SOILS AS COMPONENTS OF ECOSYSTEMS

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INTRODUCTION

Historically, because of the obvious influence of soils on plant development, the "edaphic factor" always had a place in plant environmental literature. The effect of soil was seen either as predominantly chemical or as purely physical. Some 135 years ago an extensive analysis of silicate flora versus the flora on calcareous substrate in the Tirolean Alps suggested chemical causes for species distribution. Even the generation of new species was ascribed to differences in soil chemistry. A few years afterwards, the opposite view was held, viz that soil texture and organic matter were the main factors in plant distribution. For almost a century the chemical versus physical soil theory controversy dominated the discussion of plant distribution and association.

It was not until the introduction of colloid chemistry that physical and chemical soil characteristics were combined and provided a new basis for plant ecology. Base saturation of humus and clays explained much of the differences in plant growth as well as of profile formation. Thus causal relationships between floral and all soil characteristics were established.

The physical, chemical, and colloid theories of early plant ecology considered soil as an independent environmental factor that determined subsequent vegetation. Today's system ecology views soil neither as the beginning nor as the end product of vegetation but as a compartment in a network of interactions among soil, flora, fauna, and man with his agriculture and industry. And because there seldom is a steady state, "soil" is only a phase in a succession of stages of build-up or deterioration.

Stages of build-up of soils, of net increase of minerals and humus, usually take place under natural ecosystem succession. Annual increments of minerals from substrate weathering and atmospheric input, including N fixation, are at least in part immobilized by colloids and biota. Thus there is a gradual increase in soil fertility because of the gradually increasing pool of available nutrient elements.

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On the other hand mineral pools can be reduced in size by removal of minerals with the harvested crops in excess of natural inputs and by man-made additions such as fertilization or eutrophication. Mineral pools may also be depleted by leaching of minerals upon destruction of the biological buffer by man-made biocides or loss of the colloidal buffer by accelerated humus decomposition upon defoliation, clear-cutting, or fire.

Loss of nutrient minerals in general leads to decreased productivity for long periods of time. Most of the factors listed that cause loss of nutrients are the direct or indirect results of human action. Thus there is a threat that the increasing human population will increasingly interfere with the environment and that this intervention will lead to reduced productivity. On the other hand the increasing human population requires greater photosynthetic output. Because the vegetation-bearing area on earth essentially cannot be expanded, the greater human population will need greater productivity per unit area rather than reduced productivity as may be expected under increased human interference with the nutrient cycle.

It is exactly the evaluation of conflicting effects of the increasing human density and activity on productivity that today occupies the minds and affects the research interest of many environmentalists. Productivity of natural ecosystems depends primarily on climate and nutrient supply. Energy input hardly appears to be a limiting factor; mate to either enhance or decrease productivity is not yet an urgent issue but interference with nutrient supply is of immediate importance. In order to maintain and possibly increase productivity of ecosystems we must understand the mechanism that drives the nutrient cycle and how the environmental factors affect nutrient flux.

Present awareness of the crucial issue of nutrient flow in primary and, subsequently, all productivity has brought together foresters, agriculturists, ecologists and soil scientists in a number of multidisciplinary projects. These include in-depth studies of mineral turnover in simulated ecosystems in the laboratory, single-plot studies of simple natural ecosystems, watershed analyses, and large integrated woodland projects such as are now in progress in many countries as part of the International Biological Program.

In the following pages I will present results of the last few years of study of the mechanisms, the ecology, and the analysis of mineral flow through soils. Forest ecosystems are emphasized because their mineral cycles are usually more closed than those found outside the forest. Particularly in mature stands there is great year-to-year continuity. Thus forests offer excellent sites for cycling studies. In addition, understanding and subsequent maintenance or enhancement of mineral turnover in forests is of more importance than in most other "production" ecosystems, such as grasslands and fishponds, where fertilizer amendments are commonly used to raise productivity and compensate for harvest outputs.

Emphasis will be on nutrient supply because productivity is more often checked by mineral availability than by lack of energy input. In many natural
ecosystems, especially in forests, mineral supply depends on remineralization of chemical elements that are returned to the soil in organic plant and animal debris. Therefore much of the discussion will center around recent additions to our knowledge of litter decomposition and nutrient remineralization.

There exist three main approaches to the study of mineral transfer in soils. The approach of soil chemistry focuses on chemical and colloid chemical reactions between mineral elements and the soil with its adsorption complex. The emphasis is on the chemical state and availability of the elements for subsequent plant uptake. This approach is very much at the molecular and soil particle level. At the other end of the scale is the hydrological approach which sees water as the principal mover of soil nutrients. Studies are preferably at the landscape and watershed level. Many of the mineral transfers between the various forms of input and output are treated as mass transport by flow, diffusion, and assorted black boxes for root uptake, weathering of rock, and biological remineralization. Root uptake of minerals is well documented in plant physiological literature, whereas weathering of rock has a place in geochemistry. Biological remineralization on the other hand has been studied in a variety of disciplines such as forestry, agriculture, microbiology, entomology, ecology, and pedology. Usually certain segments of the complex sequence have been studied separately, and few results of integrated studies of the entire “biological remineralization” black box have been published thus far. The main processes connected with biological remineralization are nutrient input, fragmentation and some transportation by the soil fauna, chemical decomposition and remineralization by the soil microflora, and output via root uptake. This edaphic segment of the biological cycle continuously interacts with aspects of soil chemistry and the hydrologic cycle. Space and the adsorption complex of function primarily as a rather static storage pool for minerals, whereas the hydrologic cycle tends to move minerals and bypass biological compartments. This report will mention some of the recent findings on compartments and transfer pathways in the edaphic part of the mineral cycle.

**Input of Mineral Elements and Organic Matter**

Just about 100 years ago the European forestry literature contained extensive accounts on the inputs and reservoir of mineral elements in forest litter. Foresters were impressed by the enormous mineral capital that was found locked up in the accumulated annual inputs of slowly decomposing litter. Empirical measures to unlock this store of production potential were suggested and tried. These measures were chemical (such as liming or fertilizing to boost decomposition), mechanical (discing or introducing chicken and swine to hasten mixing of litter with mineral soil), physical (ditching and draining to decrease anaerobic soil conditions, or biochemical (mixing rapidly and slowly decomposing tree species or introducing microbial or animal decomposers). Few of these methods received general acceptance be-
cause they attempted to cure a symptom rather than affect a process. In general they did not consider mineralization as part of a continuous cycle of elements that should be restored, accelerated, or optimized.

