listed are either experimentally demonstrated or widely accepted, except where otherwise indicated.

Processes which augment additions to the soil:

1. Photosynthesis: fixation of atmospheric carbon and its transfer to the soil.

2. Nitrogen fixation, both symbiotic and non-symbiotic.

3. Nutrient retrieval: the taking up of nutrients released by rock weathering in deeper layers of the soil, and their release by litter decay on the surface (not specifically demonstrated).

4. Providing favourable conditions for input of nutrients by rainfall and dust (not demonstrated).

Processes which reduce losses from the soil, making the plant/soil system more closed:

5. Protecting the soil from erosion (water and wind), thereby from loss of carbon and nutrients.

6. Trapping and recycling nutrients which would otherwise have been lost by leaching (not demonstrated).

Improvement of soil fertility through physical conditions:

7. Soils under trees generally have better physical conditions, including a higher water-holding capacity combined with good permeability and drainage, and greater erosion resistance, than non-forest soils.

Processes which affect the quality of plant residues and the timing of their transfer to the soil:

8. Promotion of a range of different qualities of plant litter, through supplying a mixture of wood and herbaceous litter (TSBF hypothesis).

9. Favourable effects of roots: growth-promoting substances in the rhizosphere (demonstrated in some cases) possibly also provision of a range of root-litter quality (TSBF hypothesis).

10. Timing of nutrient release. Under natural conditions, the provision of a steadily-decaying nutrient store in the form of soil organic matter. Under management, the potential to control timing further, e.g. through decisions on when to prune (basic TSBF hypothesis).

11. Effects of shading on microclimate, thereby on soil climate and rate of mineralization (demonstrated in some cases; TSBF hypothesis).

It is the last group of processes which is most fundamental to research in TSBF programme.

ORGANIC MATTER AND NUTRIENT CYCLING UNDER AGROFORESTRY: A COMPUTERIZED MODEL

Turning from the broad viewpoint to the specific effects of agroforestry on soils, a computerized model has been developed at ICRAF. Called Soil Changes under Agroforestry, or the SCUAF model, it is at an early stage of development and has so far been applied only to the carbon and nitrogen cycles.

The long-term objective of the model is to have the capacity to forecast the effects on soils of a specified agroforestry system. However, at present we lack firm data on some of the critical assumptions about processes, and so there is a further immediate objective. This is to draw attention to what needs to be known if such forecasts are to be made with reasonable confidence; and thus to direct research into the determination of critical data.

The carbon and nutrient cycles are complex, and there have been a number of attempts to model them, particularly the nitrogen cycle. The model under agroforestry is essentially similar to that under a single ecosystem, except that there are two components, "trees" and "crops". The tree component normally leads to a net gain in carbon or nutrients, the crop component invariably to a loss. The two components may be combined in a time-based agroforestry system - a period of cropping followed by a planted tree fallow; or in a spatially-based system, a mixture of trees and crops.

The user specifies the type of agroforestry system, and the percentages of time, or space, under trees and under crops. He might then be asked to input all the numerous variables required to quantify the cycle. Hoever, even the most comprehensive studies rarely cover all such data, and therefore use is made of a system of default values. The user inputs broad details of climate, soil and slope, and the model then assumes default values, including rates of growth, partitioning between different parts of the plant, rates of erosion and leaching, initial soil conditions, and assumptions about the manner of oxidation losses and other processes. The user is offered the opportunity to change any of these values.

Thus the inputs to the model are:

1. The physical environment.
2. The agroforestry system.
3. Initial soil conditions
4. Soil erosion.
5. Rates of plant growth: a. trees, b. crops.
6. Additions and removals by man (e.g. manure, fertilizer, crop harvest, crop residues, fuelwood harvest).
7. Assumptions about soil/plant processes.

The outputs from the model consist of tables and graphs showing changes in soil carbon and nitrogen with time. Examples of the carbon model are shown in Figure 1. Time-based systems show a dog-toothed graph, from the alternation of crops and trees, spatial systems a smooth curve. As the model is at present constructed, all systems show an approach towards an equilibrium value of soil carbon. However, feedback interactions are being developed, for example an acceleration of the rate of erosion if soil organic matter is lowered, or a slowing of plant growth where nitrogen is depleted. This leads to the possibility of including a "catastrophe situation", in which the plant cover becomes so poor, and soil humus low, that the rate of erosion accelerates rapidly.

The exciting prospect is that it has been found possible, admittedly by making many untested assumptions, to develop an agroforestry system which on the one hand is productive, and on the other, leads to a steady state in the soil at an acceptable level of fertility, namely with humus content just over half that under natural forests; the net carbon loss under crops is balanced by an equal gain under trees. The assumptions and reasoning of this model are set out in Young (1985) and later in this book.

EXAMPLES OF STUDIES OF THE EFFECTS OF TREES ON SOILS

Some references may be cited, to lend support to the points made above, and as an introduction to the kinds of studies on the effects of trees on soils that are available. This is necessarily a small selection from a substantial range of published results.

Among the many studies of nutrient cycling under rain forest, that of Golley et al. (1975) is one of the most thorough. The implications of the carbon and nitrogen cycles under forest for the design of agroforestry systems are discussed by Brunig and Sander (1983). Lundgren (1978) made a comprehensive comparison between nutrient cycling under natural forests and plantations in an area of highland Tanzania. There have been clear demonstrations of soil changes upon clearing forest for agriculture, such as that by Sanchez et al. (1983); an IBSRAM workshop on this subject was held in 1985.

As examples of work on the regenerative effects of forest fallows may be cited work by Toky and colleagues in north-eastern India, and current studies in Sri Lanka and Malaysia (Tokyo and Ramkrishnan, 1983; Andriesse and Schelhaas, 1985).

For nutrient cycling under plantation forestry, work on pine (Singh, 1982) and eucalypt (George, 1982: Turner and Lambert, 1983) may be cited, among many ohter studies. Chijoke (1980) compared the effects on soils of Gmeligna arborea and Pinus caribaea in six tropical countries. The effects of individual trees can be studied by taking soil transects from the base of the trunk to beyond the canopy (Kellman, 1980).

Among a range of FAO publications relevant to trees and soils, three of the Conservation Guides may be noted, those on watershed management, conservation in arid and semi-arid zones, and the environnmental impact of forestry (FAO, 1976, 1977; Zimmerman, 1982).

