

Mutualism: A Factor in Ecological Succession Through its Influence on Nutrient Resource Ratios

Dowon Lee*
Carl F. Jordan**

Factors Influencing Succession

Succession is a fundamental ecological concept, and the phenomena of community change through time has sparked hundreds of descriptions, commentaries, and interpretations (McIntosh, 1980). Researchers and theorists have sought long and hard to uncover underlying generalities and common causative mechanisms which could both explain observed patterns of plant and animal replacement, and predict future courses of succession on particular sites. However, the nature of the fundamental mechanisms of succession has been elusive, and there is little consensus among researchers and theorists.

Many authors have hypothesized that competition, both inter- and intra-species, is a fundamental mechanism that determines which community of plants and animals will be present at a given time along a successional sere (Salisbury 1929, Grime 1974, 1979, Diamond 1975, Pickett 1976, Wiens 1977, Pyke *et al.* 1977, Tilman 1985, Grubb 1986, Huston and Smith 1987). The changing species composition as a function of time in an abandoned field, or on a new rock surface is seen as a result of the outcome of a competitive race for the resources available at any given time.

In some interpretations, for example relay floristics, there is a continuing

*Assistant Professor of the Department of Environmental Planning at the Seoul National University.

**Institute of Ecology University of Georgia Athens, Georgia 30605, U.S.A.

competition for the resource base which itself is continually changing (Connell and Slatyer 1977). The winner(s) of the competition during a particular phase of succession becomes the dominant species, at least for a while, but the success of a particular species or community eventually becomes its downfall because the species itself changes the resources that are available, thus paving the way for other species better adapted to the new conditions.

In other interpretations such as initial floristics, the successional community depends not upon modification of the environment by the previous community, but rather simply upon what species or individuals are first to expropriate the existing resources (Egler 1954). In both relay floristics and initial floristic composition, competition is considered to be very important.

Emphasis on competition may result in part from a focus which is almost completely on higher vegetation. When the frame of reference is expanded to include higher animals, mutualistic types of interactions such as predation, protection, and transport become apparent in the regulation of ecosystem structure and function (Boucher *et al.*, 1982). Inclusion of lower organisms within one's system boundaries results in a recognition that symbiotic types of interactions can influence ecological succession (Odum and Biever 1984). Such symbioses frequently involve the microflora and fauna living in or on the soil, and because these organisms are difficult to study and manipulate, they are often neglected in successional studies. Neglect in successional theory of mutualistic interactions between higher plants and soil flora and fauna has limited our understanding of dynamics of above-ground vegetation (Cromack 1981, Rich 1984).

There are a few interactions involving soil microorganisms that are well known as influencing ecosystem function. Nitrogen fixation by root nodule bacteria, and phosphorus recycling by mycorrhizae are two examples classified as symbiotic mutualisms by Boucher *et al.* (1982). However, these authors have not included decomposers within their classification scheme of mutualistic interactions. In fact, interaction between plants and decomposers seems never to have been mentioned as a mutualism in any review of biological interactions.

In this paper, we hypothesize that mutualism between higher plants and decomposers, as well as competition between higher plants is important in succession. This is done by developing the following ideas:

1. Mutualism between higher plants and decomposers is an important regulator of the phosphorus cycle. As a result of mutualistic interactions, P becomes more soluble and thus more available to plants during the course of succession.

2. The availability of N and S also increase during succession, although not at the same rate as P. As a result of differing rates at which these elements enter the active cycle of ecosystems, ratios of nutrient resources change during the course of succession.

3. As resource ratios change, the plant communities that are best able to compete for the changing available resources change. As a result, there occurs a sequence of plant communities called a successional sere.

We also point out that:

4. When the series of interactions between higher plants and microbes begins on a nutrient-poor substrate, the resource ratios, and the plant communities dependent on those resources change in a regular and predictable sequence.

5. The cyclic influences of the above ground plant community on the decomposers and other below-ground organisms, and the influence of these in turn on the above ground plant community resembles a cybernetic system.

Mutualism in the Phosphorus Cycle

The Phosphorus Cycle

The phosphorus cycle in a terrestrial forest ecosystem is shown in Figure 1. We can begin an examination of the cycle with the roots of living trees. Inorganic phosphorus taken up by roots is translocated upward to the stem and leaves. In the leaves, it is incorporated into complex biochemical compounds such as DNA, RNA, and phospholipids. Some of these compounds may be leached from the leaves (throughfall), or exudated from the root, and provide an energy and nutrient source for whatever microbes may intercept these soluble compounds.

Some of the compounds in the plant are taken up by animals, for example by deer grazing on leaves and nematodes grazing on root hairs. Underground herbivory usually is given less attention than it deserves as a regulator of natural communities (Andersen 1987). When plants and animals die, or when trees shed leaves and fine roots, the carbon compounds enter the organic residue pool.

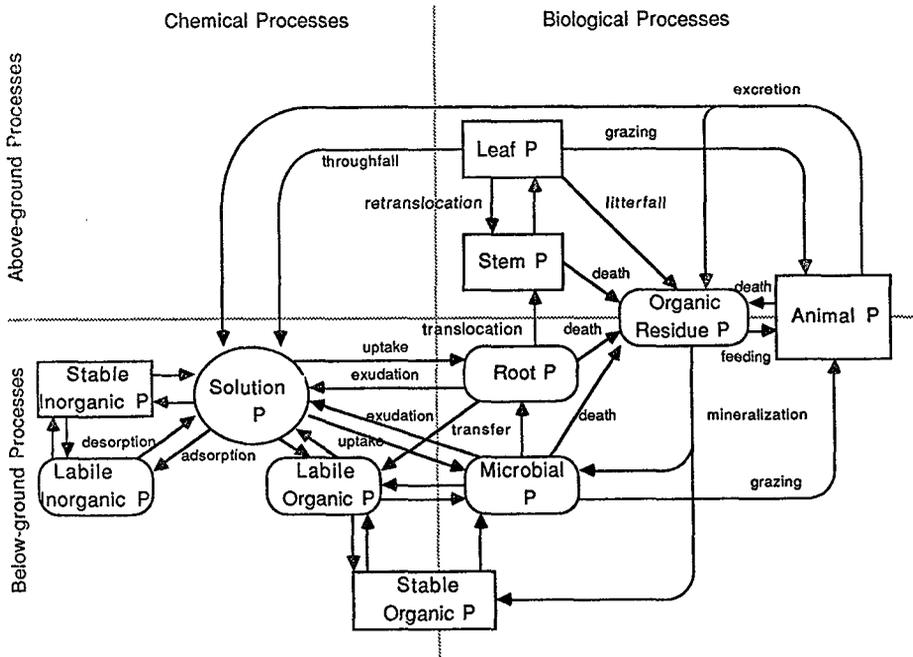


Fig. 1. Phosphorus transformations in fully closed forest ecosystems. Modified from Cole *et al.* (1977), Smeck (1985), Vitousek (1985), and Stewart and Sharpley (1987).