Approaches to measuring mineral inputs vary with the objectives of the study that is being made. In watershed studies which emphasize the hydrological cycle only input by rain may be considered. In industrial and agricultural areas particulate inputs may make up more than half of the input of elements such as Ca and Si. Presence of radon in the West Indies has been correlated with deposition of Sahara dust blown across the Atlantic by the NE tradewinds. Particulate mineral deposits from power plants are reported to follow seasonal fluctuations in consumer demand for electricity. Effects of wind velocity and rates of precipitation on the scavaging of atmospheric debris by rain received much attention in the literature on fallout from atomic explosives. Inputs of sodium and chlorine by rain depend to a large extent on oceanic storms that transport spray far inland (26, 68). Almost all sodium input to the forest floor is in rain. Similarly, about half of the potassium input is in rain. In contrast to sodium, 40% of which may originate from outside the forest, almost all (99%) of the potassium input in rain may be leached from the aboveground part of the forest and only a small amount is input into the system (99). Of the rain inputs of aluminum, iron, and manganese, about 90% comes from the aboveground vegetation. In rather unpolluted atmospheres only 20% of the sulfate sulfur in rain may originate from outside the stand, but in heavily industrialized areas most of the sulfur inputs is by addition rather than by recycling.

Part of the potential mineral input to the forest floor may be intercepted by epiphytes and possibly recycled to their hosts. Stem epiphytes may be responsible for the rather low mineral input in stemflow of temperate deciduous forest (25). Leaf epiphytes of moist tropical vegetation such as rain forests and certain coffee plantations greatly affect mineral flow. Epiphyte density increases from the crown layer down as a result of increasingly favorable moisture and nutrient influx (21). In simulated rain shower experiments epiphytes increased mineral retention by tree leaves from 1.7 to 20 times, depending on tree species and mineral (110). Retention also increases with increasing epiphyte density (69). Effectiveness of rain forest epiphytes in retaining mineral throughfall decreases in the order algae-moss-liverwort encrustations > moss masses > bromeliads > rooted epiphytes. Many of the epiphytes, and of the epiphylls in particular, only delay mineral input to the forest floor, for they eventually end up in the litter layer. Thus they may not influence the mineral balance but rather the seasonal kinetics of mineral input.

Epiphytes do affect the mineral balance of nitrogen. Many stem and leaf dwellers, in particular blue-green algae, appear to be actively fixing nitrogen from the atmosphere. In general, annual increments of N by fixation are in the order of 1-10 kg/ha (85, 93). Under favorable conditions up to 85 kg/ha may be accumulated in 1 year, as was found for an alder stand
invading an abandoned mill pond (101). Nitrogen input from rain depends greatly on the amount and periodicity of rainfall. For temperate forests this input may be 10-13 kg/ha annually (25). The combined nitrogen input from fixation and rain appears to be sufficient to maintain range productivity (93) and may be a key factor in the increasing productivity of forest sites during succession.

Much of the mineral input from throughfall is seasonal, not only because of climatological differences, but also as a result of physiological and chemical changes in the leaves. In particular, leaching of potassium greatly increases when the leaves turn yellow and cell turgor decreases. As a result of appreciable leaching before leaf fall, mineral input from throughfall may be three times the mineral input from leaf fall in a tropical rain forest (68). Even the influx in stem flow was greater than from leaf deposition. On the other hand in temperate forests the input of Ca was predominantly in falling leaves, whereas magnesium and potassium inputs were equally divided between leaf fall and throughfall (26). Of the litter influx in a mixed oak stand on good soil, only slightly over half (52%) the input by weight was from leaves (32). The rest was made up of branches (13%), twigs (17.5%), scales (4%), flowers (2.5%), acorns (3%), and 7% miscellaneous debris. These values for weight input may deviate considerably from those for input of various minerals.

In the temperate forest roughly three fourths of the total amount of cycling minerals may be returned to the forest floor in throughfall and leaf fall (26). More than 60% of the nitrogen uptake is thus returned. This figure holds for phosphorus and sulfur as well, because at least part of the way they are involved in the same protein synthesis and decomposition cycles. Other elements, such as Fe, Al, and in particular Si, are more abundant in tropical forests than in temperate forests. The annual return of Si may be as much as 770 kg/ha or 60% of the total ash content (85).

The total amount of annual mineral input to the forest floor tends to be highest in tropical forests. Among the reasons for the high input are the rather high ash content (5%) of the organic return, the continuous input in throughfall, and the relatively large mass of green parts (3% of the standing crop as compared to only 1% in temperate deciduous forests) (85).

Much of the mineral input to the forest floor in throughfall may be intercepted by soil vegetation such as mosses and lichens and be stored up for many years. Tufts of moss and lichen are reported to intercept and retain up to 99% of the dissolved and particulate mineral fallout. Thus they provide excellent monitors for past mineral input to the floor of various landscapes, in particular at higher latitudes and elevations.

**Mineral Leaching**

The most common inputs are: 1. particulate organic matter, 2. particulate inorganic fallout which may be dry fallout or scavenged from the atmosphere by rain, and 3. dissolved minerals in rain and throughfall. In addi-
tion, there are specific pathways for fixation of atmospheric N, C, and O.

In most forests the particulate organic matter forms a litter layer which intercepts inputs of particulate fallout, throughfall, and rain. Thus the litter is the first area-wide pool for all inputs to forest floor. The mineral pool in litter thus provides a good starting point for the measurement of edaphic transfer of minerals to either root uptake, the mineral soil pool, or removal by either runoff or deep leaching.

The size of the organic litter pool generally decreases from cold to warm climates, providing there is adequate moisture. The size of the mineral pool in litter decreases less rapidly because of the general paucity of minerals in cold climates and the generally high ash contents of tropical litters. Finally mineral flux rates tend to increase from cold to warm climates because of rather rapid rates of mineral loss from the litter layer in the warmer climates.