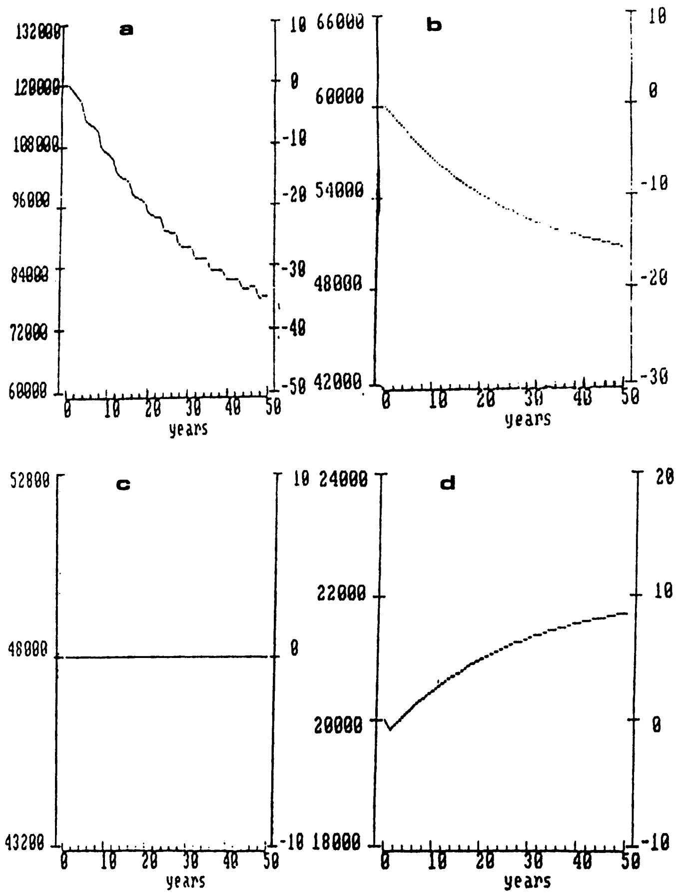


Figure 1
Outputs from the ICRAF model. Soil Changes Under Agroforestry (SCUAF). The vertical axis shows soil humus carbon, kg/ha.
a: humid climate, time-based system, 3 years crops, 3 years trees.
b and c: humid climate, spatial system, 50-50% crops-trees, starting with different levels of soil carbon; c is a steady-state system.
d: semi-arid climate, spatial system, 50-50% crops-trees, commencing on a degraded soil.

Starting points for the study of soil changes under agroforestry are the 23 papers in an ICRAF symposium (Mongi and Huxley, 1979) and the review of soil productivity aspects by Nair (1984). Nutrient cycling and the monitoring of soil changes are not included in agroforestry experimental work as often as they should be. Two examples of methods, and the kinds of result obtainable, are work on soil changes under alley cropping at IITA, Ibadan (Kang et al., (1981); and of nutrient cycling under coffee and cocoa in combination with shade trees in Costa Rica (Aranguren et al., 1982). The effects of agroforestry on soil conservation are reviewed by Wiersum (1984) and Lundgren and Nair (1985).

There is an annotated bibliography on nutrient cycling and organic matter relations of forests, with notes on almost 1000 studies, compiled by Adlard and Johnson (1983). A thorough review of the effects of agricultural tree crops on soils was made by Sanchez et al. (1984).

The ideas set out briefly in the present paper, and the implications for agroforestry of the TSBF hypotheses, are set out in more details in Chapter 6.

CONCLUSIONS

A distinctive feature of land use systems which make use of trees is the potential to combine production with conservation. The production may be of goods or services, the goods including both wood and non-wood products. The services include shade, fencing, moisture conservation, wildlife conservation and recreation. Added to these is the service of conservation of resources, through protection against water and wind erosion, and the maintenance or improvement of soil fertility. This dual role, of production with conservation, applies whether the trees are part of forestry or agroforestry land use systems.

Some aspects of the favourable effects of trees on soils are well known, and what is required is the application of this knowledge through good land use planning and management. Other aspects, particularly some of the key relationships between tree litter and soil biological processes, require further research. If some of the basic hypotheses in this area can be proven, then there are considerable opportunities for applying such knowledge to practical land development, often with relatively low-cost inputs.

ACKNOWLEDGEMENT

The SCUAF model for carbon and nitrogen cycling under agroforestry was developed jointly with Dr P M Hotten.

REFERENCES

Adlard, P.G. and J.A. Johnson 1983 Annotated bibliography: biomass estimation - nutrient cycling and organic matter relations in forest stands. Commonw. For. Inst., Oxford.

Andriesse, J.P. and R.W. Schelhaas 1985 Monitoring project of nutrient cycling in soils used for shifting cultivation under various climatic conditions in ASia. Progress Report 3. Roy Trop. Inst., Amsterdam, 58 pp.

Aranguren, J., Escalente, G. and R. Herrera 1982 Nitrogen Cycle of tropical perennial crops under shade trees. I. Coffee. II. Cacao. Plant Soil 67, 247 - 269.

Brunig, E.F. and N. Sander 1983 Ecosystem structure and functioning: some interactions of relevance to agroforestry. In: Plant research and agroforestry (ed. P.A. Huxley, ICRAF, Nairobi), 221 - 247.

Chijoke, E.O. 1980 Impact on soils of fast-growing species in lowland humid tropics. FAO Forestry Paper 21, 111 pp.

Commonwealth Science Council 1985 Soil biology and the productivity of tropical soils. Report of the planning meting CSC Tech. Pub. 176 13 pp.

FAO 1976 Convservation in arid and semi-arid zones. FAO Conservation Guide 3, 125 pp.

FAO 1977 Guidelines for watershed management. FAO Conservation Guide 1, 293 pp.

George M. 1982 Litter production and nutrient return in Eucalyptus hybrid plantations. Indian Forester 108, 253- 260.

Golley, F.B. et 4 al. 1975 Mineral cycling in tropical moist forest ecosystem. Univ. Georgia, Atehns, 248 pp.

Kang, B.T., Wilson G.F. and L. Sipkens 1981 Alley cropping maize (Zeamays L.) and leucaena (Leucaena leucocephala LAM) in Southern Nigeria. Plan Soil 63, 165 - 179.

Kellman, M. 1980 Soil conditions and nutrient cycling under natural and plantation forests in Tanzanian highlands. Swedish Univ. Agric. Sci., Uppsala, 429 pp.

Lundgren, B. (1978). Soil conditions and nutrient cycling under natural and plantation forests in Tanzanian highlands. Swedish University of Agricultural Sciences, Uppsala, 429 pp.

Lundgren, B. and P.K.R. Nair 1985 Agroforestry for soil conversation. In: Soil erosion and conservationn (Soil Conserv. Soc. Am., Ankeny), 703 -717. Reprinted as ICRAF Reprint 27, 1985.

Mongi, H.O. and P.A. Huxley 1979 Soils research in agroforestry (symposium). ICRAF, Nairobi, 584 pp.

Nair P.K.R. 1984 Soil productivity aspects of agroforestry ICRAF, Nairobi, 85 pp.

Sanchez, P.A. , Villachica, J.H. And D.E. Bandy 1983 Soil fertility dynamics after clearing a tropical rainforest in Peru. Soil Sci. Soc. Am. J. 47, 1171 - 1178.

Sanchez, P.A. et al. 1984 Tree crops as soil improvers in the humid tropics. Agric. Res. Serv., Univ. No. Carolina, Raleigh, mimeo., 64 pp.

Singh B. 1982 Nutrient content of standing crop and biological cycling in Pinus patula ecosystem. For. Ecol. Management 4, 317 - 332.

Swift, M.J. (ed) 1984 Soil biological processes and tropical soil fertility: a proposal for a collaborative programme of research. Biol. Internat. Spec. Issue 5, 38 pp.

Swift, M.J. (ed) 1985 Tropical soil biology and fertility (TSBF). Planning for research. Biol. Internat. Spec. Issue 9, 24 pp.

Toky, O.P. and P.S. Ramakrishnan 1983 Secondary succession following slash and burn agriculture in north-eastern India. J. Ecol. 71, 735 - 757.

Turner, J. and M.J. Lambert 1983 Nutrient cycling within a 27 year-old Eucalyptus grandis plantation in New South Wales. For. Ecol. Management 6, 155 - 168.