Sometimes arthropods begin the decomposition processes, but microbial decomposition is important in all cases.

In the organic residue, all nitrogen, and some sulfur is directly bonded to carbon through co-valent bonds (e.g. C-N, C-S). Breaking of these bonds by microbes is carried out by a biological need for energy, and has been called "biological mineralization" (McGill and Cole 1981). The release of nitrogen during biological mineralization seems to be incidental, and as a result, rates of release of carbon and nitrogen from soil organic matter show close correspondence (McGill *et al.*, 1975). In contrast to nitrogen, phosphorus and some sulfur is linked to carbon through ester bonds (e.g. C-O-S, C-O-P). Biochemical mineralization, defined as release of inorganic ions of P and S from an organic form through enzymatic catalysis external to the cell membrane, is strongly controlled by the supply of and need for P or S, rather than the need for energy (McGill and Cole 1981). Thus the plant-microbe interaction supplies microbes with nutrients as well as with energy.

Microbes exude or excrete some phosphorus into the labile organic and solution

pools of phosphorus. For example, some bacteria are capable of synthesizing and secreting phosphate binding protein (Anba *et al.*, 1987). In the case of mycorrhizae, P is transferred directly into the roots. Phosphorus in the soluble and labile organic pools is available for uptake by roots. However, the microbes also compete with the higher plants for the soluble and labile organic P, and the outcome of the competition depends in part on the relative abundance of populations, physical spacing in the soil, and other environmental factors. Competition becomes most evident when there is an oversupply of energy relative to nutrients. However, the competition may be lessened by microbial activities which move phosphorus from surrounding sources to labile organic and inorganic pools, and by fauna which ingest microbial cells and release soluble phosphorus.

Some organic residue is very recalcitrant, and becomes part of a stable organic pool. Phosphorus in this pool is released only very slowly by the action of microbes.

Although soluble and labile organic phosphorus can be leached from the soil into nearby streams, the amount lost in this manner is usually relatively small (Jordan 1985). A potentially much greater loss of P from the living system occurs on highly weathered acid soils, especially in the tropics and sub-tropics. Iron and aluminum, in soluble form or as hydrous oxides in solution or on clay surfaces, react with soluble phosphorus to form insoluble hydroxy phosphates (Fox and Searle 1978, Uehara and Gillman 1981, Bohn *et al.*, 1985).

Both fungi and bacteria are capable of solubilizing inorganic phosphate as well as organically bound phosphorus (Tate 1984, Thomas *et al.*, 1985). Following an early report by Gerretsen (1948), many researchers examined the relationships between production of extracellular organic compounds by microbes in the rhizosphere, and plant uptake of P from mineral sources. Important mechanisms are shown in Fig. 2.

Hydrogen ions from organic acids, released by microbes from organic residues can solubilize phosphate bound at high pH in insoluble forms such as the calcium phosphate in rock phosphate (Kucey 1983). Organic anions from decomposing litter can compete with phosphate for adsorption sites on aluminum and iron, and thus reduce the amount of phosphate that reacts with Al and Fe. The organic compounds chelate Al and Fe, and thus reduce the quantity available to react

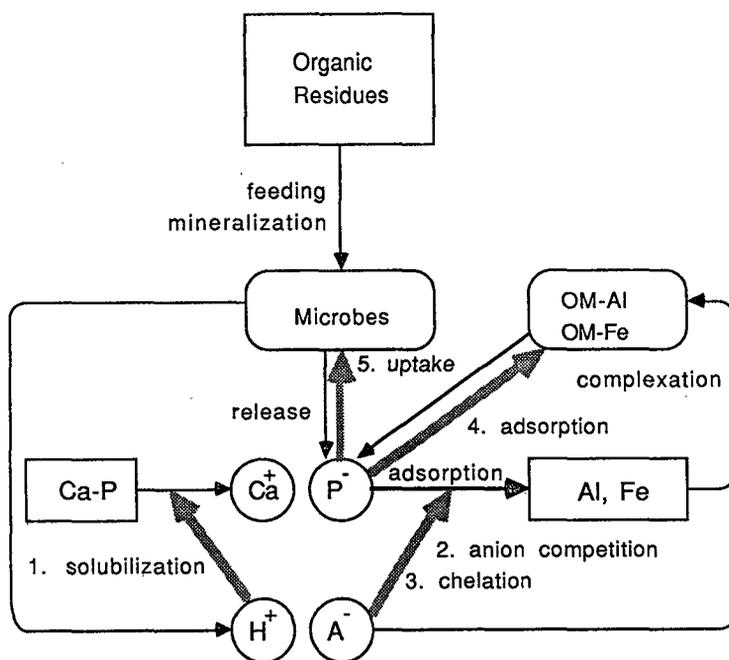


Fig. 2. Processes involving organic matter and its decomposition products which increase the availability of phosphorus to plants.

with phosphate (Young and Bache 1985, Sibanda and Young In Press). Organic matter itself can complex iron and aluminum. The metallo-organic matter complexes adsorb a relatively high amount of dissolved phosphorus (Kwong and Huang 1978, 1979), and conserves it in labile forms (Lopez Hernandez and Burnham 1974a, b). This process reduces the dissolved pool and thus accelerates the solubilization. However, the labile phosphorus is available to plant roots, whereas the aluminum and iron adsorbed phosphorus is not. Inorganic phosphorus applied to acid soils might be quickly bound by iron, and never become available to plants. However, if organic matter is present in the soil, phosphorus adsorbed to the metallo-organic matter complexes will be gradually released at a rate which more closely matches nutrient uptake by roots. This results in a more efficient use of the phosphate fertilizer.