Mineral loss from the litter layer occurs by either root uptake or by leaching. Both processes usually require that the minerals be in ionic form, though there are many exceptions. Much of the mineral input to the litter in coastal, agricultural, industrial, and tropical areas may already be in ionic form; add water and you have instant leaching. Other minerals have to be set free from the physical confines of cells and the chemical structure of frequently large organic molecules. This process of remineralization makes minerals available for subsequent leaching, uptake by roots, or retention by the soil adsorption complex in humus and clays.

Movement of water through litter is much more heterogeneous than its movement through soil and it has more horizontal displacement because of the essentially horizontal orientation of the leaf planes. Depending on the stage of decomposition of the litter, leaf species, and rate and periodicity of the flow, part of the ionic pool will move down and out of the litter. More than half of the leachable minerals, however, may remain in the litter even after severe leaching because of continuous readsoption of the moving ions (108). In addition to being adsorbed by the litter material, many of the dissolved ions may be absorbed by the soil microbes, in particular at slow flow rates or in capillary water; consequently, leaching may be further reduced by microbial immobilization. Thus during periods of rapid microbial growth because of favorable temperature, moisture, and aeration conditions, there tends to be less leaching of minerals than under cold, dry, or waterlogged conditions. Conditions for increased leaching are high microbial mortality (108), release or formation of humic and inorganic acids (39), and high rates of water movement (97). Leaves in brooks lose their mineral content faster than those in stagnant water, and those on land have the lowest mineral loss rates. Even under snow, however, leaves may lose 30 to 50% of their organic content as a result of intermittent microbial growth and frequent leaching (9). Rates of leaching differ greatly for the various elements, but over periods of several months they approximately follow the rates of weight loss of the organic donor material. Calcium tends to be lost
at similar rates as litter weight. Highly soluble mineral elements such as K and Cs are lost more rapidly than weight, whereas Mg and N contents may decrease at slower rates than litter weight. Losses tend to be exponential in time and can adequately be described by rate coefficients. Effective half-times for weight loss by deciduous leaves in temperate forests are in the order of 7 to 14 months.

Exponential decay curves are only approximations of weight loss of litter as a function of time. In the field, initial losses tend to be greater and final losses slower than indicated by the curves. The rapid initial losses are caused by massive leaching of soluble materials, both organic and inorganic, from the freshly fallen litter. This initial loss varies from year to year and depends on previous leaching on the trees as well as on the rate and frequency of leaching on the ground.

In the inorganic soil, as in the litter, dispersion of minerals by mass flow appears to be more important than ionic diffusion as a means of transport (42). Computer simulation of chromatographic transport in a heterogeneous soil system helps to explain the irregular patterns of leached minerals as found in field experiments with radionuclides. Movement of tritiated water in forest soil basically indicates a vertical movement, even on slopes, until dense soil layers are encountered. Thereafter the movement follows the layer laterally or downhill (52).

LITTER BREAKDOWN BY SOIL FAUNA

We can distinguish litter breakdown, the mechanical litter fragmentation, from litter decomposition, the chemical deterioration of tissue. Litter breakdown is mainly the work of the litter fauna, whereas decomposition is primarily microbial.

The morphology of litter breakdown can be used as an indicator of simultaneous chemical changes, such as decomposition of cellulose and lignin; to distinguish various age layers in litter; and to characterize activity by the fauna (66). Litter-feeding species have their specific patterns of leaf consumption, and animal excrements show species characteristics as well. Characteristic forms of litter feeding may be mining of the parenchyma from within; consumption of cuticle and parenchyma from either the top or bottom of a leaf; skeletonizing; simply eating small round holes, like those produced by various oribatids; or eating along the leaf edges, as do caterpillars and orthoptera. In all instances leaf contents will be opened up to microbes, leaching, and subsequent mineral removal.

The comminution or size reduction of litter fragments may increase the exposed area to 15 times that of the original leaf area. In the resulting fecal pellets, moisture-holding capacity is increased and evaporation may be decreased to one third of the same weight of unchanged leaf. Because of the globular or cylindrical forms, much of the fecal material will move down into the litter layer by gravity or washing at a more rapid rate than the original litter.
Earthworm activity also is important in the downward transportation of litter. Experimental elimination of worm populations leads to more litter remaining at the surface, less organic matter in the soil, slower humus formation, and greater total organic weight remaining (75). Greater soil porosity and humification of soil through earthworm activity leads to better aeration and moisture-holding properties of the soil (84). Because earthworm populations may have relatively large biomasses, occasionally as high as 250 g live weight/m² (114), and because they may cover relatively large vertical distances, they as well as other larger fauna may be important as microbial inoculants of organic matter and soil (13, 59).

Arrival of fecal material from both arthropods and earthworms in the more favorable moisture condition in deeper strata, the opening of cell contents, and a usual rise of litter pH during gut passage induce rapid microbial growth, particularly by bacteria (4). Net assimilation of ingested litter by soil fauna is less than 10% of the ingested material. Easily digestible sugars and proteins are utilized. Consequently, the fecal material is chemically only slightly different from the ingested matter. Mineral concentrations may be somewhat higher in the excreted material than in the ingested because part of the weight of the food has been respired. Excrement coatings of earthworm burrows have significantly higher C, N, P, and Ca concentrations than adjacent soil (46). Also, lignin contents of fecal material are higher than in ingested food, but cellulose concentrations usually remain rather constant except in snail excrements. Some litter-feeding snails are able to produce cellulase. Earthworms enrich the soil with Vitamin B₁₂, which stimulates sections of the soil microflora (4). Thus the direct effect of the fauna on mineral transfer in litter is rather small. Only from 4 to 8% of the annual input of litter energy is utilized by the soil fauna (35, 86), and the faunal turnover of minerals should be of the same order.

The part of loss of litter weight as a result of faunal activity has been evaluated by comparing loss rates in the presence and absence of fauna. In particular for leaf species with rather hard cuticles and wide C/N ratios, such as in oak leaves, chemical or physical exclusion of litter fauna by using litter bags may reduce decomposition rates by as much as one fourth. In contrast, breakdown of more readily decomposable leaves such as grassland herbage appeared to be no different in the presence or absence of litter-feeding animals (24).