Wiersum, K.F. 1984 Surface erosion under various tropical agroforestry systems. In: Symposium on effects of forest land use on erosion and slope stability (ed. C.L. O'Loughlin and A.J. Pearce, East-West Center, Hawaii), 231-240.

Young, A. 1985 The potential of agroforestry as a practical means of sustaining soil fertility. ICRAF Working Paper 34, 28 pp.

Zimmerman, R 1982 Environmental impact of forestry. FAO Conservation Guide 7, 85 pp.

2. PLANT NUTRIENT-USE EFFICIENCIES AND SOIL PROCESSES IN NATURAL AND AGRICULTURAL ECOSYSTEMS

J. M. ANDERSON
Exeter University, U.K.

SUMMARY

1. Mechanisms of nutrient cycling in natural ecosystems are described with particular reference to the effect of disturbance on nutrient retention by the system.

2. The use of trees in agriculture is discussed as to its value in maintaining soil fertility in the conversion of forest to agriculture.

3. The application of these concepts is discussed with respect to the role of trees in agroforestry systems.

INTRODUCTION

Adaptations of plant communities to nutrient-poor soils can be seen throughout the world but are particularly widespread in the tropics. Here over half of the region comprises highly weathered and leached soils (Oxisols and Ultisols) with available phosphorus concentrations usually well below those required for agricultural crops (Sanchez 1976). Yet some of the lowest fertilty soils support rainforests of massive structure and productivity (Proctor et al 1983) as a consequence of tight nutrient cycling between vegetation and soil, and efficient production per unit of limiting nutrient (Vitousek 1984). This lack of correlation between forest structure and soil fertility has promulgated many disaster in agricultural development in the tropics where land cleared of forest has failed to sustain the expected crop yields, even with fertiliser inputs, or worse, has become catastrophically eroded.

In terms of plant-soil relationships it is therefore important to differentiate between the sustained production of unmanaged systems (which may be maintained on a finely balanced nutrient capital which is very sensitive to exploitation) and the sustained yield of cropping systems. Here the depletion of the nutrient capital, by product removal and periodic disturbance to the plant-soil linkage, must be balanced by nutrient returns and residue management to sustain soil structure. An understanding of the mechanisms by which the productivity of natural systems is maintained by highly efficient nutrient cycles and the responses of the systems to disturbance may provide the means to develop better management practices for agriculture and agroforestry in the humid tropics.

MECHANISMS OF NUTRIENT CONSERVATION

A characteristic of most natural ecosystems, particularly forests, is that inputs of potentially limiting nutrients (NPK Ca and trace elements) in precipitation, weathering processes, by N fixation, and so forth are efficiently retained in soils and vegetation. The nutrient capital of the system therefore increases with time until nutrient inputs and losses reach a semi-equilibrium state representing a small through-flow of nutrients in relation to the large internal pools and fluxes. Thus in most undisturbed forest ecosystems there are negligible losses of N and P or other limiting nutrients through leaching but considerable differences in internal nutrient pools and flux pathways according to nutrient availability on high and low fertility soils.

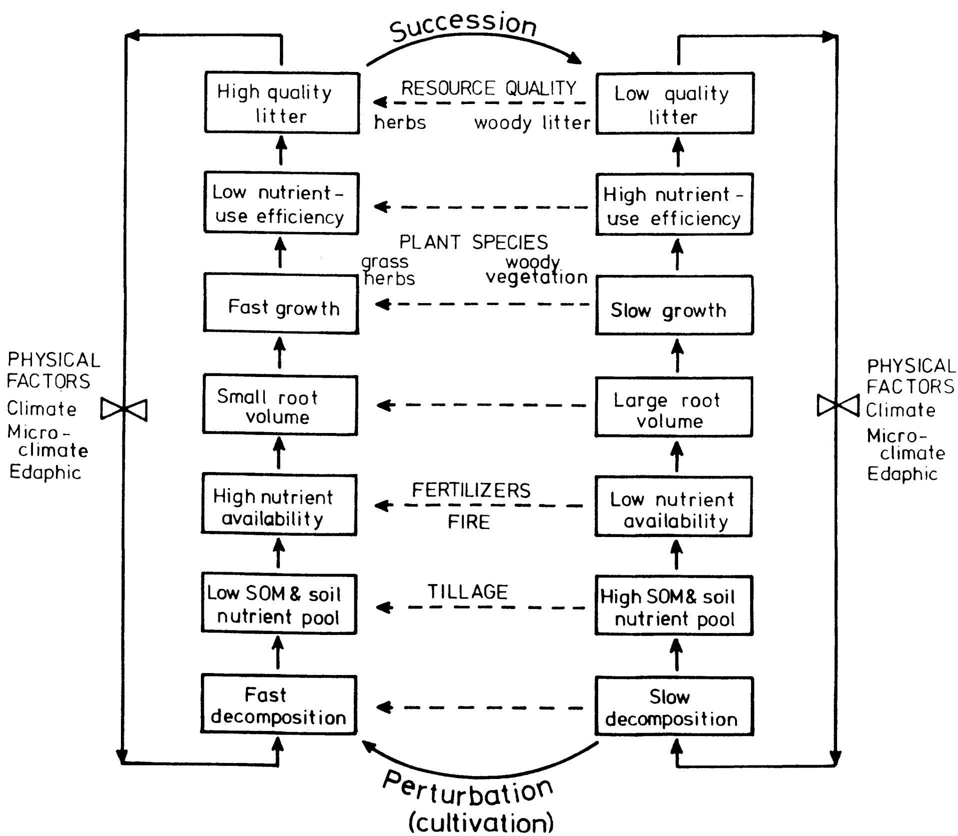
A key adaptation to nutrient limited conditions is the efficiency of nutrient use by plants since this influences the quality and quantity of resource inputs to the soil, decomposition processes and root biomass and distribution (Figure 1).

Variations in foliar concentrations of N and P according to soil nutrient availability is a generally observed phenomenon for natural vegetation and agricultural crops. If nutrient availability is high, fast-growing plants produce nutrient-rich litters which decompose rapidly (maize residues are a notable exception) and nutrient cycling between plant and soil is largely 'external' through the liter pathway. Vitousek (1984) has shown, however, that in forests on nutrient poor soils, the production of leaves or wood is more efficient per unit of N or P on nutrient poor soils than on high fertility soils. This is achieved by the selection of plant species which have low nutrient requirements, eg the N requirement of temperate deciduous forests is on average twice that of conifers in the same region (Cole and Rapp 1981). In addition, nutrients are translocated more efficiently from senescent tissues before abscission under nutrient limited conditions (Charley and Richards 1983). Evergreen, scleromorphic leaves are also associated with drought and/or nutrient stressed habitats. These leaves, which are long-lived, tough and insect resistant may be advantageous under conditions where their replacement is costly in terms of nutrients. Leaf longevity thus capitalises on photosynthetic returns over an extended time period on a 'high cost, slow profit' strategy since scleromorphic rain forest leaves have lower photosynthetic rates than plants on nutrient rich soils which operate on a fast turnover 'low cost, quick profit' strategy (Werger and Ellenbrook 1978).