Organic matter supports microbial organisms, which conserve phosphorus through uptake of dissolved forms. This will gradually be released and made available to roots.

Mutualism

We propose that the process of mineralization of organic matter is a mutualistic interaction which benefits both higher plants and decomposers. Mineralization of nutrients bound in plant and animal litter is an essential ecosystem function. This function, carried out by decomposers, transforms nutrients bound in insoluble particulate organic matter into soluble forms which can be taken up by plants. Mineralization of nutrients is the part of the plant-decomposer interaction which benefits plants, although the microbes themselves also use some of the nutrients which are mineralized.

The major benefit derived by the decomposers from this interaction is that they obtain their energy from oxidizing (or in some cases anaerobically metabolizing) the organic litter supplied mainly by plants, but in part by animals.

The relationship between higher plants and decomposers is very similar to the mycorrhizal symbiosis that exists between fungi and higher plants, with the exception that mycorrhizal fungi are physically attached to the plants, while decomposers frequently are not. The plant-decomposer interaction would fall under the category of "nonsymbiotic mutualism" which Boucher *et al.* (1982) define as mutualistic interactions in which the two species are physically unconnected.

The solubilization or mobilization of phosphorus bound by iron and aluminum in acid soils, or by calcium in basic soils also can be considered part of a mutualistic interaction. The phosphorus becomes solubilized and eventually available to higher plants as a result of microbial activity in the soil. While the microbes themselves may immediately benefit from this solubilization, the longer-term effect is to increase the soluble phosphorus in the ecosystem, thereby benefitting higher plants which may be limited by phosphorus.

While the focus in this paper is the interaction between higher plants and microbes as a mutualism which results in phosphorus for the plants and energy for the microbes, the same argument could be made for microbial nitrogen fixers which derive their energy from organic compounds in the soil.

The interaction between autotrophs and heterotrophs can be visualized as a cybernetic or feedback system (Fig. 3). The autotrophs produce biomass utilizing carbon, nitrogen, and sulfur derived from the atmosphere, and phosphorus from

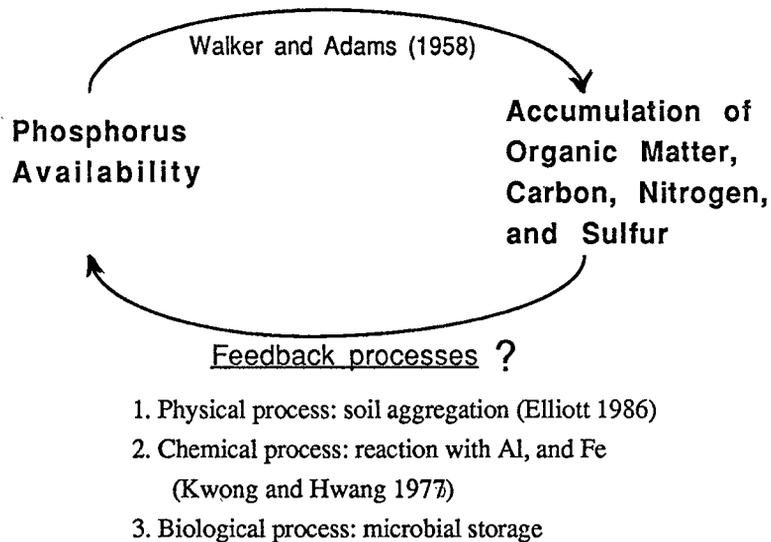


Fig. 3. Interactions of phosphorus and organic matter in soil.

the soil. Plants continually discard biomass in the form of leaf and root litter, and occasionally entire dead trees. The carbon compounds of discarded biomass serve as an energy source for microbes, which solubilize and conserve P in the soil through the processes summarized in Fig. 3. Through chemical processes, microbes solubilize P bound with calcium, iron and aluminum. Through biological processes, they incorporate the P, store it, and gradually release it so that sufficient P becomes available for uptake by higher plants. Through physical processes, microbial activity results in aggregation of soil into crumbs, blocks, and peds (Oades 1984), which may prevent leaching of P into the subsoil (Elliot, 1986). These processes result in the close control of organic matter accumulation by phosphorus availability, discussed by Walker and Adams (1958).

Succession and Mutualism

While hypotheses concerning ecological succession continue to be vigorously debated (Finegan 1984, Huston and Smith 1987, Walker and Chapin 1987), there is an emerging realization that the applicability of a particular hypothesis may depend in part upon the type of disturbance which initiates the subsequent succession (Pickett *et al.* 1987). On forest sites which have been cleared but which have not been subjected to prolonged disturbance such as cultivation, initial floristic composition may be an important determinant of the successional pattern

of species (Uhl 1987). For example, a short-term disturbance such as clear-cut logging may not seriously deplete the soil seed bank, inhibit stump sprouting, decrease soil nutrient stocks, nor decrease the micro-heterogeneity caused by piles of slash on the forest floor. Thus there are opportunities for seeds and young plants already in the area, and possessing a wide variety of environmental requirements, to grow and play a dominant role in succession.

In contrast, areas which have been cleared, cultivated for a number of years, and then abandoned, may exhibit a different pattern of succession (Uhl 1987). Soils in such areas may be relatively low in nutrients, and have few viable seeds of mature forest species. Soil surfaces may be free of litter and organic matter, and may be quite homogeneous. The micro-climate over an entire field may be quite severe, due to direct exposure to sunlight, and the erosive impact of rain. The area may not be suitable for germination of seeds of primary forest species. Succession may occur through autogenic change such as facilitation, tolerance, or inhibition (Connell and Slatyer 1977), where modification of severe initial environmental conditions by pioneer species enables other species characteristic of a later successional stage to become established.

Facilitation as a factor in succession may be very important in ecosystems on highly leached and weathered Oxisols and Udisols of the humid tropics and subtropics. In such soils, most of the entire stocks of phosphorus in the soil is held in a stable inorganic pool. In undisturbed forests, efficient P recycling enables the forest to function using only a small proportion of the total stocks in the entire system including soils. However, when forests are cut and the land used for agriculture or grazing, the P which is released from decomposing or burned trees quickly reacts with soluble iron and aluminum in the system, and becomes unavailable to the higher plants. Solubilization of this phosphorus is essential to build up biomass of a plant community on such degraded soil (Jordan 1985).

