Zambezia (1983), XI (ii).

THE DEATH OF TREES: AN ESSAY ON THE NATURAL ECONOMY OF THE FOREST*

M.J. SWIFT

Department of Biological Sciences, University of Zimbabwe

WHEN THE FACULTY of Science was founded in this university, twenty-five years ago, two chairs in the Biological Sciences were established; that of Botany and that of Zoology, a distinction which marks the traditional division of the living world into plant life and animal life. This dichotomy in life science goes back at least to the days of Aristotle but is no longer regarded as defensible by modern biologists who recognize not just two kingdoms of organisms but at least five: the unicellular *bacteria* and *protista*, and the multicellular *plants, animals* and *fungi*. This change in the categorization of the living world derives in part from an increasing recognition of a fundamental duality in the study of Biology; the thrust on the one hand to account for the readily observable diversity of nature and on the other to explain life in terms of unity in function.

UNITY AND DIVERSITY IN BIOLOGY

The diversity of living organisms is a feature of common observation and it is probable that even now only a relatively small proportion of the living species of the earth has been scientifically described, although the lists for flowering plants and vertebrate animals, the organisms with which the layman is most familiar, are relatively complete. The drive of modern biology has not been, however, to merely document in greater detail the diversity of form, function and behaviour of life but to recognize an underlying organizational unity. This change in perception has come from the application of sophisticated techniques and concepts, developed mainly for the study of chemistry and physics (Jacob, 1970; Judson, 1979).

Among the most important of these revelations has been the demonstration that the totality of an organism's character is written in a single molecule, the nucleic acid known as D.N.A. (deoxyribose nucleic acid). Moreover this genetic code, the language of life, is the same for all organisms, from bacterium to man. This insight is revolutionary in the sense that it gives a new perspective to man's view of his place in the universe (Monod, 1970; Jacob, 1982). Concomitant with this discovery is the accompanying realization that many other characteristics of 'life' — muscular movement, reproductive behaviour, sensitivity to external stimuli, nerve transmissions, even thought itself — can similarly be described in terms of the laws of physics and chemistry. 'Vitalism' seems to have been laid to rest at last.

If life has such a unified basis, then how do we account for its enormous variety? How (and why) is the diversity derived from the unity? This dialectic

---

* An inaugural lecture delivered as Professor of Botany before the University of Zimbabwe on 13 October 1983.

is the driving force of much modern biological thought and discovery. The linking concept of course is the theory of evolution.

It is just 101 years since the death of Charles Darwin; his exposition of the theory of evolution, an exposition which in its day also altered man's concept of his place in the scheme of things, continues to excite controversy. But there is no part of biological study which is not in some way informed by the theory or does not in some way impinge upon it. It is thus appropriate that the theme of my lecture is couched within an evolutionary framework and can begin from Darwin himself.

Charles Darwin was a polymath, his contribution to biology was outstandingly wide. The last book he wrote, published a year before his death in 1882, was a volume entitled *The Formation of Vegetable Mould through the Action of Worms with Observations on Their Habits* (Darwin, 1881). This book was an attempt to explain the existence of a living organic soil as a consequence of the activity of a particular group of animals, the earthworms (Satchell, 1983). That same story is an essential part of this lecture, although in this case the origin (and disappearance) of soil will be related in particular to the interaction of two other types of organism — forest trees and fungi.

AN EVOLUTIONARY STORY

The earliest steps: Molecular biology has given us insight not only to the functioning of living organisms but also to the very origins of life itself. The earliest evidence of cellular life — similar in form to present-day bacteria — dates life as far back as at least 3.4×10^9 years before present (B.P.). Interestingly, a significant component of this evidence comes from Zimbabwe where indications of fossil microbes have been found in limestone sediments from the Belingwe area, dating back about $2.5-2.8 \times 10^9$ years (Bickle, Martin and Nisbet, 1975; Nagy, Nagy, Zumberge, Sklarew and Anderson, 1977). It seems apparent, however, that even by this stage there was a considerable degree of diversity and the precellular origins of life must be placed somewhat earlier, perhaps at the start of Archean aeon about 3.9×10^9 years B.P.

It has been inferred that many of the simple organic molecules from which all known living systems are constructed — carbohydrates, amino acids, purines, pyrimidimes and lipids — would have predated these fossils. Such substances are indeed known to be present in interstellar space, to be components of meteorites and to be formed abiotically from simple inorganic precursors. The evidence for the latter process has been provided unequivocally by experimentation; under anaerobic conditions in the presence of an energy source such as ultra-violet radiation these compounds may be formed from precursors such as methane (CH_4), hydrogen cyanide (HCN), ammonia (NH_3), and water (H_2O) (Margulis, 1981). It is probable that this is a reasonable simulation of events that occurred early in the earth's history.

What remains a mystery, however, is how these 'building blocks' became polymerized to form the macromolecules that are the chemical basis of living systems. Even more crucially there is presently little evidence to show how these molecular constituents became organized into the self-perpetuating units which we call 'cells'. Whatever the solution of this, surely the most intriguing of all biological mysteries, we know that by the start of the Proterozoic aeon, 2.6×10^9 years B.P., there had already emerged cells that showed the form of oxygenic photosynthesis characteristic of all modern-day plants.

All living systems are organic in nature; that is, they are built from molecules containing carbon (C). There are fundamentally two ways in which living organisms obtain their carbon. The heterotrophs — represented in the present by the animal and fungal kingdoms and by a large majority of the bacteria and protista — obtain their carbon from preformed organic compounds. The autotrophs — the plants and a minority of bacteria and protista — utilize the inorganic compound carbon dioxide (CO_2) as a source of carbon. To utilize C the organisms must also have a source of energy. The most abundant source is that of sunlight and it is this energy which plants utilize; hence their mode of nutrition is known in full as photo-autotrophy. An alternative source of energy is that built into organic compounds — chemo-energy. The animals and the fungi and many other heterotrophs thus utilize the same organic compounds as a source of both carbon and energy and are therefore known as chemo-heterotrophs.

The earliest living organisms were probably chemo-heterotrophs utilizing abiotically formed organic compounds as sources of both carbon and energy. This was a wasting asset, however, and natural selection would have favoured organisms that utilized alternative and less readily exhaustible sources of energy and/or carbon (Broda, 1975). The most abundant source of the former was light. A considerable number of such metabolisms are known but by far the most widespread is that of oxygenic photosynthesis.

$$6CO_2 + 6H_2O \xrightarrow{hv} C_6H_{12}O_6 + 6O_2$$

In this process the energy of sunlight (hv) is used to split the water molecule, the resulting hydrogen (H) being used to reduce the CO_2 to form carbohydrate ($C_6H_{12}O_6$); the oxygen released from the water is evolved in molecular gaseous form (O_2).

The emergence and eventual dominating success of this particular biosynthetic system (Stanier, 1974) changed the pathway of evolution and the course of earth history. The system is highly efficient in thermodynamic terms and made possible the synthesis of a large biomass of organic compounds of great variety. At the same time the generation of oxygen began to change the atmosphere towards its present-day composition. The presence of an oxygen-containing atmosphere in its turn created a situation in which more efficient ways of chemo-heterotrophic utilization of the new excess of organic compounds as a source of energy (by various processes of oxidation) could evolve.