The net result of the low nutrient concentrations in leaves and other tissues, and the efficiency of 'internal' nutrient recycling is that plant materials entering the decomposer sub-system have low resource quality (high lignin and low nutrient concentrations), slow decomposition rates and a high capacity to immobilize exogenous sources of nutrients. In some cases the litter quality of trees on nutrient-poor soils is so low that favourable environmental conditions for decomposition are overridden and organic soils form under tropical forests (Figure 2) This illustrates that the mechanisms exist, through selection of tree species, to increase the organic matter content of tropical soils to high levels. However, the soil physical and chemical properties associated with these extreme conditions, as in the heath forest soils of S.E. Asia, require considerable amendment to support nutrient-demanding, annual crops such as rice. Thus the effects of tree litter on soil properties are not necessarily consistent with sustained productivity.

Figure 1

Schematic representation of process controls and feedback mechanisms in plant-soil systems. Decomposition rates of litter, nutrient availability and hence litter quality have positive and negative feed-backs on nutrient cycles in high and low fertility soils respectively. Under extreme conditions, determined by the physical controls over decomposition interacting with litter quality, the high fertility system can degrade as soil organic matter is depleted; while in the low fertility system productivity declines as nutrients are immobilised in plant residues. Most natural systems undergo less extreme cyclical shifts in these plant-soil relationships. During plant community succession a more nutrient conservative (usually tree dominated) system develops while a major disturbance increases nutrient availability and shifts plant growth forms to the less mature phase (eg temporary cultivation). The various forms of disturbance associated with cultivation feed into the plant-soil cycle at different stages to initiate and reinforce the transition to an unstable, high nutrient availability agricultrual system from a stable, natural system on low fertility soil.



Perhaps the most conspicuous adaptation of plants to nutrient poor soils is the production of a large root biomass which is usually concentrated on or near to the soil surface. The allocation of up to 70% net primary production below ground to maintain a high root: shoot biomass ratio is a characteristic of many tree species found on nutrient poor soils (Herman 1977) especially in savannas where both fire and water stress select for extensive rooting systems. This adaptation may be plastic, however, and both crop species and natural vegetation growing on a range of soil types have been found to allocate more photosynthate to root production with decreasing soil fertility (Wareing and Patrick 1975). An alternative explanation is that fine root turnover may be faster on high fertility soils (because of higher root resource quality and decomposition rates) and thus offset the low below-ground biomass values reported for these sites (Nadelhoffer et all 1985). A large perennial root biomass is highly effective in scavenging nutrients from dilute solutions, including canopy throughfall, especially in conjunction with mycorrhizas which are typically associated with roots on nutrient poor soils. The root mat is also a sink for nutrients released through weting and drying of soils when the trees are dormant and integrates the uptake of nutrients released from litters decomposing at different rates on the forest floor. The efficacy of the root mat in preventing nutrient leaching is illustrated by studies in an Amazonic forest (Stark and Jordan 1978) where 99.9% of radio-active calcium and phosphorus added to the forest floor was absorbed or taken up by roots and only 0.1% of the activity was recorded below the rooting zone. Mineral-N is scavenged by roots with a similarly high efficiency and the soil water below the root mat in undisturbed forest usually contains very low concentrations of nitrate (Figure 3). In contrast, nitrate is very mobile in soils under arable agriculture and losses to the crop rooting system (other than through denitrification) are set by the depth of the wetting front in relation to rooting depth. Most nitrate is found in the top 15cm at the start of the rains in tropical agricultural soils and is leached down the profile at rates of about 0.5 mm mm^{-1} rain in Alfisols and 1-5 mm mm^{-1} rain in Ultisols.

Figure 2
Litter (o) and soil organic matter (o) standing crops in forest systems from the northern boreal region to the equator. Data for rain forests to the south of the equator are plotted the same degrees north. From Anderson and Swift (1983).

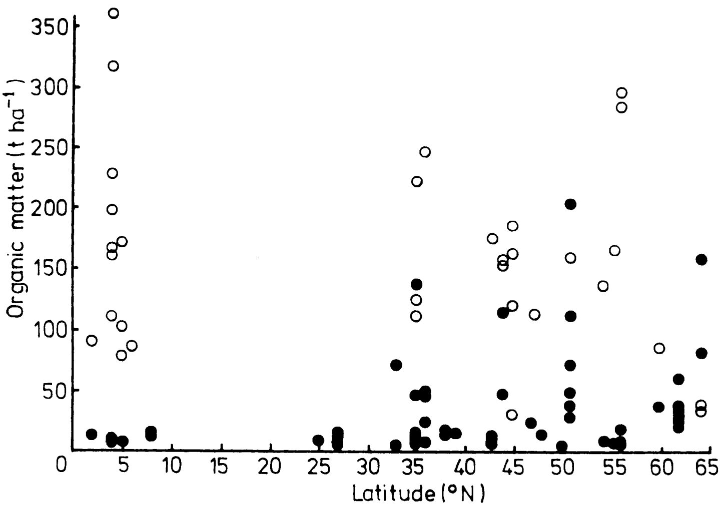
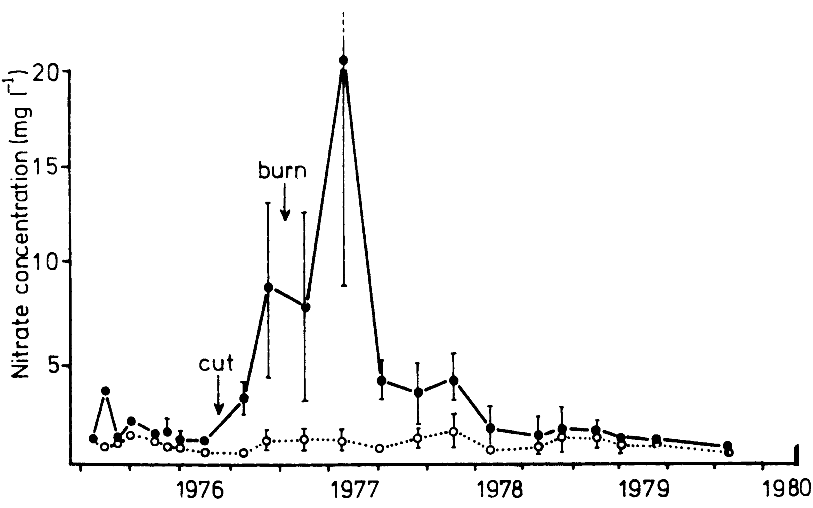


Figure 3
Nitrate concentrations (mean ± 95% confidence limits) in the soil water of a cut, burned and abandoned forest plot (o) and an undisturbed forest control (o) in the Amazon Territory of Venezuela. From Jordan (1985).



EFFECTS OF PERTURBATIONS

The concept that the nutrient capital of ecosystems is conserved except during irregular periods of catastrophic perturbation, including fire and clear felling (Fig. 3), is generally supported by studies on forested catchments in temperate and tropical regions (Jordan et al 1972). Thus losses of nutrients from the system are generally negligible despite major storm events, individual tree falls and canopy defoliation by insects. This nutrient retention depends firstly upon the integrity of the plant-soil link or, if the rooting system is disrupted, upon the capacity of micro-organisms to immobilize nitrogen in resources, such as wood, with a high C : N ratio. But the local effects of the disturbance to vegetation cover may be to temporarily shift the nutrient dynamics of the system into a different mode: the changed soil microclimate and disrupted plant rooting systems result in enhanced nutrient availability to regrowth vegetation; litter resource quality is higher (higher nutrient concentrations and lower proportions of woody materials) and nutrient turnover is faster (Figure 1). The system reverts to a more conservative nutrient cycle as canopy closure is regained.