When secondary succession occurs on this type of soil, mutualism, facilitation, and succession work in a deviation amplifying system. The initial plant community on such degraded soil might be herbs or sparse grasses. The organic litter is sparse, but as it decomposes in the surface soil, a small amount of bound phosphorus is released into a labile form. As a result of slightly improved soil fertility, a larger biomass accumulates, which in turn produces a greater amount

of organic litter, and this causes a greater mobilization of phosphorus. The sequence continues until factors other than nutrients limit biomass accumulation.

The idea of a mutualistic interaction resulting in greater nutrient availability also would be applicable to primary succession on rocks. In this case, the carbon compounds that supply the first decomposers would be from decomposing algae, lichens, and other simple plants that typically colonize rock surfaces.

In neither secondary succession on degraded oxisols, nor on rock surfaces is phosphorus the only limiting nutrient, nor is it the first nutrient to limit succession. The gradual mobilization of many nutrients during the course of succession is an integral part of the successional process. The mobilization of the nutrients, and the ratio of nutrients present at any particular point in the successional series strongly influences the plant community which is dominant at that time. This point will be explored more fully, utilizing the resource ratio concept, reviewed in the next section.

Resource Ratios and Ecosystem Dynamics

The resource ratio concept embodies the idea that the ratio between resources such as nutrient elements controls the biota, which in turn modify the environment. The resource ratio concept has been applied to various ecological systems.

Marine ecosystems

Redfield (1958) synthesized a number of ideas regarding the chemistry of planktonic organisms and the chemistry of the marine environment into a scheme that suggested extensive control by the biota over the chemistry of some elements in sea-water and oxygen in the atmosphere. These general relationships form a basic stoichiometric model for the control of C, N, O and P chemistry in sea water (Bolin *et al.* 1983).

Evolutionary Time

The earth's biota has changed quantitatively and qualitatively through the earth's history. Differences have evolved in the ways and rates at which species can extract and sequester elements. These differences have led to ecological

differences in the ability to compete for nutrients (assuming competitive conditions) or to survive in a particular environment even without competition. This is part of the basis for niche differentiation, which leads in turn to predictable outcomes of competition, geographical distribution, and succession (Reiners 1986). However, the changing biota of the earth throughout evolutionary history has simultaneously altered the biogeochemical cycles of the earth, and consequently influenced the pathways of evolution (Rich 1984).

The sequential dominance of elements during evolution of anaerobic prokaryotic organisms began with carbon. The first heterotrophic organisms obtained carbon through anaerobic glycolysis, while in primitive autotrophs there evolved the ability to fix atmospheric carbon dioxide into reduced organic compounds. Closely correlated with CO₂ fixation evolved the ability to fix atmospheric nitrogen (Margulis 1970).

With the evolution of the apparatus of genetics, the first major barrier to the spread of living systems was overcome. As a result, the pace of development of life must have been enormously accelerated. This acceleration of metabolism must have led to severe competition for unstable compounds that were required for synthetic reactions. Pathways which would produce these activated compounds from more abundant intermediates would have evolved. Such pathways must have included those involving substrate-level phosphorylation that are found in organisms today (Hall 1971). Species with the ability to sequester necessary elements for genetic replication and phosphorylation, especially the elements sulfur and phosphorus, must have conveyed a competitive advantage. The sequence in which inorganic elements appear to have been incorporated into organic compounds during the evolution of life could have been C, N, S and then P. As each element was added into the biosphere, resource ratios changed, and subsequent evolutionary opportunities were thereby altered.

Primary Succession

Bolin *et al.* (1983) suggested that changing resource ratios might be a characteristic of succession in natural terrestrial ecosystems forming on newly exposed land surfaces or rocks, such as would occur following formation of a volcano, or melting of a glacier. The development of biota and soils on such sites

requires first the fixation of carbon from CO_2 by photosynthesis. The next step is nitrogen fixation by symbiotic or non-symbiotic micro-organisms. Rates of N fixation become limited as sulfur and phosphorus which are essential for nitrogen fixation become scarce. Relatively higher abundances of these elements become essential to further successional development, and thus S and P become next in the sequence of resources which constrain successional development. Microbes which can mobilize these nutrients from the environment play an essential role. As their activities increase, nitrogen fixation can then continue, and biomass of the ecosystem increases. The forest canopy becomes thick and closed, and little light reaches the forest floor. Light becomes the limiting resource. Plants evolve a large, complicated structure, and competition for light becomes paramount.

Soil formation

A concept similar to the resource ratio idea has been proposed for the process of soil formation. Walker (1965) suggested a sequence of nutrient elements which, each in their turn, dominate the process of soil formation. The sequence is the reverse of the sequence for primary plant succession. The reason is, there is an order of magnitude difference in the time scales between succession and soil formation. In the soil formation time scale, the rendering of nutrients from unweathered rock to a soluble state is only a very small fraction of the time for a soil weathering sequence. Important changes only occur when nutrient elements begin to become unavailable, due to very long term weathering processes.

The first important change occurs when rocks and primary minerals become depleted of phosphorus (stage A, Fig. 4). At this stage, the only source of phosphorus for most plants is probably from the mineralization of organic forms. Because of phosphate fixation by iron and aluminum in the soil, plant-available phosphorus in the soil declines. Walker (1965) summarized the sequence in Fig. 4 by saying: "After stage A has been passed, levels of carbon, nitrogen, sulphur, and phosphorus become increasingly out of phase. Carbon may increase for a time, because photosynthesis by successful plants may still maintain a high return of litter, and decomposition may be retarded by low pH. Organic nitrogen and sulfur must be lost from the system in some way, and C/N, C/S and C/P ratios in the organic matter increase. Finally carbon contents may decline, possibly because