The decomposition, by oxidation, of organic molecules can take place in the absence of oxygen. This indeed was the basis of heterotrophy before the appearance of oxygenic photosynthesis. Many bacteria living in anaerobic environments do this today, but it is essentially an inefficient method of utilizing the chemical energy locked in organic molecules because it never goes to completion. Six-carbon sugars (e.g. $C_6H_{12}O_6$-glucose), for instance, are commonly converted only as far as forming two three-carbon acids. In the presence of oxygen this breakdown can be taken to completion ($6CO_2 + 6H_2O$) — a total reversal of the synthetic equation given above. This form of nutrition is given the general term of 'respiration' and is characteristic of the higher plants, the animals and the fungi of today. In the plants it is just a complement of their synthetic process — a way of using the energy fixed into the sugar molecules by photosynthesis. In the animals and fungi, and in many bacteria and protists, it is the major means of capturing both energy and carbon.

It was only following the emergence of these two highly efficient forms of aerobic metabolism that the multicellular organisms evolved. At the start of the Phanerozoic era about 0.6×10^9 years B.P. the origin of these organisms— the ancestors of the plants, animals and fungi of today — from the simpler bacteria-like life which had preceded it was almost as large a step in evolution as the origin of cellular life itself and in its turn has provoked a deal of recent speculation (Margulis, 1981). Whatever the nature of the early beginning, the succeeding 200 million years produced a great diversity of aquatic plants, and it was probably from ancestors resembling today's green algae that the first terrestrial plants evolved.

Tree making: The first plants to emerge on to land were essentially aquatic in habit and probably very simple in form. That is to say that they were flattened (dorsiventral), adopting a habit that pressed them closely to the surface of the earth. This form gives two advantages; the ability to spread laterally ensures rapid cover of the land surface and gains maximum benefit from the sun's rays; at the same time the plant remains in contact with the earth so that it can absorb the water which runs on the surface and with it take up the essential nutrients which are to be found in soil (nitrogen (N), phosphorous (P), calcium (Ca), potassium (K), magnesium (Mg), etc.). This lateral spread was soon succeeded by vertical growth. The earliest form of vertical growth may well have been the raising of a spore-producing head above the ground, as is found in the mosses and liverworts of today. This enables the plant to gain the advantage of wind as a dispersal agent instead of relying on water in the manner of its ancestors. But plants also gain other advantages in vertical growth. A plant taller than its neighbours retains maximum benefit from the sunlight but can also over-shade its neighbours. Vertical growth combined with a laterally spreading canopy has a strong competitive advantage. The great imperative of plant evolution was thus the climb towards the sun; and its culmination was the production of the tree.

The tree is the optimum plant form for life on earth and before the intervention of man the major part of the earth's surface was naturally covered in vegetation of a tree-like form. Trees have an essentially polar structure in contrast to aquatic plants. At one end they have a canopy — a crown of leaves which is the photosynthetic system of the plant. At the other end is the root system, the site of absorption of water and mineral nutrients. Linking these two essential systems is the trunk which is a feature of plants dictated by the problem of life on land, for the upward growth of terrestrial plants brings three major attendant difficulties which must be overcome.

Firstly there is the problem of dessication. Life on land is dry and the plants must cover themselves with impermeable coats, the cuticle and the bark, to prevent excessive loss of water by evaporation.

The second problem is that of transport; if the photosynthetic surface is raised above the ground, then it loses direct contact with the source of water and nutrients in the soil which are essential to its growth. It is, therefore, necessary for there to be a development of a transport system within the plant, conducting the water and the nutrient from the soil to the photosynthetic system above (Raven, 1977). Correspondingly, there is a need to transport sugars downwards to the roots which are an intrinsically heterotrophic part of the tree.

The third problem, attendant upon this growth towards the sun and the development of the internal transport system, is the need for rigidity in the plant. Plants living in water or plants living simply on the surface of the soil have no need for structural rigidity. But for a plant to grow tall it must be able to stand on its own and to withstand the compressive forces imposed on it by lateral winds. The plant cell walls of algae and of the simpler earth-bound plants are composed almost entirely of polysaccharides of which the commonest component is cellulose. Cellulose is simply a chain of sugar molecules linked together to form a very long unbranched macro-molecule; these molecular chains themselves aggregate to form fibrils and these fibrils wind round in the cell wall, and give it some strength (Fig. 1a). This form of cell wall is indeed quite tough; we know this because we use cotton fibre (which is almost pure cellulose) to make textiles; we also use cellulose to make paper and cardboard. But this strength is a tensile strength, a strength which withstands tearing or shearing stress; it does not have to withstand forces of compression. Cellulose walls unless stiffened by turgor pressure — the pressure of cells filled with water — do not have a great degree of rigidity. Cellulose molecules and those of the other polysaccharides also have the property of attracting and absorbing water. This renders them soft and pliable as we know from the way in which cotton fibre or paper may be wetted. Cellulose walls are thus not tough enough to build trees from. An important stage in the evolution of the terrestrial plants came when another type of chemical component was added to the polysaccharide cell wall — the molecule lignin.

Lignin is an entirely different type of chemical from cellulose and the other polysaccharides (Fig. 1b). First of all, it is not built from sugars; it is built from a series of aromatic compounds known as phenylpropanes, which have hydrocarbon side chains. Moreover these units are not linked in a regular linear form, as in cellulose, but in a highly branched fashion. Whereas cellulose resembles a chain of equal-sized links, lignin is more like a piece of wire-netting which is snipped in a number of places and then folded around in a rather random fashion.

Lignin has two properties which contribute to its importance in cell walls. First of all, its much more diffuse non-linear structure means that it can fold around the fibrillar structure of the cellulose molecule like hardened cement round a metal scaffolding. In this way the lignin fills in the spaces between the fibres of the cellulose and other polysaccharides and this in-filling itself gives added strength to the cell wall. Secondly the lignin molecule is hydrophobic, that is to say it repells water. Lignified cell walls, instead of having the tendency to absorb water with the attendant loss of strength, are water repellent and their rigidity is much enhanced by this property (see Wainwright, Biggs, Currey and Gosline, 1976, for a general discussion of strengthening in plants).

Trees have been described as the apogee of plant evolution but of course there are many thousands of plant species that are not trees. At the edges of the forest and in the drier parts of the world, where tree building is not possible because of limitations on the supply of water and the extreme dessication of the environment, the vegetation may be dominated by grasses or shrubs. These areas are, however, relatively uncommon. Of the entire area of the land surface capable of supporting vegetation over 70 per cent was originally occupied by forest and woodland. Within the forest itself there are many non-tree plants; plants which can tolerate the shade cast by the forest trees but benefit from the stable and benign environment created by the forest — the epiphytes and climbers of the canopy and the herbs and shrubs of the floor.

The forest also provides the habitat for a great diversity of heterotrophic organisms — the animals, the protists, the fungi and the bacteria. These organisms have co-evolved with the forest. Their emergence in evolution is dependent upon, and the product of, the evolution of the plants. Among these we can focus on one group as of particular significance to the functioning of the forest — the fungi.