These shifts in the dynamic balance between nutrient immobilization and release in soils and vegetation are the basic mechanisms underpinning the practice of shifting cultivation in the tropics (Nye and Greenland 1964). When practiced on small plots with an adequate fallow period it is an ecologically sound analogue of gap phase regeneration and causes negligible nutrient losses to the forest ecosystem as a whole. But with increasing frequency or duration, area and intensity of disturbance, the regulatory mechanisms of nutrient conservation break down and the system inevitably degrades unless skillfully and intensively managed (Greenland 1975). The effects of frequent fires are particularly deleterious on acid soils. Burning increases the availability of P by raising the soil pH but it also converts Ca and K to soluble forms which are susceptible to leaching and depletes the nitrogen capital by nitrate leaching (Figure 3) and nitrogen volatilization. The loss of N through fires depends upon the proportion o biomass above and below groun exposed to the fire, the efficiency of the burn and the temperature of the fire (up to 70% N volatilised at 700°C). During an experimental burn of a secondary forest in Costa Rica, 30% of the initial amount of carbon in slash, 22% of the nitrogen and 49% of the sulphur were volatilised (Ewel et all 1981).

It is also well established that cultivation practices, and particularly mechanical tillage, result in a decline in the humus content of the soil. This is a consequence of changes in the soil thermal regime, disruption of soil aggregates and changes in the quality and quantity of plant residues returned to the soil (Swift and Sanchez 1984). Soil physical properties show a concomitant decline with humus content. The reduction in soil infiltrability is particularly marked in the conversion of forest to arable agriculture (Wilkinson and Aina 1976), Lal et al 1980) leaving the soils susceptible to surface run off and erosion. Aside from compaction from tillage operations, the decrease in soil faunal populations due to cultural practices is a major contributory factor to the changes in soil structure. Aina (1984) recorded equilibrium infiltration rates of 82 lhr^{-1} under forest fallow in Nigeria in contrast to 6 lhr^{-1} for adjacent plots which had been under continuous cassava cultivation for 12 years. Earthworm channels, with diameters up to 8 - 10 mm, and modal frequencies in the range 3 - 5 mm, channels m^{-2} mainly in the 1 - 3 mm diameter range. Total porosity was 58% for the soils under forest and 38% for soils under cultivation with pores greater than 60 um (transmission pores) making up 35% and 10% of total porosities respectively.

The net result of perturbations to all the integrated components of the forest ecosystem is a precipitant shift from a high nutrient efficiency system to a low nutrient efficiency system with a massive loss of nutrient capital. The replacement system, under continuous cultivation, is maintained by high input/output fluxes in relation to the plan and soil nutrient pools and is thus inherently unstable. Productivity declines when the nutrient regime is insufficient to support the low nutrient-efficiency crop species and succession of wild species is prevented which can produce more biomass with fewer nutrients.

THE AMELIORATIVE EFFECTS OF TREES

The restorative value of forest fallow is generally recognised and linked to the regrowth of deep rooted trees and shrubs, which recycle plant nutrients from considerable depth in the soil profile, and build up soil organic matter. During the fallow period, plant cover and litter protect the soil from the impact of raindrops, and the roots bind the soils, increase water infiltration and reduce run off and soil erosion. The shade conditions and surface litter cover also promote a diverse and active soil biota which maintain beneficial soil physical and chemical conditions. Most herbaceous crops are selected for their food and pest resistant properties and not for their nutrient use efficiency or ameliorative effects on soils. The replacement of forest by herbaceous species and the effect of the agricultural practices, positively reinforce the shift away from a balanced ecosystem. The incorporation of trees into agricultural systems, under the many agroforestry options, provides a means of capitalizing the food cropping potential of the fast cycling system and the stablizing effects of perennials on soil properties and nutrient regeneration. The two main variants in agroforestry for continuous crop production are the simultaneous and sequential cropping systems.

In alley cropping, typically maize interspersed with Leucaena leucocephala or Gliricidia sepium hedges (Kang et al 1981), the two component systems are established simultaneously; though in these cases the tree produces a rapidly decaying nitrogen source and the maize residues form a low quality mulch.

The use of tree species which produce low quality litters as mulch, such as Acioa barterii, either for interspacing with Leucaena or cultivating with crops producing high quality residues which decompose rapidly, eg cowpea, provide further options for managing soil biological processes and nutrient recycling. Pilot studies suggest that maize yields, without fertilizers, can be doubled using N-fixing tree mulches with yields maintained under drought conditions. But the nutrient dynamics of these systems have not been studied in detail. In particular more information is needed on the phenology of the trees and crop plants in relation to spatial and temporal patterns of nutrient mineralization and uptake. In addition, studies on the root architecture of different species (how the soil volume is exploited horizontally and in depth) are critical for designing the optimum spacing and combinations of species for effective nutrient use and conservation.

Sequential cropping systems may follow a simulation of natural succession in which species which naturally follow intensive cultivation are replaced by species with greater economic value. For example a cropping sequence might consist of (a) annuals and plants whose roots and stems are harvested (b) bananas and plantains (c) palms (d) cacao, rubber or commercial timber species (Jordan 1985). Thus the effects of nutrient-efficient species on soils are gained without a tree fallow.

Tree intercropping provides a permanent or transitional cropping system which is highly conservative of nutrients in the conversion of forest to agriculture. In this system the economically desirable crop is an understorey species (eg cacao) planted beneath larger trees, sometimes N fixers, which provide shade and sustain soil fertility through nutrient restoration by deep rooted species.

In conclusion, trees provide a means of manipulating both general and specific soil properties and processes in land reclamation, and in establishing sustainable agriculture for food, fodder and fuel. Improvements in soil fertility, and control of erosion and catchment hydrology are general benefits of re-afforestation (with some exceptions). On the other hand the selection of particular trees species adapted to local soil conditions can be used:

(i) to change the balance of cations returned to the soil surface in litter;
(ii) to build up soil organic matter;
(iii) to provide for fast or slow decomposing mulches to control nutrient release to crops and
(iv) to enhance soil fauna activities (and hence soil physical properties). The manipulative potential of tree root systems has yet to be investigated.

It is, however, of central importance, in attempting to manage soil biological processes, to recognise the integrated nature of the plant-soil properties and that by altering one component variable, such as the elimination or addition of earthworms or changing litter quality, the whole system can shift its equilibrium state over a period of time.

REFERENCES

Aina, P.O. (1984). Contribution of earthworms to porosity and water infiltration in a tropical soil under forest and long-term cultivation. Pedobiologia, 26, 131-136.

Anderson, J.M. and Swift, M.J. (1983). Decomposition in tropical forests. In Tropical Rain Forest : Ecology and Management (Eds Sutton, S.L., Whitmore, T.C. and Chadwick, A.C.) pp 207-309. Blackwell Scientific Publications, Oxford.

Charley, J.L. and Richards, B.N. (1983). Nutrient allocation in plant communities : mineral cycling in terrestrial ecosystems. In Physiological Plant Ecology IV Ecosystem Processes (Eds Lange, O.L., Nobel, P.S., Osmond, C.B. and Ziegler, H.) pp 5-45. Springer Verlag, Berlin.

Cole, D.W. and Rapp, M. (1981). Elemental cycling in forest ecosystems. In Dynamic Properties of Forest Ecosystems (Ed Reichle, D.E.) pp 341-409. Cambridge University Press, Cambridge.