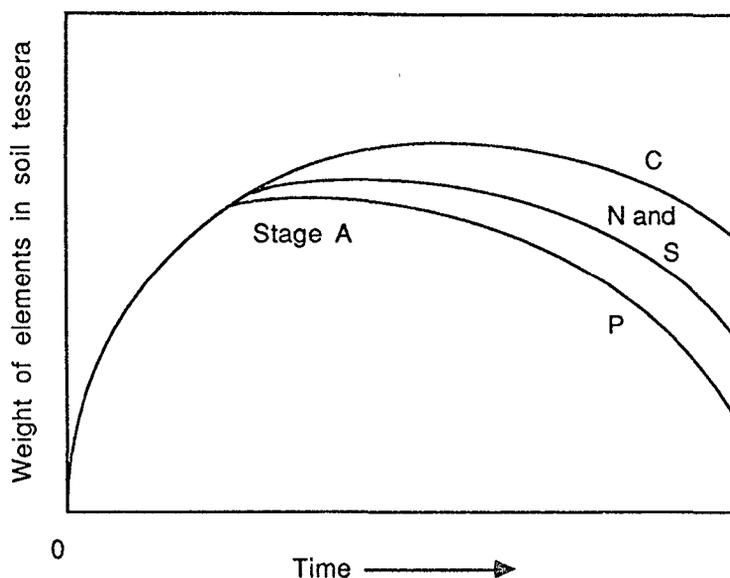


Fig. 4. Idealized changes in levels of carbon, nitrogen, sulfur, and phosphorus in soil organic matter, in a chronosequence of soils in a humid climate. If S and P are expressed in the same units, N and C will be approximately $10 \times$ and $100 \times$, respectively (From Walker 1965) ("Tessera" refers to the soil profile).

photosynthesis by even the most tolerant plants is eventually restricted, giving lower returns of litter."

The sequence in which nutrient elements become limiting—P, then S, then N—may be influenced by the relative strengths by which the oxidized forms of these elements are held by mineral soil. Phosphate is adsorbed most strongly by soils, followed by sulfate, and then nitrate (Kinjo and Pratt 1971). The factor governing accumulation of organic matter in many soils ultimately is phosphorus (Walker and Adams 1958).

Decomposer Succession

Although usually not specifically stated, the resource ratio concept appears in the literature on decomposer succession. Garrett (1951, 1963) and Griffin (1972) hypothesized that fungal succession on decomposing organic matter such as leaf litter could be described in terms of the decomposability of the carbohydrates on which they live. Initial colonizers are sugar fungi which utilize low molecular weight saccharides. They are followed by decomposers of cellulose or comparable polysaccharides, and finally by decomposers of lignin, tannin, keratin, and other

derivatives of carbohydrates. The successional direction may be caused in part by increasing phosphorus requirements of the biotic groups, since the more refractory carbohydrates later in the successional sequence require relatively more phosphorylation to be broken down to monosaccharides. However, this hypothesis is not adequate to explain many observed patterns of fungal succession (Swift *et al.* 1979). They have proposed a more general pattern of succession in decomposing branch and stump wood (Fig. 5). They emphasize that the decomposer community operating at any time is probably determined by resource quality factors such as ratios of C to N and P. The ratio between carbon and nutrient elements in decomposing organic matter such as leaf litter declines as a function of time. As decomposition proceeds, the C/nutrient ratio declines as C is lost through respiration of decomposer organisms. However, if a nutrient becomes limiting, it is immobilized and conserved until the ratio of C to this nutrient once again becomes favorable for decomposition (Swift *et al.* 1979).

In mineral soil low in nutrient elements, fungi are usually dominant over bacteria since fungi can utilize some bacterially undecomposable substrates (Ingham *et al.* 1986). Early stages of succession on nutrient-poor organic substrate also is dominated by fungi. Tribe (1960) found that on pure cellulose, bacteria

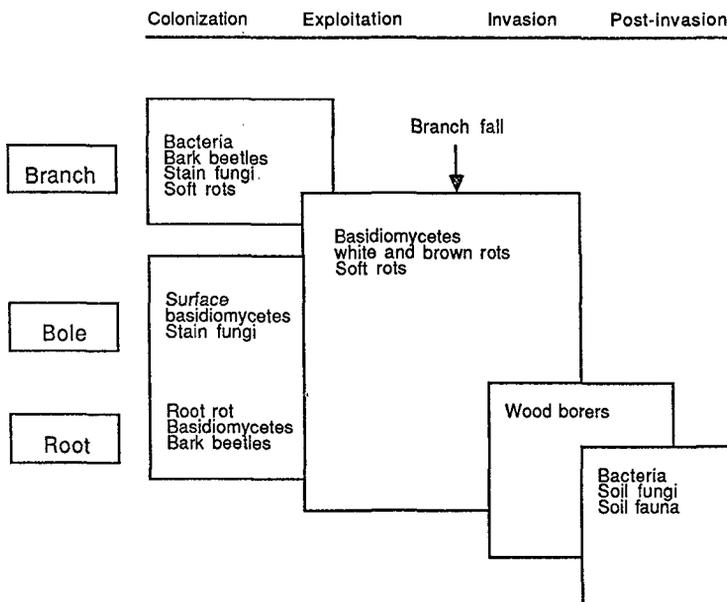


Fig. 5. Patterns of succession in decomposing branch and stump wood (From Swift, 1979).

were relatively uncommon during the initial fungal phase and caused little lysis of the cellulose. As the fungal mycelia got older, bacteria proliferated and induced an increase of nematodes and protozoa.

In natural systems, succession on nutrient poor substrates such as old logs or straw is often dominated in early stages by fungi. This is due in part to the "bridging" ability, that is, their ability to extend their hyphal network from nitrogen-poor substrate into the soil where nutrients are more readily available (Holland and Coleman 1987). Other mechanisms cited through which fungi appear to utilize nitrogen efficiently during early successional stages are: re-use of mycelial N by internal translocation of cytoplasmic contents from old to young cells; production of extracellular lytic enzymes which render cell walls available for assimilation by younger cells; preferential allocation of N to metabolically active systems. As a result, some types of fungi can utilize substrates such as heartwood with a C/N ratio on the order of 1000/1. The white rot fungi can produce cellulases even at a C/N ratio of 2000/1 (Charley and Richards 1983).

As a result of fungal activity, C/N ratios are reduced, and conditions become more favorable for bacteria. Bacterial decomposition is usually stimulated by addition of nitrogen (Baath *et al.* 1978). Lower ratios of N to P in bacteria than in fungi (Reiners 1986) suggests that increases in phosphorus availability also may favor bacteria relative to fungi.