Biomass of litter and soil fauna is another clue to the limitations of faunal effects on litter decay. In tropical rain forests faunal mass (12 g/m²) was estimated as only 0.03% of the total organic mass (68). Activity of abundant and prominent nest-building termites represented only 0.25% of the annual energy input in litter fall (106). Larger biomasses (100 g/m²) may be encountered in temperate deciduous forests and subtropical rain forests (54). Horizontal distribution of species within ecosystems is influenced by nonenvironmental causes such as social instinct, sexual attraction, care for offspring, and by environment-induced choice of sites for predation,
feeding, and egg deposition. A synecological cause for heterogeneous distribution is a plant effect reported for soil microfauna (79) and similar to the rhizosphere effect of microbes. Small animals appear to be more numerous and active around roots than in soil away from roots.

Vertical distribution and activity of microarthropods has been estimated from their $^{45}$Ca ingestion in microcosm experiments. Of the total ingestion 41% occurred in fresh litter, 39% in year-old litter, and 20% in deeper layers (57). This vertical distribution is also a chronological distribution for substrate with new litter on top and the oldest litter below. Other time sequences in faunal mass and activity are seasonal and successional with rhythmic changes of specific faunal synusia, in particular of carabids and collemboles (28). Periodicity of individual species also appears to be directed to maintenance of a positive energy balance by restricting activity under low-temperature and moisture regimes (72).

Mineral contents of the faunal pool tend to be small because of the limited biomass. Concentrations of N, P, and K in larval tissues, in particular, tend to be higher than in the base food (78). Whether mineral concentrations in consumers will be higher than in the food is a matter of supply and demand. Sodium may be considerably concentrated because it is required in animal tissue and it may be low in vegetable food because plants do not require it. Similarly, calcium may be considerably concentrated in insects and isopods with calcified exoskeletons (38). Mineral concentrations in predators and their preys are in general equal and thus, except for some mineral elements used in growth, reproduction, or molting, excretion will equal ingestion. As argued before, mineral concentrations in excreta tend to be slightly higher than in ingested material due to metabolic elimination of C, H, and O from the dry weight.

Because the relationship between minerals in the food source and the consumer is rather stable, trophic relationships within food webs can be established quite easily by using food tagged with radioisotopes (16, 17, 57, 107). Concentration and lag in appearance of the radioisotopes in the consumers indicate what, when, and where feeding took place (65). For instance, fungivores show rather high initial isotope levels because fungi tend to concentrate various elements. Predators of saprovores show, after a several-day lag period, isotope concentrations only slightly above food base level.

Mineral concentrations and biomass of the fauna provide an estimate of the faunal mineral pool. Mineral turnover rates by the fauna can be derived from mineral uptake or elimination curves using radioactive food or animals respectively (22). Measurement of rate of evolution of CO$_2$ provides an alternate parameter for metabolic turnover. Separation of CO$_2$ evolved from plant roots, animals, and microbes, as well as the separation of CO$_2$ evolved from the various litter strata, has been successful (16, 112). Total biomass is not a useful parameter for mineral turnover of CO$_2$ evolution because turnover rates per gram of biomass are much higher for small ani-
mals than for large ones. Oxygen consumption (44) and CO₂ production (54) by nematodes are around ten times larger than those by the same mass of earthworms. Consequently, the estimated 5 g/m² of nematodes in temperate forests (44) may turn over minerals at a greater rate than do earthworms.

Temperature is the main environmental factor affecting turnover rates. For a particular population, respiration will double for each 10°C increment within the normal range of field temperatures (80, 112). Turnover rates at different latitudes not only respond to the differences in temperature but also to the population and biomass differences that were mentioned earlier. As a result respiration rates are highest in subtropical lowland forests with mean temperatures of around 16°C, lower in the warmer tropical rain forests and in the cooler temperate forests, and lowest in alpine shrub vegetations (54).

The relatively small mineral pool as well as the limited faunal contribution to energy transfer and loss of weight of decomposing litter indicate that the fauna is of little direct consequence to the total cycle of minerals of an ecosystem. Recently it has been suggested that the primary effect of the soil fauna is indirect rather than direct (34). There are many indications that this is so. Increased mineral leaching as a result of comminution has already been pointed out and additional effects on the microbial action will be discussed in the following section.

**Litter Decomposition by the Microflora**

The mass of the decomposer microflora consists primarily of bacteria, fungi, actinomycetes, and yeasts. Their main effects on mineral transfer are temporary immobilization of minerals in the microbial tissue mass and re-mineralization, which usually means that minerals are released in ionic form.

The microbial mass consists mainly of fungal mycelium. Fungal mycelium lengths may be as much as 10 km/g of substrate with masses in the order of 10 g/m². Unresolved, however, is the question of how much of the mycelium is active, inactive but living, or dead. Estimates of live versus dead mycelia based on uptake of vital stain indicate that the percent dead mycelial mass increases with increasing depth and with increasing pH. Increases in both these parameters tend to be accompanied by decreasing numbers of bacteria and actinomycetes, which are the main decomposers of dead mycelia.

In the last few years more realistic insight into the mass, form, distribution, and behavior of the microbial mass has been obtained by direct methods of counting, observation (48, 73, 76), and cultivation (2). Observation of microbial growth from natural soil substrate into rectangular capillaries reflect population composition, appearance, mass, and activity. Direct popu-
lation estimates appear to be from one to two orders of magnitude greater than those based on laboratory colony counts.

Current efforts to estimate microbial mass by physical separation through zonal centrifugation (11) or by using chemical qualities such as densities of ATP, DAP, and catalase (90) in soil are directed toward finding acceptable conversion factors for various populations under changing environmental conditions. Other conventions proposed to indicate microbial performance in soils are richness and activity indices (83). For a richness index, soils are ranked according to the numbers of bacteria in each of a series of physiological groups, such as denitrifiers, pectin decomposers, etc. The soil with the lowest sum of rank numbers is "richest." The activity index of a soil is the sum of all bacteria in the various physiological groups divided by the total number of bacteria on soil extract agar. Thus activity index is an indication of the physiological and competitive vigor of the microflora in a particular soil.