Ewell, J., Berish, C., Brown, B., Price, N. and Raich, J. (1981) Slash and burn impacts on a Costa Rican wet forest site. Ecology, 62, 816-829.

Greenland, D.J. (1975). Bringing the green revolution to the shifting cultivator. Science, 190, 841-844.

Hermann, R.K. (1977). Growth and production of tree roots : a review. In The Belowground Ecosytem : A Synthesis of Plant - Associated Processes (ED Marshall, J.K.), pp 7-28. Range Science Department Series No. 26. Colorado State University, Fort Collins.

Jordan, D.F. (1985). Nutrient Cycling in Tropical Forest Ecosystems. Wiley & Sons, New York.

Jordan, C.F., Kline, J.R. and Sasscer, D.S. (1972). Relative stability of mineral cycles in forest ecosystems. American Naturalist, 106, 237-253.

Kang, B.T., Wilson, G.F. and Sipkens, L. (1981). Alley cropping maize (Zea mays L.) and leucaena (Leucaena leucocephala Lam) in southern Nigeria. Plant and Soil, 63, 165-179.

Lal, R., de Vleeschauwer, D. and Malafa Ngenje, R. (1980). Changes in properties of a newly cleared tropical alfisol as affected by mulching. Soil Science Society of America Journal, 44, 827-833.

Nadelhoffer, K.J., Aber, J.D. and Melillo, J.M. (1985). Fine roots, net primary production and soil nitrogen availability : a new hypothesis, Ecology, 66, 1377-1390.

Nye, P.H., and Greenland, D.J. (1964). Changes in soil after clearing tropical forest. Plant and Soil, 21, 101-112.

Proctor, J., Anderson, J.M., Chai, P. and Vallack, H.W. (1983). Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak. I. Forest environment, structure and floristics. Journal of Ecology, 71, 237-260.

Sanchez, P.A. (1976). Properties and Management of Soils in the Tropics. Wiley, New York.

Stark, N.M. and Jordan, C.F. (1978). Nutrient retention by the rootmat of an Amazonian rain forest. Ecology, 59, 434-437.

Swift, M.J. and Sanchez, P.A. (1984). Biological management of tropical soil fertility for sustained productivity. Nature and Resources, 10, 1-8.

Vitousek, P. (1984). Litterfall, nutrient cycling and nutrient limitation in tropical forests. Ecology, 65, 285-298.

Wareing, P.F. and Patrick, J. (1979). Source-sink relations and the partitioning of assimilates in the plant. In Photosynthesis and Productivity in Different Environments (Ed Cooper, J.P.), pp 481-500. Cambridge University Press, Cambridge.

Werger, M.J.A. and Ellenbroek, G.A. (1978). Leaf size and leaf consistence of a riverine forest formation along a climatic gradient. Oecologia, 34, 297-308.

Wilkinson, E.E. and Aina, P.O. (1976). Infiltration of water into two Nigerian soils under secondary forest and subsequent arable cultivation. Geoderman, 15, 51-59.

3. INTEGRATION OF NUTRIENT CYCLING IN THE PLANT-SOIL SYSTEM; THE ROLE OF BIOLOGICAL PROCESSES

M. J. SWIFT

University of Zimbabwe, Harare

(IUBS/UNESCO : Tropical Soil Biology and Fertility Project)

SUMMARY

The relationship between the biological processes of litter decomposition, humus synthesis and humus breakdown are reviewed. The possible influence of trees on these processes is indicated as the basis for potential soil amelioration. The need for further research into the links between plant inputs (as above and below ground litter), soil organic matter status and soil fertility is emphasised.

INTRODUCTION

The objective of the Tropical Soil Biology and Fertility Project (TSBF) is "to determine the management options for improving tropical soil fertility through biological processes". This objective was formulated on the premise that the sustainable productivity of natural ecosystems is derived to an important extent from the biological processes of litter and soil such as those of decomposition and humus synthesis. Fertility is dependent not only on the maintenance of these activities at certain critical levels but even more importantly on their functioning as an integrated sysem with regulatory mechanisms operating in a synchronised manner.

Whilst relatively closed and integrated soil systems may be characteristic of natural ecosystems, man's activities often have the effect of uncoupling them. The end-effects of this disruption have been extensivley catalogued but there is very little information on the operation of the processes at a mechanistic level. This lack of understanding at a fundamental ecological level means that we have very little predictive capacity about the quantitative effects of these practices. Even more worrying is our inability to predict the functional mechanisms of potentially ameliorative practices. Among these, the planting of trees on degraded or 'problem' soils is a commonly advocated practice. It is an act of faith that trees have beneficial effects and that their presence results in restored or improved fertility. Little, however, is known of the mechanism of these effects. To enable the adoption of sensible policies for soil amelioration, we must be able to fit tree species with soil type and condition for a given climatic zone and have a good probability of predicting the outcome in terms of changed soil conditions. This we are unable to do under current lack of mechanistic insight.

The TSBF project has proposed a research methodology for examining some of the key questions concerning the integrated functioning of the soil system. Some of these ideas will be outlined here with specific reference to the potential ameliorative effects of trees.

THE SOIL SYSTEM

One way in which biological processes in the soil can be seen operating as an integrated system is in relation to the flux of mineral nutrient elements. A relatively simple version of such a nutrient cycling model is given in Fig 1. The diagram may be made more explicit by detailing the biochemical processes and the groups of organisms involved. Three processes may be selected for particular attention however, those of litter decomposition, soil organic matter (SOM) formation and SOM decomposition. These processes are general, and crucial to the integrated cycling of key elements such as N, P and S in all soils Equally significantly they are also potentially accessible to management.

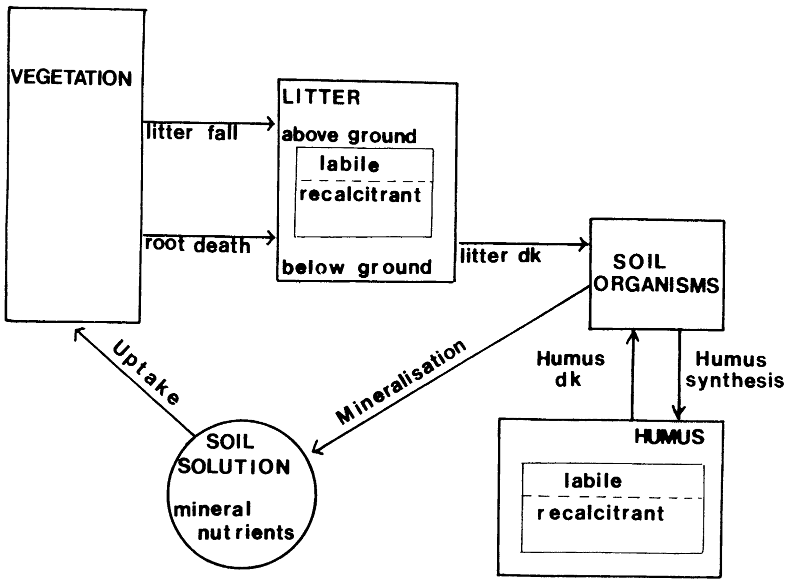


Figure 1: Integrated nutrient cycling in the plant-litter-soil system. The diagram shows some of the main processes influencing the flux of nutrients between plant and soil.