Resource Ratios and Secondary Succession

Tilman (1985) has hypothesized that the resource-ratio concept can be used to explain plant succession. The hypothesis says that during the process of succession, the ratio of different nutrient elements in the ecosystem to each other, and to light, is continually changing due to the influence of the various species. The combination of resources available at any one time influences the species that colonize the site. Because the colonizing species efficiently utilize these resources, they influence their availability, with the result that the new relative abundance of resources favors a new complement of species. Tilman (1985) summarizes the concept as follows: "The gradient through time in the relative availability of a limiting soil resource and light will sequentially favor the species that are superior

competitors at particular ratios.”

In Tilman's model for succession in mesic terrestrial habitats, nitrogen frequently is the initial major limiting resource. Vitousek and White (1981) also stressed the importance of nitrogen in the early stages of succession. Due to nitrogen limitations, species with nitrogen fixing capabilities or associations are relatively successful, and nitrogen usually becomes more plentiful. With abundant nitrogen, the canopy of the plant community becomes thicker and denser, and amount of light near the forest floor becomes reduced. At this stage, species that are superior competitors for light become dominant. In this model, nitrogen and light are inversely related along a successional sere, and the occurrence of a plant along the sere should depend on the point along the soil-resource-light gradient at which the plant is a superior competitor.

Resource Ratios and Succession on Nutrient-Poor Substrates

We propose that during ecosystem aggradation on nutrient-poor substrate such as cultivated and abandoned oxisols and ultisols in the tropics and sub-tropics, carbon, nitrogen, sulfur, and phosphorus, in that order, limit the progress of succession; and each of the limiting resources is sequentially overcome, in some cases by mutualism between plants and microbes, and succession proceeds until the next element is limiting.

During succession on bare rock, carbon is the first limiting element, followed by N, S, and P. In old abandoned fields, where nutrient levels are low, but where the first colonizers are higher plants which fix relatively large amounts of carbon per unit soil compared to lower plants, the sequence begins with nitrogen.

Regardless of the state of chemical weathering of parent materials in the soil, the sequence of limiting nutrient elements begins with nitrogen (Tilman 1985), because this element is not part of rock or soil minerals. When the successional sere is on soils in which the rock minerals are relatively unweathered chemically, as seems to be the case for the sites studied by Tilman (1985), the sequence jumps from nitrogen to light, the resource considered by Tilman (1985) to be the ultimate limiting resource in succession. When succession occurs on soils which are highly weathered chemically such as Oxisols and Ultisols, sulfur and phosphorus enter the sequence between nitrogen and light, as limiting resources.

Nitrogen limitation is overcome, due to the appearance of nitrogen fixing organisms. The mutualistic interaction between higher plants and nitrogen fixing bacteria overcomes nitrogen as a resource limiting succession. After nitrogen becomes more readily available, sulfur and phosphorus seem to become barriers, because of the need of nitrogen fixing organisms for these nutrients. The sequence in which the limitation is overcome depends on their relative availability in the environment. If most of the labile sulfur and phosphorus in the soil is associated with organic matter, then it is the rate at which each is released which determines their relative availability. Since some sulfur is carbon bonded, sulfur is released concurrently with nitrogen by organisms seeking energy. However, all phosphorus is ester bonded, and is supplied through mineralization by enzymes in response to the need for this specific element (Stewart *et al.* 1983). Thus a sulfur limitation may be more readily overcome than a phosphorus limitation.

A consideration of nutrient supply outside the organic ecosystem also argues for phosphorus as the ultimate limiting nutrient. Compared to phosphate, there is a higher sulfate concentration in precipitation (Galloway *et al.* 1982), and a higher mobility of sulfate in the soil (Kinjo and Pratt 1971).

The rates at which elements accumulate as a function of time in an aggrading ecosystem on highly weathered, nutrient poor rocks occur in the sequence shown in Fig. 6A. This results in relative patterns of accumulation of the elements shown in 6B. The changing ratios of C, N, S, and P are illustrated in Fig. 7. In terms of total abundance, C is always greatest, followed by N, S, and P. But as a function of time, C is limiting only during the first part of the sequence. Nitrogen is the next element to cease being limiting, and as its relative abundance increases, sulfur and phosphorus remain limiting. If sulfur is more readily available than phosphorus, its ratio to carbon will decrease more quickly, and sulfur deficiency is overcome sooner. Finally, only phosphorus has a relatively low ratio to carbon, and gradually that ratio narrows.

The first inflection point (following stage I) of each element's curve in Fig. 7 illustrates the relative point in time at which that element no longer is limiting. Thus, at the point where the line for carbon begins to flatten out, N, S and P remain as limiting factors. Where the nitrogen curve flattens, only S and P are limiting, and when the sulfur curve flattens, only S and P are limiting, and

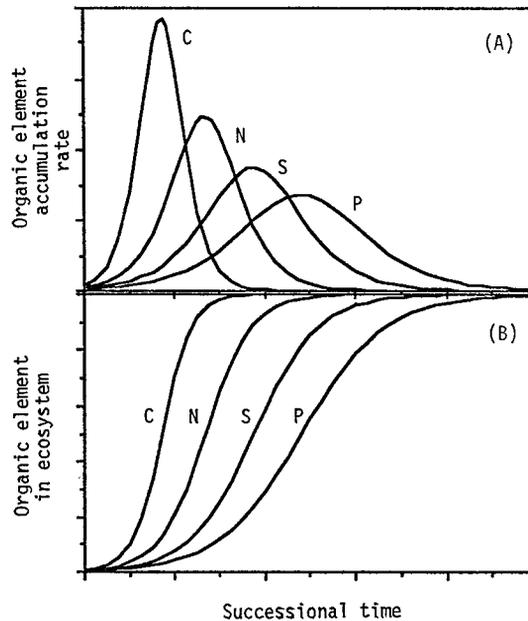


Fig. 6. Hypothetical curves representing rates of element accumulation (A), and amounts of elements accumulated in a terrestrial successional primary sere (B), during the aggrading phase of the ecosystem. A secondary sere would begin with nitrogen instead of carbon. If S and P are expressed in the same units, N and C will be approximately 10 ×, and 100 ×, respectively.

when the sulfur curve flattens, only phosphorus is a limiting nutrient. Once the ratio of phosphorus to carbon reaches its minimum, light theoretically would become limiting.