Evolution of the decomposer system: Most fungi obtain their food from the most direct and obvious of sources within the forest — the plants. Access to this food source may be attained by creation of an intimate association directly

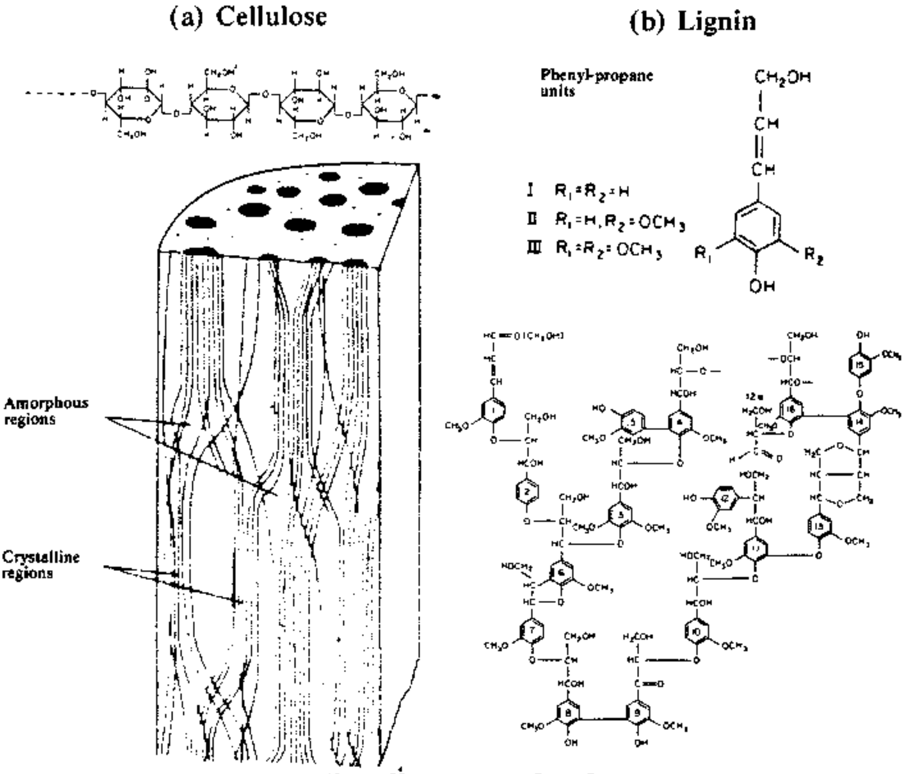

Figure 1: Structure of cell wall macromolecules.
(a) Cellulose. The upper diagram shows part of a single molecule with the glucose units joined together in a repetitive unbranching chain which may be several thousand units in length; the lower diagram shows the aggregation of cellulose chains to form fibrils which form a 'scaffolding' for the cell wall.
(b) Lignin. The upper configuration shows the basic phenyl-propane unit; the lower configuration illustrates a portion of a molecule showing the highly branched non-repetitive structure (from Swift, Heal and Anderson, 1979).

between living fungus and living plant. In some instances this association may be mutually beneficial; the fungus penetrates into the roots of the plant and absorbs sugar produced by photosynthesis by direct transfer from the plant cells; in return the thread-like fungal hyphae, which ramify out into the soil, aid in the absorption of mineral nutrients such as N and P which are transferred to the plants. Such associations are widespread in modern vegetation and ancient in origin, having been detected even in the primitive root systems of the earliest of vascular plants (Malloch, Pirozynski and Raven, 1980). Some authorities have even speculated that such mutualism was essential to the evolution of efficient absorptive systems in plants (Pirozynski and Malloch, 1975), although others have seen this type of association as a later feature in fungal evolution (Lewis, 1974).

A second group of fungi also associate with the living plant but on a shorter-term basis. They parasitize the plant by penetrating into the living tissue and secreting poisons which kill it. The dead plant can then become food for the fungus. My first research work here in Zimbabwe was concerned with this type of parasitic association between fungi and plants (Swift, 1964; 1972) but my present interest and the theme of this lecture relates to a third type of fungal behaviour.

Trees, like all living organisms are mortal. Parts of the tree, in the normal course of events, die and fall to the forest floor, creating a litter of twigs, branches, leaves, petals, bud scales. A huge variety of fungi use this dead organic matter as their source of food. These fungi are the only group of organisms in the living world that possess the enzymes capable of breaking down not only the simpler sugars, amino acids and proteins of the plant cells but also the cellulose, other polysaccharides and in particular the lignin, cutin and suberin of the plant cell wall. In so doing they liberate energy and nutrients for their own growth. But during that breakdown process, which we call the process of decomposition, they bring about two other events which are of great and indeed essential significance to the functioning of the forest. These two processes are the processes of mineralization and of humification (soil organic matter formation).

Mineralization is that part of the decomposition process in which essential elements such as N, P, S and others are converted from an organic form (that is in the form which they are found within leaves, twigs, roots or in the carcasses of animals) to an inorganic form (e.g. NH_4^+, $NO_3^{/}$, $PO_4^{//}$, $SO_4^{//}$). In the organic form, combined with carbon, these nutrients cannot be taken up by plant roots. Conversion from the organic to the inorganic form is thus essential for the vegetational productivity of any ecosystem (Swift, Heal and Anderson, 1979).

Decomposition is never a complete process, however. There is always a residue of organic material left from the activitiy of the decomposer organisms. The material which is left is quite different from the starting material. And of these residues the most important are the group of chemical molecules known as humus. The humus components (humic and fulvic acids and bitumens) have molecular structures quite different from those of the sugars, cellulose, proteins, amino acids and other molecules found in plant or microbial cells, although these molecules, particularly lignin and certain microbial pigments, form the precursors for their synthesis. It may indeed be hypothesized that the appearance of abundant humus is a product of the incorporation of lignin in plants and the appearance during evolution of lignin-degrading fungi. Like cellulose and lignin the humic molecules are polymeric and like lignin they lack a linear repetitive structure. The molecular core of the humus molecules is in each case aromatic but non-aromatic moieties resembling carbohydrates, peptides and organic acids are also detectable within the molecules; the exact structure, however, remains unresolved. The humus molecules also contain significant contents of nitrogen, phosphorous and sulphur, which is one of the main reasons why the presence of humus in soil adds to soil fertility. The humus molecules are highly resistant to decomposition but they do decay at a very slow rate, releasing their nutrients to the soil solution. Where a large mass of humus has accumulated this contributes a very important and stable component to the nutrient cycle. Humus is negatively charged and retains high levels of cations on the soil. The presence of humus also improves the soil by forming complexes with the mineral components such as clay, giving a more stable physical structure and improving its ability to hold moisture and to withstand compaction.

I have emphasized the role of fungi in decomposition but they do not do this alone. Many of the invertebrate animals, protists and bacteria are also involved in decomposition. Indeed, evolution has produced some very close and intimate relations between various representatives of these groups of hetrorophic organisms. It is perhaps better to think not just of the evolution of organisms but of the evolution of systems — on the one hand of the vegetation system and on the other of the decomposer system. These two systems are co-ordinated, and have co-evolved to produce the major biological components of the ecosystem.