Biomass estimates are usually between 1 and 10 g/m² for fungi, and less than 1 g/m² for bacteria. Bacterial populations may fluctuate greatly and may reach 30 g/m² on calcareous mull. Mineral contents vary greatly because, like higher plants and in apparent contrast to animals, microbes can absorb certain mineral elements such as K and Ca in luxury consumption.

Microbial concentrations of C, H, O, N, P, and S, however, appear in rather constant ratios and consequently as rather constant percentages of microbial weight. Spores and other propagules usually have two to four times higher mineral concentrations than vegetative stages to provide priming capital for the new growth.

The mineral contents of the microbial pool are both extremely difficult to leach out and unavailable for primary production. Mineral uptake by microbes and subsequent immobilization can take place from soil solution, detrital protoplasm, the soil adsorption complex, or from enzymatic breakdown of organic molecules that contain mineral elements. The much-studied processes of cellulose and hemicellulose breakdown do not yield minerals directly but provide energy and make cell contents available for subsequent mineral uptake. Consequently, cellulolytic activity may be used as an equivalent to mineral turnover.

Microbial immobilization of minerals starts even before litter fall. In spring when mineral concentrations in leaves are highest (78) and when energy is in its most available form, rates of microbial uptake of minerals in frass, aphid exudate, and flowers and scales are high (40). Just before leaf fall there is a flux of minerals and nutrients leached from senescent leaves. This influx into the forest floor primes decomposition of old litter and a flush.

Microbial colonization of the subsequent influx of new litter is usually extremely rapid with bacteria more evident than in later stages of decay. Gross mineral immobilization in these young early stages may be as high as
60% of the leachable mobile content of highly soluble minerals (108). The amounts of minor elements immobilized by the microflora tend to be proportional to their concentration in and leachability from the substrate. Concentrations decrease with the aging of the population and almost quantitative releases take place when microbial populations are killed off by freezing or drying. More than half of the released material, however, may be readSORBED onto the litter or immobilized by subsequent microflora before it can leach out of the substrate.

Because of favorable moisture and temperature conditions and a continuous influx of new litter with relatively high N content, in tropical rain forests the momentum of initial breakdown is never lost. Resulting rates of CO₂ evolution are continuously high and mineral half-lives are short (37, 102, 109). In temperate forests, rates of biological turnover are checked by low winter temperatures and slow removal of toxic metabolites (74, 89). Turnover resumes in spring at usually lower rates than those in autumn. In mull, decomposition cycles take less than 1 year; in moder it usually takes somewhat over a year; and litter decay in more soil may take from 2 to several years.

Mineralization and immobilization of substrate minerals follow each other in successive cycles. Cycle frequency depends primarily on freezing and drying, faunal activity, and succession. Some of the microbial succession is in the form of a matrix of successive as well as simultaneous waves depending on substrate availability. This matrix may be repeated and varied at any time.

Microbial innocula are rather omnipresent and frequently inactive. Most visible bacteria are associated with soil organic matter even though the surface of this matter may make up only 15% of the surface of all soil particles (47). Based on calculations relating population and available energy input, microbes persist under starvation conditions much of the time. When new food is made available by opening up of a cell, import of fecal material, or death of a microbe or animal, a succession starts on the newly available material, its breakdown products, its moribund decomposers, and their exudates. Decomposition of a simple molecule such as glucose may proceed along three different pathways, each presumably with its own successional population waves (64). Hydrolysate of extracellular polysaccharide such as of Rhizobium may yield six different amino sugars (92). In addition to the effects of breakdown products on population development there are a number of compounds, such as tannin, that affect the breakdown of other products and thus mineral turnover. Tannin, which is the fourth abundant leaf litter component after cellulose, hemicellulose, and lignin, contains only C, H, and O, just like the other three components. Consequently, it does not directly contribute to the nutrient element pool. Presence of tannin, however, can retard decomposition of chitin, protein, and pectin and, thus mineralization of N, P, S, and Ca (61).

The recycling of minerals within the litter-fauna-microbe system may be
quite effective in retaining elements. As an example, 27% of highly soluble and biologically nonessential Cs was still present in tropical rain forest litter after 6 months of decay and exposure to heavy rains (53). Biological retention is particularly effective for essential elements such as nitrogen and phosphorus. In contrast, metabolic losses of CO$_2$ and H$_2$O decrease, C, H, and O contents of the decomposing material. Consequently, the C/N ratio will decrease and percent of N and P will increase during decomposition. In temperate and boreal forests there is additional nitrogen exchange with the mineral soil. Added ammonia N becomes rapidly immobilized and in turn microbial N is remineralized. Both ammonia N and cellular N may inter­change with the native soil N and cause part of it to become remineralized (56). Differences in nitrogen regimes of different soils appear to be, to a large extent, the result of their different immobilization-remineralization properties (81). In addition to the biological cycles, apparent nonbiological immobilization of nitrate N has been reported. The amount of nitrogen thus immobilized appears to be inversely related to the square root of the diameter of the soil particles (88).

An additional effect of the microflora on mineral cycles takes place through the mobilization of minerals from inorganic soil material, primarily as a result of acid formation. In 7 days under laboratory conditions a *Peni­cillium* species mobilized 31% of Si, 11% of Al, 64% of Fe, and 59% of Mg in basalt. Analysis of the rock suggested transformation of its crystalline structure into amorphous silicates (87). Mobilization of inorganic phospho­rus by lactic acid-producing bacteria can increase the P uptake by vegetation. Strains adapted to local soil conditions appear to be particularly effective (94).

The driving potential of the biological transfer of minerals is contained in the available energy input. The availability of energy decreases with time as the most easily decomposable litter components are utilized first. The rates of transfer are limited by suboptimal environmental conditions, mainly temperature and moisture. Availability as a function of time, temperature, and moisture content of the litter can explain 88% of the variability of litter breakdown measured as evolution of CO$_2$. The amount of CO$_2$ evolved is in turn closely related to the loss of organic material, and loss of litter weight parallels net losses of various minerals from the litter (111). Thus temperature and moisture, or CO$_2$ evolution, may be useful driving functions in models for turnover of certain minerals. In most temperate forests and in rain forests where moisture conditions are mostly adequate for microbial activity, variations in mineral turnover rates are primarily governed by temperature. Under less humid conditions microbial activity is affected mainly by soil moisture (58, 96).