Following the inflection point for P during stage II, nutrient elements no longer limit succession, and light may become the limiting resource. The second inflection point (following stage II), which could occur hundreds or thousands of years after the first, illustrates the beginning of ecosystem degradation. This is the shifting resource ratio proposed by Walker (1965), who focused on chemical changes in soil after a mature ecosystem with maximum biomass has been attained. Phosphorus is the first element depleted from such a system, because losses from the biological portion of the ecosystem are not compensated as readily as are S and N. Phosphorus again becomes limiting, and ecosystem degradation begins as postulated by Walker (1965).

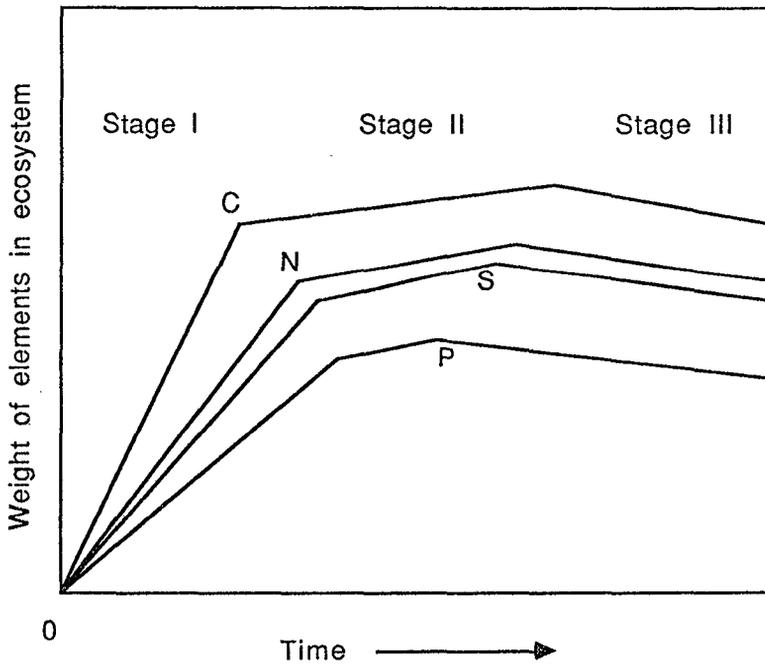


Fig. 7. Idealized changes in levels of carbon, nitrogen, sulfur, and phosphorus in the organic fraction of an ecosystem during succession. Stage I is probably exponential, but is represented linearly here. If S and P are expressed in the same units, N and C will be approximately $10 \times$ and $100 \times$ respectively.

The Ecosystem as a Cybernetic System

Engleberg and Boyarsky (1979) have asserted that ecosystems are not cybernetic systems, because there is no information flow which stabilizes ecosystems at a fixed set point. Patten and Odum (1981) rebutted their argument by stating that neither a discrete information flow nor a fixed set point is necessary for system regulation. Interactions between species, they maintain, is a non-discrete form of information flow that enables an ecosystem to function, although not always at the same point (for example at the same level of productivity), but nevertheless to keep functioning. We suggest that the cyclic influences of the above ground plant community on the decomposers and other below-ground organisms, and the influence of these in turn on the above ground plant community is an example of the type of cybernetic system described by Patten and Odum.

Conclusion

Changing resource availabilities and requirements are an important factor in successional sequences. In aggrading ecosystems beginning on bare rock, carbon may be the first limiting resource. In secondary succession, nitrogen usually is the first nutrient element which ceases to become limiting, and on nutrient poor soils, it is followed by sulfur, and then phosphorus. In degrading ecosystems, the sequence may be reversed. The changes in resource abundance during aggradation come about in part through the influence of microbial activity. Microbes depend on the autotrophs for their energy supply, while autotrophs depend on microbes for their nutrient supply. This mutualistic relationship appears to be an important regulator of ecosystem function, and of ecological succession on nutrient poor soils.

Summary

Mutualism as well as competition is important in succession. Plant communities change the resource base upon which they survive through mutualistic interaction with microbes. The changing resource base in turn causes a change in the plant communities which depend on the resources. When a series of these interactions begins on a nutrient-poor substrate, the ratio of resources often changes in a regular and predictable sequence. The resultant change in plant communities may be considered to be succession.

Literature Cited

- Anba, J., . Pages, A. Bernadac, and C. Iazdunski. 1987. New insights into the export machinery through studies on the synthesis of phosphate-binding protein in *Escherichia coli*. Pages 73-77 in A. Toriani-Gorini, F.G. Rothman, S. Silver, A. Wright, and E. Yagil eds. Phosphate Metabolism and Cellular Regulation in Microorganisms. Amer. Soc. Microbiology. Washington, D.C.
- Andersen, D.C. 1987. Below-ground herbivory in natural communities: a review emphasizing fossorial animals. Q. Rev. Biol. 62: 261-286.

- Bååth, E., U. Lohm, B. Lundgren, T. Rosswall, B. Soderstrom, B. Sohlenius, and A. Wiren. 1978. The effect of nitrogen and carbon supply on the development of soil organism populations and pine seedlings: a microcosm experiment. *Oikos* 31: 153-163.
- Bohn, H.L., B.L. McNeal, and G.A. O'Connor. 1985. *Soil Chemistry*. Wiley, N. Y. (pg. 341).
- Bolin, B., P.J. Crutzen, P.M. Vitousek, R.G. Woodmansee, E.D. Goldberg, and R.B. Cook. 1983. Interactions of biogeochemical cycles. Pages 1-39 in B. Bolin and R.B. Cook eds. *The Major Biogeochemical Cycles and Their Interactions*. SCOPE 21. Wiley, Chichester, England.
- Boucher, D.H. 1982. The ecology of mutualism. *Ann. Rev. Ecol. Syst.* 13: 315-347.
- Charley, J.L. and B.N. Richards. 1983. Nutrient allocation in plant communities: mineral cycling in terrestrial ecosystems. Pages 6-45 in O.L. Lange, P.S. Nobel, C.B. Osmond, and H. Ziegler eds. *Physiological Plant Ecology IV. Ecosystem Processes: Mineral Cycling, Productivity and Man's Influence*. Springer-Verlag, Berlin.
- Chauhan, B.S., J.W.B. Stewart, and E.A. Paul. 1979. Effect of carbon additions on soil, labile inorganic, organic and microbially held phosphate. *Can. J. Soil Sci.* 59: 387-396.
- Chauhan, B.S., J.W.B. Stewart, and E.A. Paul. 1981. Effect of labile inorganic phosphate status and organic carbon additions on the microbial uptake of phosphorus in soils. *Can. J. Soil Sci.* 61: 373-385.
- Cloud, P. 1974. Evolution of ecosystems. *Am. Sci.* 62: 54-66.
- Cole, C.V., G.S. Innis, and J.W.B. Stewart. 1977. Simulation of phosphorus cycling in semi-arid grasslands. *Ecology* 58: 1-15.
- Connell, J.H. and R.O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *Am. Nat.* 111: 1119-1144.
- Cromack, K. 1981. Below-ground processes in forest succession. Pages 361-373 in D.C. West, H.H. Shugart, and D.B. Botkin eds. *Forest Succession, Concepts and Application*. Springer-Verlag, N. Y.
- Diamond, J.M. 1975. Assmby of species communities. pp.342-444 in M.L. Cody