THE NATURAL ECONOMY OF THE FOREST

To talk of the evolution of the decomposer system is tantamount to talking of the evolution of the soil. The substratum colonized by the first plants inhabiting the land was largely bare rock covered in a fine dust of mineral particles. As such it had little capacity to retain a reservoir of the soluble mineral nutrients that are essential to plants. It was only with the addition of organic components to this substratum that a soil began to develop that was able to accumulate a level of fertility capable of supporting a high level of vegetational productivity.

Thus there has developed, through the evolution of plant life on land, an inextricable relationship between five elements which comprise the essential components of any ecosystem (Fig. 2). The climate and parent rock of the area are predetermining factors which establish the overall potential of the vegetation system. This latter system is the source, through autotrophic synthesis, of the organic content of the ecosystem. The heterotrophic animals and micro-organisms of the decomposer system feed upon the organic matter and the product of this activity, interacting with the minerals derived from the parent rock, is the soil. This soil is the reservoir of the fertility of the ecosystem, a fertility evolved over many centuries by the interactions of the biotic and abiotic components. These inter-relations are so intimate that ecologists with knowledge of the climate and parent rock of an area of the world can predict the types of vegetation and soil that it will sustain.

The decomposer system thus comprises an essential component of the 'natural economy of the forest'. This economy is based on a currency of nutrients, such as the elements of nitrogen, phosphorous, potassium, sulphur and calcium. The pattern of the economy is a cycle of these nutrients between the organic tissues of the living trees and the organic and inorganic components of soil (Fig. 2). The continued fertility of the forest system depends on this economy being in balance and that is achieved by the exact but antithetic correspondence of the synthetic productivity of the vegetation and the decomposer activity of the soil organisms.

It is widely believed that the climactic ecosystems of the world are in steady state with regard to their productivity and nutrient cycling (Bormann and Likens, 1979). Every patch of vegetation is a mosaic of the youthful, the mature and the senescent. The forest contains, for instance, a mixture of seedlings, saplings and mature and dying trees. In balance the biomass (the living weight of the forest) remains constant. It is added to annually by plant production; it is depleted by death and decomposition. The balance between these two is essentially an equilibrium between the autotrophic and heterotrophic forms of metabolism that we saw emerging so early in the history of life, an equilibrium between the two anti-parallel processes, plant production and decomposition. The sustainability of a forest, or any other type of vegetation, depends on the maintenance of function of both of these processes, for as we have seen they are inter-dependent components of the natural economy. Estimates of the natural extent of vegetation on the world's surface suggest that about 70 per cent of the land surface is productive, the remainder (the hot and cold deserts) being virtually incapable of supporting vegetation. About two thirds of this productive area (that is about 7.4×10^9 ha) was covered in vegetation dominated by trees (including the coniferous forests of the boreal zones, the temperate forests of the mid-latitudes, the woodlands and woodland-savannas of the subtropics and the equatorial rain forests). In contrast, grasslands (including the open savannas) probably originally comprised only about 18 per cent of the productive area (Whittaker, 1975). This distribution has, however, dramatically changed in the last ten thousand years as a result of man's activity. The present estimate of the extent of tree-dominated vegetation is now about only 2.6×10^9 ha, that is about one third of the original area (O.E.A., 1978).

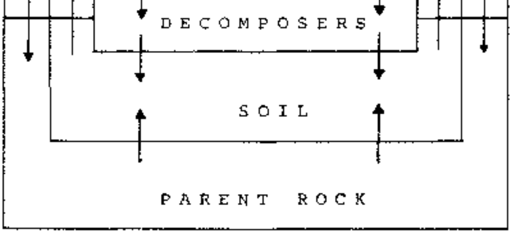

Figure 2: The relationship between the fundamental components that determine the functioning of a natural ecosystem (see text for details).

The clearance of the forest: The forested area stood at about 4.8×10^9 ha in 1950. Thus the extent of clearance in the last thirty years has been almost as great as in the whole previous ten thousand years of man's social history. Present signs show that whilst the rate of clearing may have levelled off in the temperate zone, in the tropics it is actually still accelerating (O.E.A., 1978). The main sites of deforestation in the last two decades have been the Tropical Rain Forests. In some areas — Indonesia, Malaysia, the Phillipines — there is very little left of the original forest and West Africa and Central America are fast approaching the same condition (Ranjitsinh, 1979; Melillo *et al.*, 1983). What are the reasons for the removal of forest? Is this a good and necessary thing, essential for man's survival, or is it short-sighted and self-destructive?

Trees are cut largely for one or more of three reasons. Firstly they may be cut for commercial utilization, as timber or pulpwood; this is the major incentive for the present clearance of the tropical rainforest but it should be noted that the utilization of this timber and pulp is largely outside the tropical zone. Secondly trees are cut to provide fuel, the major source of local (as opposed to export) utilization. It has been estimated that on the African continent over 85 per cent of the wood that is cut annually is used for fuel whereas in North America only 4 per cent of utilization is for this purpose (F.A.O., 1979). The third purpose for forest clearance is to provide land for agricultural use.

The effects of clearance: When wood is removed from a forest, whether for timber or fuel, the natural economy of the forest is disrupted. Countries which sell their trees are exporting more than the timber: they are also selling the nutrients previously locked into the biomass of the forest. When the forest is used for fuel, then the nutrients may also be lost unless efforts are made to return the ash to site. In both cases it is important that new stocks of trees be introduced, for ecological as well as economic reasons. Harvest need not be critical in itself if efforts are made to ensure that the forest is replenished — by planting new trees or by encouraging natural regrowth — because vegetation is resilient and capable of regenerating new nutrient stocks if given time. By this means ecosystem stability may be fairly readily regained. But if these proper precautions are not taken the harvest of the timber may also be a harvest of the soil. There is now well documented evidence from many parts of the world of the effects of clear-felling forest cover. An outstanding example of studies of this kind was done in the U.S.A. at the Hubbard Brook Forest in New Hampshire, a deciduous forest of temperate region trees such as birch, beech and maple (Likens *et al.*, 1977). Studies of the stream waters flowing out of this forest showed them to be remarkably stable in their nutrient content even though the rainfall (and therefore streamflow) varied markedly from year to year (see controls in Fig. 3). Clear-felling a catchment of its trees had a marked effect on water output from the land to stream, increasing the output by 30 to 40 per cent. The concentration of nutrient ions in that outflow increased even more dramatically (Fig. 3). The most significant increase was in NO_3-N which showed 46 times higher loss from the clear-felled catchment than from a control forested catchment. The amount of N lost in three years following felling was roughly equivalent to the total N previously held in the vegetation. Similar effects could be noted for other nutrients. The main reason for these losses is the uncoupling of vegetation from decomposers. The decomposers carry on with their activity, re-generating inorganic nutrients, but there are no plants to take them up; it is as though a thick black line is drawn across Fig. 2, separating vegetation from soil.

The Hubbard Brook experiment is an extreme case because re-growth was prevented by use of herbicides; but the lessons are quite clear. Massive losses of nutrients will occur unless steps are taken to encourage rapid regrowth to re-stabilize the system. The clear-felling operation should also be so structured that there is always a buffer of standing vegetation in the catchment to stabilize the hydrology and prevent irreversible loss of nutrient.