Additional factors that affect mineral turnover which will be more difficult to model are cultural measures such as clear-cutting (37, 50, 107), burning (108), and flooding causing anaerobiosis. The resulting extreme temperature and moisture regimes require constraints on the model func-
Clear-cutting results in extremely rapid mineralization through increased aeration, raised temperatures, more severe wetting and drying cycles, and more severe leaching. The increased mineralization, together with elimination of all or much of the root uptake, may increase net mineral losses of nitrate N, K, and Al (12). Burning of surface litter represents an exaggerated case of the clear-cutting syndrome. Charred litter residues, however, may readSORb part of the mobilized minerals and protect them from subsequent leaching (108). Anaerobiosis on the other hand greatly impedes rates of breakdown and may lead to increased mineral pools without an increase in turnover rates.

Cultural measures, as mentioned above, as well as inherent properties of the litter input, may cause litter decay not to proceed exponentially. Moreover, net immobilization of several elements as shown above is not proportional to rates of organic matter oxidation. These departures from the basic exponential models, as well as differences in available mineral soil pool size and in turnover times by two to three orders of magnitude, complicate prediction of mineral kinetics in litter and soil. On the other hand, annual mineral fluxes of widely different forests are surprisingly similar (82), presumably as a result of similar nutrient demands and energy inputs to the primary producers.

**HIGHER PLANTS AND MINERAL TURNOVER IN SOIL**

The higher plants affect mineral turnover in soils by their uptake of mineral elements from the soil pool, by retaining mineral elements in the standing crop, and by returning minerals contained in debris of primary production to the soil. This return can be assessed from litter fall and root mortality. In a steady-state condition, mineral uptake by a stand should approximate mineral return. Most estimates of uptake, however, have been made on production forests with annual increase in standing crop. The annual uptake or mineral requirement of such stands has been calculated as the sum of the net mineral increment in the standing crop (retention) and mineral return in litter and roots (29). This flux in temperate forests may be in the order of 95 kg of N, 7.5 kg of P, 15 kg of Mg, and 75 kg of K per hectare per year. Uptake of Ca was in the order of 100 kg/ha per yr but this may vary greatly as a result of luxury consumption depending on Ca availability in the soil pool. In order to maintain productivity in production stands, the accumulated production removed in the harvest should be compensated for by fixation, by input from fallout and rain, and by weathering.

Establishing significant ratios for the fluxes of biologically important elements, formulation of the relationships between mineral concentrations in the uptake flux and in the soil solution, and determination of the relevant climatological parameters are indicated as the prime objectives for the ecological approach to soil-plant systems (100). Movement of bioelements through soil to roots is passive. The entropies for water and gas fluxes are in the order of $10^9$ and $10^7$ cal deg$^{-1}$ ha$^{-1}$ yr$^{-1}$ respectively. Corresponding
values for bioelements are between $10^2$ and $10^4$ (99). Consequently, evapo-transpiration by aboveground plant parts driving water movement near roots may be an important force in mineral transfer. The amount of minerals in the water movement depends on mineralization-immobilization relationships. Factors favoring biological immobilization were discussed above. Physicochemical immobilization is beyond the scope of this chapter; however, biological activity can affect nutrient availability by changing the oxidative state of mineral elements and consequently their mobility and their acceptability for root uptake (95). For instance the amount of organic matter affects the pH and consequent Fe valency and the quantity of Fe released. Because plants prefer the ferrous form and because Fe uptake is proportional to its concentration in the soil solution, organic matter content of soil may greatly effect Fe uptake by plants.

Uptake in proportion to soil solution applies to many of the bionutrients including Mg and Al. On the other hand, Na is discriminated against and K and Ca are taken up selectively. This implies that uptake of most elements can be greater than strictly required for growth when there is an ample supply of these elements in the soil solution. Tropical soil solutions and vegetation are high in Fe, Si, and Al contents. Plants on dolomitic substrate are high in Mg and those on calcareous substrate contain more Ca per unit weight than do their counterparts on sandstone (31). In extreme cases mineral levels in soil solution may lead to either deficiency or toxicity (41). In either case the plant's metabolism will be affected, and with it the turnover of minerals. These phenomena are only poorly understood at the community level. Community uptake studies between deficient and toxic levels show that there is a rather good correlation between mineral supply of the soil and mineral content of the vegetation. Consequently, phytochemical groups of plants based on mineral content and ecosociological groups based on soil richness appear to be well related (31). So-called nitrophilic plants on rich sites accumulate relatively high concentrations of ash, in particular K (7 to 8%), rather high concentrations of N, and sometimes considerable amounts of P. Mull sites are characterized by somewhat lower contents of K (up to 7%) and total ash. On occasion Mn may replace Ca on these sites. On acid mull usually less K and Ca is found and total ash contents are about average. On moder total ash contents usually range from 6% to 10%, ond on mor only 4.5% to 6% ash is usual, with about only 1% K. In particular, plants with a wide ecological amplitude may reflect this entire range of differences in mineral accumulation.

Differences in mineral uptake are not only a function of mineral supply but may also be related to inherent or adaptive root properties. Roots of dicots tend to have higher cation exchange capacity than those of monocots. Within the dicots, roots of communities on poor acid soil appear to have lower cation exchange capacity than roots of communities on neutral or alkaline soils that are rich in nutrients (91).

Rates of net mineral uptake can be assessed from accumulation in grow-
ing vegetation, in particular in temperate and monsoon deciduous forests with their considerable annual fluctuations in mineral pool in the standing crop. Amount of litter fall and root mortality can also indicate amount of mineral flux from soil to vegetation. Rates of CO₂ evolution by roots, reflecting the energy spent to achieve mineral uptake, might provide another measure for mineral flux into roots, at least within a community. To my knowledge, this approach has not yet been explored in the field, partly because of the difficulty of separating root respiration from faunal and microbial respiration. Similarly ATP content of roots might be considered as a measure for mineral uptake.