LITTER DECOMPOSITION

The rate of decomposition of any litter component (or resource) has been described as being regulated by three categories of factor, the physical environment (P), the resource quality (Q) and the community of decomposer organisms (O), (Swift, Heal & Anderson, 1979). These factors operate interactively in a complex manner but can be pictured as a hierarchy (Fig 2).

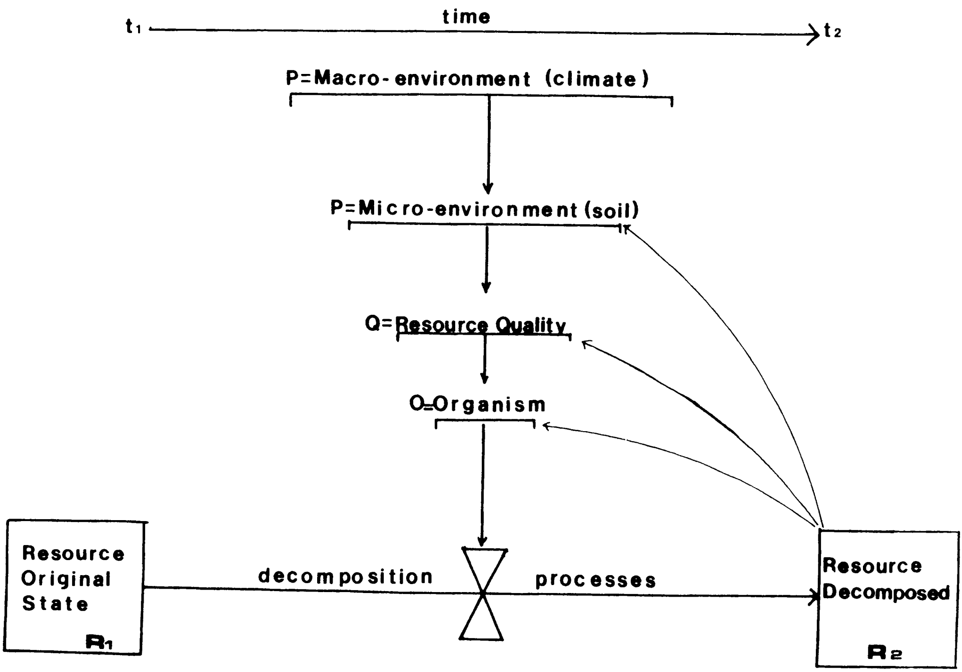


Figure 2: Regulation of the processes of decomposition. The processes of decomposition are pictured as being influenced by three groups of regulatory factors; O, the organisms of the decomposer community; Q, the quality of the organic matter (resource) being decomposed; and P, the physical environment. Although these factors are arranged in an hierarchy, feedback interactions also occur.

The overall limits to the decomposition rate are set by the climate of the region, in particular in the tropics by the rainfall period. These limits may be narrowed by specific micro-environnmental (including edaphic) factors. Within this matrix of environmental determination the actual rate of decay of the resource will be determined by its intrinsic character - its resource quality. Even within the same environment, resources decay at widely varying rates (Table 1). The characteristics determining this are complex but are though to include nutrient content, degree of lignification and the presence or absence of allelopathic molecules. Crudely speaking low quality (slow decomposing) litters ae characterised by low N and P and high lignin; high-Q by high N and P and low lignin. All these factors influence the activity of the decomposer organisms. A final regulatory influence, still further narrowing the limits established by P and Q, may thus be the composition and/or biomass of the decomposer community (Anderson, Leonard, Ineson and Huish, 1985; Swift and Heal 1986 in press).

TABLE 1: The influence of resource quality on rate of decomposition. Calculated times for 95% weight loss for different litter components in a rainforest in Panama (Healy & Swift unpublished date)

(a) Main litter components - calculated from Litter Fall to Standing Crop ratios (yrs).

Fruit	**Leaf**	**Palmfrond**	**Twigs**	**Branches**
0,3	1,2	1,9	5,6	19,4

(b) Different leaf species - calculated from observed decay results in coarse mesh litter bags (months)

Quararibea Asterolepis	Gustavia superba	Anacardium excelsum	Miconia argentea	Oenocarpus* panamanus
2,3	4,7	7,4	9,8	12,1

*lamina of palmfrond

This simple model can be placed within the context of soil amelioration. In the conditions addressed here the soil environment may be extreme and will operate as a severely limiting factor within the hierarchy. An extreme example of this is the sodic or alkaline soil conditions described by Khanduja (Chapter 3) and Abrol (Chapter 3). Lowered fertility due to nutrient loss and/or development of low pH are equally relevant and more general examples however.

If amelioration of these soils by the use of trees can be achieved through the agency of decomposition processes, then it must operate not only by a direct effect on soil but through its influence on the quality and on organism variables which lie below the edaphic environment in the hierarchy. Q and O effects will have subsequent feed-back to influence the edaphic environment (Fig 2) and it may be hypothesised that these are the pathways of amelioration. Trees influence the soil they are growing in by changing its microclimate and moisture regime, litter and soil organic matter both being mediators of these effects. The presence of trees also changes the context of decomposition processes. This can perhaps best be illustrated by considering an agro-sylvicultural system (such as alley cropping) in comparison with a monocultural crop as illustrated by Young and by Bashir Jama et al in Chapter 5.

The litter characteristics of the two systems differ greatly; the introduction of trees is likely to increase the amount of litter, particularly the below-ground litter due to perennial root systems; lengthen the time period of litter input; and in particular, widen the spectrum of resource quality. Whilst a monoculture crop will generally have only a few types of resource differing only marginally in their decay rates, trees produce twigs, branches and leaves (and perhaps woody or fleshy fruits) and fine and woody roots. It has been hypothesised in the TSBF proposals that this situation will tend to stabilise nutrient cycling in the soil with a consequent increase in sustainable fertility (Swift 1984, 1985).

The improved physical condition of the soil due to the presence of trees will also affect the nature of the decomposer community. Such changes can be described in general population terms but the influence of such changes on patterns of nutrient cycling remains to be determined (Lavelle 1983, 1984).

Changes in the patterns of nutrient cycling through the litter component are expected to take place in degraded or overcultivated soils under the influence of trees. These are hypothesised to be a progressive change from an open (leaky) system with a relatively few dominant pathways of nutrient flux to a more complex, integrated and consequently closed (tight) nutrient cycling systems.

With respect to potential for management of the system, the best option seems to lie in manipulation of the composition, timing and location of the litter inputs. This can be done by choice of appropriate tree species, including mixtures, and their management practices (e.g. pruning, lopping, biomass transfer).

SOIL ORGANIC MATTER

Although exceptions can be advanced for specific soil types under particular conditions, sustainable fertility is generally supposed to relate closely to the equilibrium level of organic matter found in a soil. The commonly listed beneficial influences of soil organic matter (SOM) include improved soil aggregation and stability, increased water holding capacity, increased cation exchange capacity, decreased fixation of P, and increased content of organic N, P and S. SOM also stabilises nutrient cycling in a manner analogous to low-Q litters by acting as a 'slow release' reservoir of these elements. Despite these commonly perceived benefits, it is difficult to postulate a clear quantitative relationship between SOM content and the productivity of soil as this appears to vary in relation to other features of the soil. Indeed SOM content is a highly variable feature of soils as Sanchez, Gichuru and Katz (1982) have shown. Whilst major soil groups may show characteristic ranges, there is considerable variation within each group. This analysis confirms those of earlier authors (e.g. Birch and

Friend, 1956; Smith, Samuels and Cermuda 1951) on showing that there is little substance to the commonly advanced generalisation that the organic content of a tropical soil is necessarily lower than that of a comparable temperate soil.