The process of loss may be further aggravated by other practices such as burning. During burning the organic matter is oxidized and many elements are converted to inorganic form. This may be regarded as a bypassing of the decomposition process, and some benefits of this rapid 'fertilization' may be seen. But much of this nutrient is commonly lost by run-off and leaching at the onset of the first rains — again because of the absence of established plant root systems. It is in just these circumstances — lack of plants and natural litter cover — that soil erosion will occur. Much has been written and publicized in Zimbabwe on this topic. Whitlow (1980) has shown the extent of tree clearance that has taken place in the last twenty years and his writings and others (Elwell and Stocking, 1975) have demonstrated the correlation between this and the development of massive areas of soil erosion.

The effects described above are local disruptions of the integrated functioning of the natural ecosystem; most of these effects can be controlled by sensible management, being problems that are more economic, social and

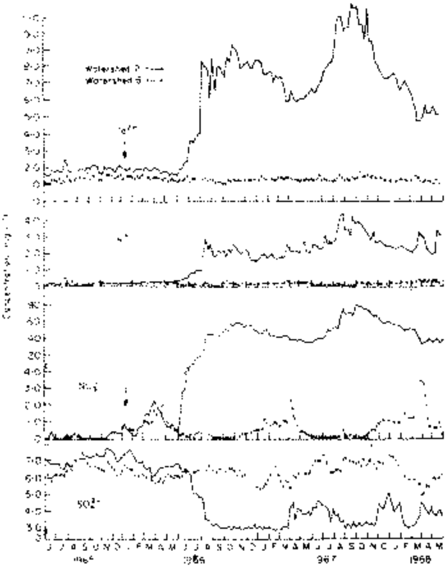

Figure 3: Nutrient losses from a forested catchment at Hubbard Brook Experimental Forest, U.S.A. The graphs show variation with time in the concentration of ions in the streamwater draining two catchments. The broken line is for a catchment which retained its tree cover throughout the experiment (= control); the solid line is for a catchment which was clear-felled in December 1965. Note the change of scale for concentration of nitrate ions (from Swift, Heal and Anderson, 1979).

political than of an intractable biological nature. But the massive extent of clearance has had effects which are global as well as local. The structure of the ecosystem described earlier postulates a balance between production (by plants) and decomposition (by fungi and their allies) (Fig. 2). This balance of the economy was described in terms of a currency of the essential elements. One such element is carbon; and a balance of production and decomposition implies a balance between the uptake of CO_2 from the atmosphere by the plants and its release back to the atmosphere by the decomposers. The circumstances described above, in which massive areas of forest are burned or decomposed without replacement by equally productive vegetation, suggest that an imbalance may develop in the carbon budget. This can indeed be verified; the CO_2 content of the atmosphere has risen steadily for the last two decades and it is predicted that by the year 2030 it will have reached double the concentration present at the start of this century (Houghton *et al.,* 1983). Forest harvest and decay is only one component of this increase (the largest is the burning of fossil fuels) but it is nonetheless a significant factor. The consequences of doubling the CO_2 content of the atmosphere can be debated (e.g. see Clark, 1982; Idso, 1982), but there can be little doubt that they must be taken seriously.

Another major component of the increase in global CO_2 derives from the conversion of forest to agricultural use. This, the third of our categories of deforestation, also results in disruption of the natural economy; in this event it is replaced by an agricultural economy.

THE MANAGED ECONOMY OF CULTIVATED LAND

The domestication of plants: I have already referred to the clearance of forest for agricultural land. It has been estimated that there are about 3.2×10^9 hectares of land suited to arable agriculture, most of it in the forest biomes. At present, only 1.4×10^9 hectares are so used, i.e. about 44 per cent of the convertible area. Nonethless, on our previous estimate that represents about 20 per cent of the original forest reserve and 30 per cent of what has already been cleared — a substantial extent of conversion. It is, therefore, appropriate to ask at this point how efficient the conversion has been.

During the ten-thousand year history of man as a cultivator he has utilized several thousand species of plants as crops. Of these, less than two hundred are economically or nutritionally significant in the world today and the major part of the world's nutritional requirement is supplied by only fifteen species. Most of these species were domesticated at the very onset of agricultural history in one of a number of centres of origin recognized around the world (Harlan, 1975). In broad terms two types of plant domestication can be recognized; vegeculture is the growing of root or tuber crops (such as yams, sweet and irish potatoes, cassava), a practice which probably originated in the tropical lowlands at the margin of forest and savanna; and granoculture, the propagation of plants by seed, which largely originated in the sub-tropical belts of Central America and the Middle East. Most of the seed plants of primary importance are derived from two families, the grasses and the legumes. One of the interesting features of these plants is that they fall into the group that the botanist would call ruderals. In common parlance such plants are termed weeds; the farmer's definition of a weed is a plant growing in the wrong place, that is competing with crop plants. To a botanist or an ecologist a weed or ruderal species is a plant with a certain set of characteristics: rapid growth, rapid setting of seed, efficient dispersal, an annual life cycle, relatively large seeds with good reserves, and an efficient seed dormancy physiology (Grime, 1979). All these characteristics adapt plants to competitively colonize disturbed areas. The natural distribution of such plants is thus in clearings of natural vegetation, at forest margins, and on unstable hillsides — situations which are mimicked by man when he clears land for agriculture, settlement or roads. It has indeed been postulated that it is just because of these 'weedy' characteristics that these cereal grasses and legumes were domesticated by man (Hawkes, 1969). During the phase of man's evolution when he was sedentary, relying for his food on fishing, small-range hunting and the gathering of plants, such organisms might well have become the weeds of his rubbish heaps and of the cleared spaces round his village. It was an easy but important step when man first gathered the seed and planted it deliberately in ground cleared for the purpose. It was an even more significant one when he started selecting seed for planting from among the diverse groups of 'weeds' which were available as food plants.

Over the centuries this selection has operated to produce the handful of primary arable species that currently occupy the attention of the world's agriculturalists. The most recent, most sophisticated and most productive phase of this ten-thousand year evolution has been the Green Revolution — the breeding of ultra-high yielding varieties of wheat and rice and more latterly hybrid maize (Borlaug, 1968; Wellhausen, 1978). The consequence of this process is that cereal grasses now occupy over 50 per cent of the arable hectarage of the world and supply an even higher proportion of the world's basic nutritional requirement. This conversion of natural forest to cultivated 'grassland' clearly represents a major ecological change and we must now examine its consequences.

The economy of cultivated land: The practice of agriculture introduces a new economy into an area in place of the natural economy of the forest. The harvest of 5 metric tons of grain from a hectare of land will remove something like 100kg of N, 20kg of P and 25kg of K. In an area previously covered with Temperate Deciduous Forest this might be equivalent to between 2 and 5 per cent of the total reserves of these nutrients in the soil. In tropical regions where the reservoir of soil nutrients is generally lower this harvest may be equivalent to 10 or even 15 per cent of the stock. Clearly such a level of depletion cannot be maintained indefinitely.

Cultivation also affects the natural economy in other ways. I have already described how the soil is a product of the equilibrium between the vegetation system and the decomposer system. Changing the vegetation system from a diverse forest to a cereal monoculture alters this equilibrium in a drastic way. The litter input to the soil may be less than half that of the forest and additionally contains a much lower proportion of lignin. This results in a decrease in the extent of humus formation. At the same time the rate of humus breakdown is markedly accelerated by tillage practices which tend to break up soil particles, increase the soil temperature and expose it to more aerobic conditions. As a result the introduction of 'conventional' agricultural practices invariably results in a decrease in the content of soil organic matter. The inevitable consequences are a further depletion of soil-nutrient reservoirs (Fig. 4), loss in the quality of the soil structure and a decreased moisture-holding capacity.