Estimates of root respiration vary from only a fraction of litter respiration to more than three times that (70, 71, 112). Methodology and interpretation still need much improvement. The methods used and the operational as well as climatological conditions under which they are used greatly affect the experimental results. Correct measurement of CO₂ evolution by the various soil biota could offer a rather unified method for measuring the respective amounts of work performed by them in the predominantly aerobic environment of the forest floor.

In addition to the physicochemical effects of the soil and plant characteristics, mineral uptake by the roots is also affected by soil biota. Earthworms have been shown to increase aeration and moisture retention through burrowing and changing soil aggregate composition. Consequently, root respiration may be enhanced and the wilting point may be lowered (84). The direct effects of earthworms on mineral transport were mentioned earlier.

The mycorrhiza of many if not most of the forest trees are the most dramatic examples of direct microbial interference with root function. Species of trees introduced into new sites without their root-associated microbes may require inoculation with soil from their original site in order to obtain their usual mineral uptake (8). The root-microbe association may result in 3.5 times greater uptake of P, 75% more K, and 85% more N in the trees. Whether or not this increase mineral uptake is the result of direct enhancement of mineral transport into the plant or whether the effect is at least in part indirect through stimulation of plant growth by microbial metabolites remains a subject for future study.

The greatest effect of mycorrhiza on mineral cycling may be found in the “direct mineral cycling” theory (104). This theory refers to the almost closed cycle of minerals from litter to microflora to tree roots in tropical lowland rain forests. Often the litter layer is only two or three leaves thick and tightly interwoven by fungi and roots. The mineral soil underneath is almost devoid of organic matter or fungal growth and presumably hardly takes part in the mineral cycle. Despite the rapid leaf decay and heavy rainfall (53), 6 months after introduction into the litter layer only 1% of the introduced Cs and Sr were found in the underlying soil. Apparently the heavily weathered and leached soil of tropical rain forests contains a limited pool of mobile bioelements. As a result, clearing of a rainforest de-
SOILS AS COMPONENTS OF ECOSYSTEMS

The preceding sections dealt with specific parts of the mineral cycle in soil from the input of minerals, mainly from plants, to their leaching in water; their exposure to leaching; microbial decomposition as a result of litter comminution by the fauna; subsequent immobilization-remineralization cycles by the microflora; and then reabsorption into the plants. The role of the mineral soil hardly entered into this picture, not because it is unimportant, but because it has been extensively studied and documented. In contrast, the role of the soil biota, the prime movers of the more important minerals, has received less attention.

The direct entry of mineral soil to the available nutrient pool is by weathering. The amount of mineral weathered is mostly calculated as the unaccounted for difference between input and output of that mineral in soil. Consequently, its calculated value contains all the elements of error in measurement as well as annual differences among various inputs and outputs. Estimates of mineral weathering have been reported for tropical forests (68) and for temperate forests (12).

As indicated before, microbes may play a role in mineral release by direct contact with the rock. They may also be involved indirectly by the formation of humic acid and CO$_2$, which may move passively through the soil and which at suitable sites may act in the release of minerals. This action is particularly evident in mine drainage, where microbial oxidation of iron sulfide may yield considerable quantities of sulfuric acid (10). Weathering
of Al-silicates may also be the result of acid production by microbes. Other minerals such as quartz may be mobilized by alkaline microbial products. Microbes also may mobilize minerals such as iron through reduction. A more direct effect of microbes on mineral mobilization is through the action of bacterial and algal slimes (3). Since the rates of mineral release from the crystalline matrix are not proportional to their relative concentrations there may be important changes in the composition of the remaining rock.

Nonbiologic weathering may be the result of leaching, oxidation, reduction, acidification, etc.—rather like the processes invoked by the microflora. In another parallel with microbial mobilization of minerals, it appears that repeated freezing and thawing mobilizes K from crystal lattices into the labile pool (45). Thus mineral release and subsequent fluxes in soil leachate upon freezing and thawing may well be the result of combined biological and nonbiological remineralization.

In contrast to mineral mobilization by weathering, there may be immobilization of minerals by formation of insoluble salts from which nutrients are available for root uptake in only insignificant amounts. This may happen through changes in valency, through changes of oxidative state as with Fe, or through changes in pH as for P. Resulting net immobilization may locally lead to deficiencies, such as of Fe and P (19). In rain forests, however, most P is recycled directly via the roots and bypasses the mineral soil (62). Nitrate salts are not available in the mineral soil because of high solubility. Consequently, the inorganic soil pool of immobile N cannot be counted on as a reserve pool (103). The organic soil pool of immobile N may, particularly at higher latitudes, contain many times more nitrogen than is present in the more active parts of the N cycle. Remobilization from this organic pool may be extremely slow. Resulting turnover rates may be in the order of $10^3$ years. Reasons for the accumulation and unavailability are not clear. Differences in percent nitrogen between temperate and tropical organic input are perpetuated throughout decomposition and humus formation. Ratios for C/N in litter of boreal and some temperate species tend to be higher, because of higher lignin and cellulose content, than those of many tropical species. Higher temperature, higher percent nitrogen, and often higher pH in tropical litter, as compared to litter of colder areas, favor bacterial over fungal decomposition. Because of higher N content, more of the tropical litter can be broken down without requirement of additional nitrogen. Bacteria tend to accumulate less and respire more of their substrate than do fungi, whereas both tend to recycle nitrogen effectively. As a result C/N ratios decrease in both tropical and temperate litter during decomposition. However, relative to nitrogen content, more carbon is respired in tropical than in temperate litter. Consequently, final C/N ratios are still smaller in tropical than in temperate humus, even when the initial C/N ratios of the litter are the same. Ammonia is more common in the tropics, while nitrate is the common form of nitrogen in boreal areas (51). As a result little or no humus is left in tropical forest with a C/N ratio of around
8, close to that of bacterial tissue, whereas in colder climates more humus remains with higher C/N ratios, above 12 and similar to that of fungal tissue. Undecomposed soil organic matter may still contain a considerable amount of carbohydrate (49). Carbohydrate-induced anaerobiosis in turn may lead to loss of nitrogen through formation of nitrous oxide and nitrogen gas by denitrifying bacteria (14).