The idea that tropical soils should have low organic contents is based on the perception that rates of organic matter decomposition are higher under the hot wet conditions characteristic of these regions. Certainly the rate of decline in SOM content under cultivation is high in the tropics but it was pointed out many years ago by Greenland and Nye (1959) that in assessing the standing stock of humus, consideration must be given to rates of synthesis as well as rates of breakdown. Both of these factors are thought to be very substantially affected by the vegetational cover. Young (1985 and Chapters 1 & 5) has made this the basis of his predictive model for soil organic matter content under different cropping and vegetational regimes. it is appropriate therefore to briefly consider the mechanisms of both processes.

(i) Humus Decomposition

Lack of specific insight into the chemical structure of humus has resulted in little progress being made in the definition of mechanisms of breakdown. As a general proposition, however, it could be assumed that this is under the regulatory influence of the same set of factors as plant litter (Fig 2). With regard to climatic variables there is little doubt that this is so; the temperature and moisture regime and access to oxygen are all regarded as features influencing the rate of breakdown of humus. The existence of a quality spectrum in soil organic matter is also implicit in most recent models of SOM dynamics. At least two fractions are commonly recognised; a labile fraction which may be substantially decomposed in periods ranging from a year to a decade or two, and a recalcitrant fraction which may persist for many hundreds of years (e.g. see Van Veen, Ladd and Frissel, 1984). The rate of breakdown of each of these components may be further affected by physical complexing with clays. The implication is that components of humus have different chemical and physical properties which determine their rate of decomposition, which can be regarded as analogous to the concept of resource quality as applied to litter. Unfortunately the ability to fractionate SOM is at present very limited, as is the chemical definition of the different fractions. Thus it is not clear whether the existence of only two fractions is sufficiently explicit to predict SOM turnover. Nor is it certain whether it is justifiable to describe the two fractions from different soils as directly equivalent.

Nonetheless it is possible to hypothesise a two stage process of SOM decline during degradation of soil condition; first that the rate of humus decomposition increases due to changes in physical conditions and that this decline is due to breakdown of the more labile fractions; and thence secondly that the resultant equilibrium level is less diverse in fractional quality and is dominated by the most refractory components. This might result in a substantial decrease in the capacity of the SOM to serve as a nutrient source i.e. the decline in fertility will be greater than is signalled by change in total content alone.

Restoration of the quantity and quality of SOM is thus dependent on increasing the rate of SOM synthesis.

Humus synthesis

The mechanisms proposed for humus synthesis can broadly be grouped into two categories. The first group of theories proposes that humus molecules are synthesised directly from the breakdown products of litter decomposition; alternatively it is postulated that there is a more distant relationship between litter decomposition and humus synthesis. This latter set of theories suggests that microbial catabolism of plant molecules is more complete and that the precursors of humus are products of microbial anabolism with melanin synthesis being a pathway of particular importance (see Hayes and Swift 1978; Stevenson 1982 for general accounts). It is entirely possible of course that both processes occur but whatever the specific pathway, humus synthesis may rightly be regarded as a by-product of litter decomposition. It is energetically fuelled by the catabolic activities of decomposition and irrespective of whether decomposition products are direct precursors of humus or not, their constituent elements certainly are, as incorporation experiments demonstrate. For instance Mayaudon and Simonart (1959a, b) have shown that 14C from materials such as cellulose and lignin is incorporated in humus molecules within 30 days of addition of soil. The implication of fungi in humus synthesis makes it likely that there are microbial species common to the process of decomposition and humification. Unfortunately, however, there is little detailed information of this.

Thus the environmental and biotic context of humus synthesis may be the same as that of litter decomposition. It is a controversial question however as to whether there is a link between the quality factor in litter decomposition and that in humus formation. For instance, it is not known whether humus quantity and quality is related to the lignin content of the litter from which it is formed. Such evidence as exists is contradictory; it is most certainly, however, a question demanding further investigation.

In the present context, this question may be posed in the following form; whether the increase in SOM content observed under fallow (i.e. tree vegetation = Greenland & Nye 1959) is a product not only of the increased quantity of litter input but also of the broadened spectrum of resource quality.

CONCLUSIONS

There seems to be good evidence that the presence of trees promotes the development of tight nutrient cycling regimes in soil. This ameliorative influence is effected through a number of mechanisms. These include; changes in the soil environment (i.e. water regime, texture, thermal and gaseous properties) that favour satisfied nutrient cycles; and direct quantitative and qualitative alterations to the bio-chemical pathways of nutrient cycling associated with changes in the microfloral and faunistic composition of the soil community. Each of these effects relates in some way to the organic status of the soil which is fuelled by the plant litter input. It is therefore proposed that the patterns and rates of litter decomposition should be an important focus of research in any attempt to determine the mechanisms for the ameliorative effects of trees on soil. It is moreover clear that in this respect the below-ground (i.e. root) input of litter warrants special attention both because it is ever-present in the system and because so little is known of its particular role.

REFERENCES

Anderson, J.M., Leonard, M.A., Ineson, P. and Huish, S. (1985) Faunal Biomass: a key component of a general model of nitrogen mineralisation. Soil Biology and Biochemistry, 17, 735-737.

Greenland, D.J. & Nye, P.H. (1959) Increases in the carbon and nitrogen contents of tropical soils under natural fallows. Journal of Soil Science, 10, 284-299.

Hayes, M.H.B. & Swift, R.S. (1978) The chemistry of soil organic colloids In: D.J. Greenland & M.H.B. Hayes Eds, The chemistry of soil constituents, pp 179-320. John Wiley & Sons, Cochester.

Lavelle, P. (1983) The soil fauna of tropical savannas I. The community structure II. The earthworms In: Tropical savannas Ed. F. Bourlier, pp 477-484, 485-504, Elsevier, Amsterdam.

Lavell, P. (1984) The soil system in the humid tropics Biology International, 9, 2-17

Sanchez, P.A., Gichuru, M.P. & Katz, L.B. (1982) Organic matter in major soils of the tropical and temperate regions. Proceeds of the 12th International Congress on Soil Science, New Delhi, 99-114.

Stevenson, F.J. (1982) Humus chemistry. John Wiley, New York.

Swift, M.J. (ed) (1984) Soil biological processes and tropical soil fertility : a proposal for a collaborative programme of research. Biology International Special Issue 5, International Union of Biological Sciences, Paris.

Swift, M.J. and Heal, O.W. (1986) Theoretical considerations of microbial succession and growth strategies : intellectual exercise or practical necessity? (In pess: Proceedings of Symposium on Microbial Community of Soil, Federaton of European Microbiological Societies).

Swift, M.J., Heal, O.W. and Anderson, J.M. (1979) Decomposition in terrestrial ecosystems. Blackwell Scientific Publications, Oxford.

Van Veen, J.A., Ladd, J.N. and Frissel, M.J. (1984) Modelling C and N turnover through the microbial biomass in soil. Plant and Soil, 76, 257-274.

Young, A. (1985) The potential of agroforestry as a practical means of sustaining soil fertility. ICRAF Working Paper, 34, 1-28.