Natural ecosystems have a vegetational cover the whole year round; crop ecosystems often remain bare of vegetation during the intervals between growing seasons. In some cases, because of practices such as burning, they are also devoid of any cover of litter. These conditions are those, as we have already seen, which promote soil erosion and nutrient loss by leaching and run-off. Even under relatively careful management of the crop residues (litter) the proportion of nutrient return to the plant from decomposition may not be as great as in a natural ecosystem. Both plant growth and decompositon are commonly triggered by the arrival of favourable seasonal conditions (an increase in temperature and day-length in temperate zones, the onset of rain in the tropics). In natural ecosystems the vegetation and the decomposers are both adapted to benefit from this. In a crop ecosystem the two systems are at the mercy of man. If the farmer does not manipulate both vegetation (planting at the correct time) and the soil (introducing crop residues at the correct time) then the tight 'coupling' between the two systems may be disrupted. One consequence of this may be, for instance, that nutrients are released from the crop residues before the crop roots are sufficiently grown to benefit from their presence. In these circumstances much of the released nutrient may be lost through leaching (Anderson and Swift, 1983; Swift, 1983).

The agricultural ecosystem is thence a different and intrinsically less productive ecosystem than the one it replaces. The intervention of man in the evolution of his crops is equally an intervention in the evolution of the soil. The soil selected in this way is less fertile and less productive than the natural soil. It should be stressed that this is an inevitable and unavoidable consequence of the practice of agriculture, in contrast to the excessive and catastrophic effects of deforestation for timber and fuelwood described earlier which can be prevented by sensible management. And most agriculture is, of course, practised under conditions of sensible management. Man's ingenuity is enormous and he has evolved many ways in which he can practise productive arable agriculture against this inevitable decline in soil fertility.

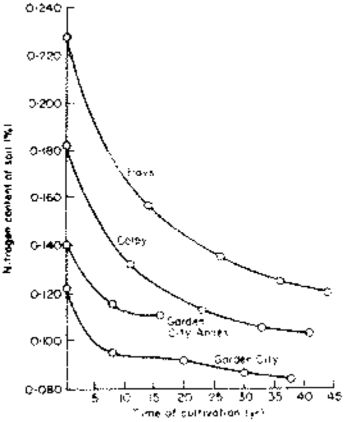

Figure 4: Depletion of the nutrient reserves in soil following cultivation. The graph shows the nitrogen content of four prairie soils from the U.S.A. over the forty-year period following conversion from natural grassland to cereal cultivation. The depletion in N is associated with a parallel decrease in the humus content (from Swift, Heal and Anderson, 1979).

Broadly speaking there have been two types of solution: that of the intensive farming characteristic of the higher latitudes in which farming is sedentary in nature and the impoverishment of the soil is subsidized by the import of synthetic inorganic fertilizer; and secondly that of the extensive farming characteristic of much of the tropics where a shifting cultivation of one kind or another is practised (Ruthenberg, 1980). In this latter case soil impoverishment is reversed by allowing the return of the forest in the form of a fallow, which alternates with periods of cultivation in any given area. Thus in shifting agriculture there is also a subsidy — the holding of a large area of land out of cultivation at any one time.

These two types of farming may be respectively characterized, at their extremes, as technological and ecological, in terms of the resources on which they depend. The high-yielding technological farm of North America utilizes intensively bred, genetically specialized varieties of crop plants grown as monocultures at very high densities. Soils are prepared by deep mechanized ploughing and are fed with water, with macro and micronutrients and with chemicals to combat weeds, pests and diseases. The supply of all these materials is dependent on an energy subsidy largely petrochemical in origin, and on industrial processing. The soil in this type of agriculture is treated simply as a rooting medium and the biological processes are bypassed (Fig. 5); in some cases the soil may even be sterilized before planting. The crop may also be harvested by mechanical means.

In contrast the gardener of a food plot in the Tropical Rain Forest of Papua New Guinea clears an area from the forest and prepares the soil by hand or with a stick. He plants possibly twenty or more species of crop. Each crop is genetically variable as the seed or roots are gathered from the previous crop without any particular selection. The garden may have a complex structure with a tree layer, a shrub layer and a variety of ground plants. All the resources utilized are indigenous and the farmer is totally dependent on the natural fertility of the soil for the level of yield he obtains. In terms of the ratio of energy output to energy input such a method of farming may be more efficient than one relying on technological subsidy (Black, 1971; Rapaport, 1971); in terms of

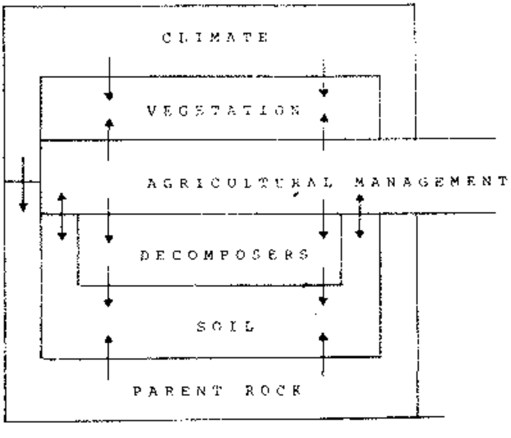

Figure 5: The intervention of agricultural management into the functioning of an ecosystem (compare with Fig. 2).

the absolute yield per unit area, however, the technological farm is many times more productive.

The world food crisis: The predicted rate of global population increase necessitates a doubling in world food output in the next twenty years in order that we may stand still, let alone make up the enormous nutritional deficit which currently exists. This requirement is most acute in the tropical regions where the major part of the population growth will occur. The demand for increased food production can be met in one of two ways. Firstly, by bringing more of the potentially arable land into effective production; secondly by increasing yields per unit area of land. The figures quoted earlier show that there is plenty of suitable land still available — 56 per cent of the 3.2×10^9 hectares of potentially arable land remain unconverted and most of this is in the tropics. But the cost of clearance on this scale in environmental terms may be very high, and a good deal of the land is probably only marginally suitable in any case. The real key to the food deficit surely lies in increasing the effectiveness of conversion of the land, that is in finding means of increasing the yield.

TOWARDS A MIXED ECONOMY

The obvious method of increasing yield would seem to lie in introducing productive technological farming on a much wider scale than is currently practised. Attempts at this were made with some measure of success during the last decade; the Green Revolution in Mexico and India produced spectacular increase in yield under some conditions. In other instances, however, the introduction of the high-yielding varieties has not had the predicted success and indeed has brought unforeseen problems of both an agricultural and a sociological nature (Borgstrom, 1973; Pearse, 1980). There are, however, two broad categories of constraint that place limits on the expansion of technological farming. Firstly there are economic limits; for this type of farming requires a very high subsidy from the other sectors of the economy, much of it petroleum-based, in order to provide fertilizer, fuel and pesticides. Whilst grain yields have gone up by factors of almost two in the last two decades, the cost of producing the same amount of grain has more than tripled. If this type of farming is to be expanded its energetic efficiency must be improved.