The rapid and almost quantitative recycling of nitrogen and the relatively high rates of nitrogen fixation in tropical forests may explain why their litter usually has a greater percent N than litter of temperate and boreal forest, in which there is a continuous drain of nitrogen into the seemingly ever increasing soil humus pool and in which rates of nitrogen fixation are relatively slow. Productivity of temperate forests tends to be smaller than that of tropical forests, providing moisture is not a limiting factor. Annual inputs of energy do not differ greatly with latitude because the higher the latitude the greater the length of day during the growing season. Temperature per se usually is not regarded to be a limiting factor to primary productivity. Microbial activity, and consequently remineralization, however, is temperature dependent. It appears likely that at least in part the slower rates of remineralization, and thus of rates at which nutrients are made available, may limit production in colder climates. This hypothesis may be substantiated by occasional high rates of productivity on alluvial sites with considerable nutrient influx in temperate and cold climates.

Slow rates of mineralization and long interruptions of mineralization during winter, when there is no root uptake, may also allow leaching and loss of nutrients in cold climates. Low rates of evaporation and resulting anaerobic conditions tend to inhibit the remineralization process as well. Thus there are various reasons why low temperatures may reduce forest productivity below the growing potential of the primary producers in cool climates. Nitrogen, the supply of which largely appears to depend on biological input, would be highly affected by temperature. Resulting differences in nitrogen content in primary producers may then be perpetuated and possibly amplified in subsequent litter decomposition, humus formation, and remineralization.

From the preceding it is clear that, when looking at the impact of soils on ecosystems, one must consider all components of soils including biota and organic matter. In addition to the direct roles of the various soil components there are equally important interactions between compartments, like those between fauna and microbes, plants and microbes, and the system's components and climatic factors. For example, the latter may serve the mineral transfer from litter to fauna, microbes, soil, and leachate as it is affected by interacting moisture and moisture regimes. Transfer that under adequate moisture conditions followed the litter-fauna-microbe-soil pathway shifted to a litter-microbe-soil pathway under temperature-precipitation interactions that resulted in periodic drying of the litter. Presumably the microflora's greater metabolic flexibility enabled the microbes to overcome
the interrupting effect of drying on mineralization better than did the fauna (113).

Intricate pathways will also be found within the microbial populations with repeated transfers between and among fungi. Upon aging, these are lysed and consumed by bacteria and actinomycetes, which may be incorporated in protozoa or nematodes and in turn may fall prey to bacteria and actinomycetes, etc. The outcome is a rather controlled and buffered release of minerals. Especially for biologically essential elements, release from the biological buffer may be slow. Thus there is slow net mineralization but very rapid gross turnover.

Repeated cycling in subsystems may also take place in coprophagous insects, particularly those that reingest their own feces. Several arthropods and earthworm species are known to ingest litter only after partial decomposition by microflora. Evidently microbial conversion of cellulose and lignin to microbial protein increases the available caloric content of the litter to the point that it will yield net energy for litter feeders. Similarly coprophagous insects will starve or not show net gain on undigested litter. The microbial bloom on their feces, however, provides adequate nutrition and feces may be reingested several times over. This sequence leads to loss of most C, H, and O and to preservation of nutrient elements, in particular N (15).

The efficient recycling of minerals in forest systems may in part account for the rather low nutrient requirements of forests, as compared to agriculture. For the same weight produced, forests are reported (6) to require two and one half times less N and six times less P and K than the average agricultural crop. This difference also reflects the greater ash content of agricultural crops than of forest products. Lysimeter and watershed studies confirm the relatively small losses of nutrient elements from undisturbed forest as compared to those of agricultural land.

The network of mineral transfer pathways appears to be involved and quite different for various elements (113). Much of the internal turnover in subsystems can be treated as black boxes by considering only turnover rates and pool size. One of the earlier stated objectives was to obtain relative measures of nutrient turnover. Various comparisons of mineral loss rates from litter can be made from published effective half-times (55, 97). A mineral variant of Jenny’s breakdown coefficient shows that annual input/((input + litter) × 100 in beech forests approaches 15 for mass and C; 10 for N, P, and S; and 25 for Ca and K (63). These numbers again indicate effective preservation of N, P, and S relative to overall weight loss. They also confirm similar behavior of these three elements. These data indicate furthermore that K/P and C/N ratios change during litter decomposition. This is in contrast to their reported constancy in other parts of the cycle (20, 30).

Turnover times for the entire system, calculated as total pool/turnover rate, vary from 0.08 yr for K to 133 yr for N in a tropical rain forest (68).
Turnover times of some other elements in the same forest decrease in the order Mg > Ca > H > C > Mn > Na > P. There is a rather large difference between turnover times of N and P. This difference is apparently the result of the large phosphorus influx of 135 g/m² yr relative to a total phosphorus stock of 67 g/m² as compared to a nitrogen inflow of 10.2 g/m² yr and a nitrogen stock of 136 g/m² in organic matter. The large P influx stems predominantly from rain.

Complete mineral cycles for several systems combined have come from watershed studies. Out of necessity these studies do not give results in great depth. They have given considerable insight into the interaction of landscape components, especially the land-water interactions. They also have demonstrated disruptive effects of forest clearing on mineral cycles and subsequent mineral losses. As much as one complete year's N turnover has been lost during the first year after clearing of temperate forests, and net losses of K increased 20-fold (12). Watershed studies also have led to some of the more complete models—conceptual, empirical, or predictive (18, 23). Detailed studies, such as those of the internal recycling of minerals in microscopic subsystems, and landscape-scale studies on mineral movement in watersheds together are providing insight into driving forces and rates of transfer, as well as the importance of the various pathways needed for predictive models of the function of soils in ecosystems.

Recent interest in optimizing use of our environment has resulted in numerous surveys of energetic and mineral cycles (6, 67, 68, 77, 86) and, in particular, of the transformations in soil (1, 27, 33) and of environmental effects thereupon (103, 105). The purpose of the present survey was to indicate some of the mineral cycling literature of the last 2 or 3 years and to point out some of the areas where progress has been made or where further work is needed. The emerging picture is one of soils as habitats of interacting biota, which are the prime agents in maintaining and elevating local levels of fertility and thus of perpetuating species composition and the level of activity of the ecosystem (5, 31, 43, 98).
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