The second constraint is potentially even more serious; it is biological. Many soils in the tropics do not seem to be able to bear the intensity of cultivation that is required to produce this type of yield from monoculture farming. There is perhaps an evolutionary lesson to be learned from the fact that the cultivation most characteristic of tropical areas is of the ecological type where conservation of the soil is at a premium — a lesson that has been learned by a painful process of trial and error over the centuries.

But shifting cultivation is an equally unviable solution for the modern world. In many parts of the tropics the population pressures are such that the length of fallow period has already been drastically shortened to levels where natural regeneration of soil fertility is no longer possible. In many places it has been abandoned in favour of continuous cropping regimes with either negligible or no fertilizer inputs at all, with the consequence of ever-decreasing yields (Ruthenberg, 1980). It seems clear that for these fragile tropical soils a different and more radical type of solution is required (Sanchez and Salinas,

1981) — one which is reliant upon not the technological nor the ecological approach alone, but one which benefits from insight into both. This type of approach might be described as a 'mixed economy' — partly that of agriculture, partly that of the forest.

The return of the forest: The absolute necessity for tree-planting is realized as a matter of high priority in this country and in many others throughout Africa and the tropics. This perception is based very largely on the high demand for fuelwood in an increasingly energy starved world (Eckholm, 1976). But it has also been recognized that the re-introduction of trees to the agricultural economy can have other benefits. This has led to a developing interest in the practice of agroforestry.

Agroforestry is a term which embraces a wide range of different practices but basically means a land-use system that combines the production of annual crops and/or animals with the growth of trees. Its fundamental feature is that the combination of trees with other types of land-use produces a viable and sustainable farming system (King, 1978; Lundgren and Raintree, 1983).

Agroforestry systems have a large variety of possible structures. The choice of combination for trees and agriculture practice depends not only on economic but also on ecological and social considerations. In economic terms the tree of choice may be primarily for fuelwood, for timber or for the yield of a food or cash crop. Whatever the decision in this respect, careful planning and management can also provide indirect ecological benefits to the agricultural system with which it is combined, whether that is arable or involves livestock production. The trees can be used to ameliorate soil degradation (Mongi and Huxley, 1979). The permanent cover of litter and roots at key positions on the catchment area stabilizes the soil and prevents erosion and nutrient losses by leaching and run-off. The presence of the tree crop may indeed improve the hydrological status of the farm area, as Whitlow (1983), for example, has recently pointed out. The trees can also be used to improve the fertility of the soil. Their roots reach deeper into soil and nutrient capture into the vegetational zone is much greater than with shallow-rooting species. The presence of mutualistic associations between fungi and the roots of the trees (see above) can further enhance the extent of nutrient capture. The production of abundant litter including components with high lignin content improves the organic-matter status of the soil as well as stabilizing the soil surface and enhancing infiltration. By ingenious choice of tree species litter production may be maintained through a large partof the year. The litter from the trees may be used as mulch and compost for arable crops. In addition to their effects on soil, blocks of trees may act as reservoirs of biological control agents against the pest and diseases of the crop plants. The trees provide shade and increase the humidity of the area and can be used to nurture the crop plants by providing a buffer against extreme environmental conditions.

Whatever the economic benefits sought from the tree the choice should be made on an ecological basis. The trees selected should be adapted to growth in the climatic conditions of the area concerned and should be shown to have a beneficial relationship with the soil type in which they are grown. There is a huge wealth of species available and there is no need to confine choice to Central American pine species or Australian gum trees (N.A.S., 1975; Okigbo, 1977). Much research on suitable provenances is already being done in various parts of the tropical zone including Tanzania, India and Central America.

The yields of farm-produce from agroforestry systems are in some cases as high as can be obtained in the short term from more intensive farming. But in many cases they fall short. The over-riding advantage lies, however, in the sustainability of this yield. Conversion to agroforestry, however, is complex; it takes a considerable period of time to establish a system at its sustainable level, that is where all parts of the cycle are yielding on a repetitive pattern. During this period of establishment, therefore, some degree of subsidy may be required. Finally the planning must include a sociological component. Agroforestry must be planned on an ecological scale. The boundaries for agroforestry units must be determined by the hydrological character of the area; that is to say they are the same boundaries as those of natural ecosystems, those of the catchment area. These boundaries do not coincide with the boundaries of man's social organizations. So the introduction of agroforestry means land-use planning which cuts across land-tenure systems.

For all these reasons it is essential that the biological scientist, the agricultural scientist and the social scientist work together in planning the research and implementation criteria for rural agricultural development (Hoekstra and Kuguru, 1983). This university has made significant contributions to developing collaboration of this kind already but I believe that it has more to make. One of the steps in this must be to turn its attention to trees, which means that at some stage forestry must be a part of its curriculum. But this does not just mean forestry in the production sense but forestry as a means of re-introducing the tree into our way of life (F.A.O., 1978). Forestry must be integrated with agriculture, with ecology and with all other aspects of natural resources utilization and planning.

EPILOGUE: MAN AND THE TREE

In the earliest stages of his own evolution man was an animal of the African savanna. He roamed areas similar to those still found in the untouched parts of Zimbabwe today. He lived in some type of equilibrium with that environment. At times its harshness defeated him but in general he used it to his advantage. In any event the trees were one of his benefits — as a source of shade, of food, of firewood, of tools and eventually of material to build his home. But man has killed the trees and now he has to live without them. And with the death of trees so also the soil has died. It is time now for a new stage in man's evolution, a stage in which he learns to live again with the trees. As a master of them, using them to his own advantage, using them to supply his wants, using them above all to rebuild the soils he has destroyed. But using them with respect and with understanding. It is after all possible that, if man does not learn to do this, the tree will finally re-inherit the earth after mankind has become extinct by his own self-destructive action.

Bibliography

ANDERSON, J.M. and SWIFT, M.J. 1983 'Decomposition in tropical forests', in S.L. Sutton, T.C. Whitmore and A.C. Chadwick (eds), *Tropical Rain Forest: Ecology and Management* (Oxford, Blackwell Scientific Publications), 287–399.

BICKLE, M.J., MARTIN, A. and NISBET, E.G. 1975 'Basaltic and periodic komatiites and stromatolites above a basal unconformity in the the Belingwe greenstone belt, Rhodesia', *Earth and Planetary Science Letters*, XXVII, 155–62.

BLACK, J.N. 1971 'Energy relations in crop production — a preliminary survey', *Annals of Applied Biology*, LXVII, 272.

BORGSTROM, G. 1973 *World Food Resources* (Aylesbury, Intertext).

BORLAUG, N.E. 1968 'Wheat breeding and its impact on world food supply', *Proceedings of the Third International Wheat Genetics Symposium*, 1–36.

BORMANN, F.H. and LIKENS, G.E., 1979 *Pattern and Process in a Forested Ecosystem* (New York, Springer-Verlag).

BRODA, E 1975 *The Evolution of the Bioenergetic Processes* (Oxford Pergamon Press).

CLARK, W.C. 1982 *Carbon Dioxide Review: 1982* (Oxford, Oxford Univ. Press).

DARWIN, C. 1881 *The Formation of Vegetable Mould through the Action of Worms with Observations on Their Habits* (London, John Murray).

ECKHOLM, E.P. 1976 *Losing Ground: Environmental Stress and World Food Prospects* (Oxford, Pergamon Press).

ELWELL, H.A. and STOCKING, M.A. 1975 'Parameters for estimating annual runoff and soil loss from agricultural lands in Rhodesia', *Water Resources Research*, XI, 601–5.

F.A.O. 1978 *Forestry for Local Community Development.* (Rome, Food & Agriculture Organization of the United Nations, Forestry Paper 7).

1979 *Forestry for Rural Communities* (Rome, Food & Agriculture Organization of the United Nations, Forestry Department).

GRIME, J.P. 1979 *Plant Strategies and Vegetation Processes* (Chichester, John Wiley).

HARLAN, J.R. 1975 *Crops and Man* (Madison WI, American Society of Agronomy).

HAWKES, J.G. 1969 'The ecological background of plant domestication', in P.J. Ucko and G.W. Dimbleby (eds), *The Domestication and Exploitation of Plants and Animals* (London, Duckworth), 17–30.

HOEKSTRA, D. and KUGURU, F.M. (eds) 1983 *Agroforestry Systems for Small-Scale Farmers* (Nairobi, International Council for Research in Agroforestry).

HOUGHTON, R.A., HOBBIE, J.E., MELILLO, J.M., MOORE, B., PETERSON, B.J., SHAVER, G.R. and WOODWELL, G.M. 1983 'Changes in the carbon content of terrestrial biota and soils between 1860 and 1980: A net release of CO_2 to the atmosphere' (in press).

IDSO, S.B. 1982 *Carbon Dioxide: Friend or Foe?* (Tempe AZ, I.B.R. Press).

JACOB, F. 1970 *The Logic of Life: a History of Heredity* (New York, Pantheon Books).

JACOB, F. 1982 *The Possible and the Actual* (Seattle, Univ. of Washington Press).

JUDSON, H.F. 1979 *The Eighth Day of Creation: The Makers of the Revolution in Biology* (New York, Simon Schuster).

KING, K.S.F. 1978 'Agroforestry (a new system of land management)', in *Agroforestry Proceedings of the 50th Symposium on Tropical Agriculture* (Amsterdam, Dep. of Agricultural Research, Bulletin 303).

LEWIS, D.H. 1974 'Micro-organisms and plants: The evolution of parasitism and mutualism', *Symposium of the Society of General Microbiology*, XXIV, 367–92.

LIKENS, G.E., BORMANN, F.H., PIERCE, R.S., EATON, J.S. and JOHNSON, N.M. 1977 *Biogeochemistry of a Forested Ecosystem* (New York, Springer-Verlag).

LUNDGREN, B and RAINTREE, J.B. 1983 'Agroforestry', in B. Nestel (ed.), *Potentials and Challenges in Asia* (Jakarta, National Agricultural Research Institute), 37–49.

MALLOCH, D.W., PIROZYNSKI, K.A. and RAVEN, P.H. 1980 'Ecological and evolutionary significance of mycorrhizal symbioses in vascular plants', *Proceedings of the National Academy of Sciences, U.S.A.*, LXXVII, 2113–18.

MARGULIS, L. 1981 *Symbiosis in Cell Evolution: Life and Its Environment on the Early Earth* (San Francisco, Freeman).

MELILLO, J.M., PALM, C.A., HOUGHTON, R.A., WOODWELL, G.M. and MYERS, N. 1983 'A comparison of two recent estimates of disturbance in tropical forests' (in press).

MONGI, H.O. and HUXLEY, P.A. (eds) 1979 *Soils Research in Agroforestry* (Nairobi, International Council for Research in Agroforestry).

MONOD, J. 1970 *Chance and Necessity* (Glasgow, William Collins).

NAGY, B., NAGY, L.A., ZUMBERGE, J.E., SKLAREW, D.S. and ANDERSON, P. 1977 'Indications of a biological and biochemical evolutionary trend during the Archean and early Proterozoic', *Precambrian Research*, V, 109–20.

N.A.S. 1975 *Underexploited Tropical Plants with Promising Economic Values* (Washington DC, National Academy of Sciences).

O.E.A. 1978 *Tropical Deforestation: Proceedings of the U.S. Strategy Conference* (Washington DC, U.S. Department of State, Office of Environmental Affairs).

OKIGBO, B.N. 1977 'Neglected plants of horticultural importance in traditional farming systems of tropical Africa', *Acta Horticultura,* LIII, 131–50.

PEARSE, A. 1980 *Seeds of Plenty, Seeds of Want* (Oxford, Clarendon Press).

PIROZYNSKI, K.A. and MALLOCH, D.W. 1975 'The origin of land plants: A matter of mycotropism', *Biosystems,* VI, 153–64.

RANJITSINH, M.K. 1979 'Forest destruction in Asia and the South Pacific', *Ambio,* VIII, 192–201.

RAPAPORT, R.A. 1971 'The flow of energy in an agricultural society', *Scientific American,* CCXXV, 116–32.

RAVEN, J.A. 1977 'The evolution of vascular plants in relation to supracellular transport processes', *Advances in Botanical Research,* V, 153–82.

RUTHENBERG, H. 1980 *Farming Systems in the Tropics* (Oxford, Clarendon Press, 3rd edn).

SANCHEZ, P.A. and SALINAS, J.G. 1981 'Low-input technology for managing oxisols and ultosols in tropical America', *Advanced Agronomy,* XXXIV, 279–406.

SATCHELL, J.E. (ed.) 1983 *Earthworm Ecology: From Darwin to Vermiculture* (London, Chapman & Hall).

STANIER, R.Y. 1974 'The origins of photosynthesis in eukaryotes', *Symposium of the Society of General Microbiology,* XXIV, 219–40.

SWIFT, M.J. 1964 'The Biology of *Armillaria mellea* in Central Africa' (London, Univ. of London, Ph.D. thesis).

1972 'The ecology of *Armillaria mellea* (Vahl (Ex Fries.) in the indigenous and exotic woodlands of Rhodesia', *Forestry,* XV, 67–86.

1983 'Soil biology and soil fertility in the tropics', *Zimbabwe Science News,* XVI, 223–7.

SWIFT, M.J., HEAL, O.W. and ANDERSON, J.M. 1979 *Decomposition in Terrestrial Ecosystems* (Oxford, Blackwell Scientific Publications).

WAINWRIGHT, S.A., BIGGS, W.D., CURREY, J.D. and GOSLINE, J.M. 1976 *Mechanical Design in Organisms* (London, Edward Arnold).

WELLHAUSEN, E.J. 1978 'Recent developments in maize breeding in the tropics', in D.B. Walden (ed.), *Maize Breeding and Genetics* (New York, John Wiley), 59–84.

WHITLOW, J.R. 1980 *Deforestation in Zimbabwe: Problems and Prospects* (Salisbury, Univ. of Zimbabwe, Supplement to *Zambezia).*

1983 'Hydrological implications of land use in Africa with particular reference to Zimbabwe', *Zimbabwe Agricultural Journal,* LXXX, 193–212.

WHITTAKER, R.H. 1975 *Communities and Ecosystems* (London, Collier-MacMillan, 2nd edn).