- and J.M. Diamond, Eds. *Ecology and Evolution of Communities*. Harvard Univ., Cambridge, Mass.
- Egler, F.E. 1954. Vegetation science concepts. I. Initial floristic composition: a factor in old field vegetation development. *Vegetatio* 4: 412-417.
- Elliot, E.T. 1986. Aggregate structure and carbon, nitrogen, and phosphorus in native and cultivated soils. *Soil Sci. Soc. Am. J.* 50: 627-633.
- Egelberg, J. and L.L. Boyarsky. 1979. The noncybernetic nature of ecosystems. *Am. Nat.* 114: 317-324.
- Finegan, B. 1984. Forest succession. *Nature* 312: 109-114.
- Fox, R.L., and P.G.E. Searle. 1978. Phosphate adsorption by soils of the tropics. Pages 97-119 in M. Stelly ed *Diversity of Soils in the Tropics*. ASA Special Pub. NO. 34. Amer. Soc. of Agronomy, Madison, Wis.
- Galloway, J.N., G.E. Likens, W.C. Keene, and J.M. Miller. 1982. The composition of precipitation in remote areas of the world. *J. Geophysical Res.* 87: 8771-8786.
- Garrett, S.D. 1951. Ecological groups of soil fungi: a survey of substrate relationships. *New Phytol.* 50: 149-166.
- Garrett, S.D. 1963. *Soil Fungi and Soil Fertility*. Pergamon Press, Oxford.
- Gerretsen, F.C. 1948. The influence of microorganisms on the phosphate intake by the plant. *Plant and Soil* 1: 51-81.
- Griffin, D.M. 1972. *Ecology of Soil Fungi*. Chapman and Hall, London.
- Grime, J.P. 1974. Vegetation classification by reference to strategies. *Nature (Lond.)* 250: 26-31.
- Grime, J.P. 1979. *Plant Strategies and Vegetation Processes*. Wiley, New York.
- Grubb, P.J. 1986. The ecology of establishment. Pages 83-97 in A.D. Bradshaw, D.A. Goode, and A.E. Thorpe eds. *Ecology and Design in Landscape*. Symp. Br. Ecol. Soc. 24. Blackwell, Oxford.
- Hall, J.B. 1971. Evolution of the prokaryotes. *J. Theor. Biol.* 30: 429-454.
- Holland, E.A. and D.C. Coleman. 1987. Litter placement effects on microbial and organic matter dynamics in an agroecosystem. *Ecology* 68: 425-433.
- Huston, M. and T. Smith. 1987. Plant succession: life history and competition. *Am. Nat.* 130: 168-198.
- Ingham E.R., C. Cambardella, and D.C. Coleman. 1986. Manipulation of

- bacteria, fungi and protozoa by biocides in lodgepole pine forest soil microcosms: effects on organism interactions and nitrogen mineralization. *Can. J. Soil Sci.* 66: 261-272.
- Jordan, C.F. 1985. *Nutrient Cycling in Tropical Forest Ecosystems*. Wiley, Chichester.
- Kinjo, T. and P.F. Pratt. 1971. Nitrate adsorption: II. competition with chloride, sulfate, and phosphate. *Soil Sci. Soc. Amer. Proc.* 35: 725-728.
- Kucey, R.M.N. 1983. Phosphate solubilizing bacteria and fungi in various cultivated and virgin Alberta soils. *Can. J. Soil Sci.* 63: 671-678.
- Kwong, K.F.N. and P.M. Huang. 1978. Sorption of phosphate by hydrolytic reaction products of aluminum. *Nature* 271: 336-338.
- Kwong, K.F.N. and P.M. Huang. 1979. Surface reactivity of aluminum hydroxides precipitated in the presence of low molecular weight organic acids. *Soil Sci. Soc. Am. J.* 43: 1107-1113.
- Lopez-Hernandez, D. and C.P. Burnham. 1947a. The covariance of phosphate sorption with other soil properties in some British and tropical soils. *J. Soil Sci.* 25: 196-206.
- Lopez-Hernandez, D. and C.P. Burnham. 1947b. The effect of pH on phosphate adsorption in soils. *J. Soil Sci.* 25: 207-216.
- Margulis, L. 1970. *Origin of Eukaryotic Cells*. Yale Univ. Press. New Haven.
- McGill, W.B., J.A. Shields, and E.A. Paul. 1975. Relation between carbon and nitrogen turnover in soil organic fractions of microbial origin. *Soil Biol. Biochem.* 7: 57-63.
- McGill, W.B. and C.V. Cole. 1981. Comparative aspects of cycling of organic C, N, S and P through soil organic matter. *Geoderma* 26: 267-286.
- McIntosh, R.P. 1980. The relationship between succession and the recovery process in ecosystems. pp.11-62 *in* J. Cairns (ed). *The Recovery Process in Damaged Ecosystems*. Ann Arbor Science Pubs. Ann Arbor, Mich.
- Odum, E.P. and L.J. Biever. 1984. Resource quality, mutualism, and energy partitioning in food chains. *Am. Nat.* 124: 360-376.
- Patten, B.C., and E.P. Odum. 1981. The cybernetic nature of ecosystems. *Am. Nat.* 118: 886-895.
- Pickett, S.T.A. 1976. Succession: an evolutionary interpretation. *Am. Nat.* 110:

- 107-119.
- Pyke, G.H., H.R. Pulliam and E.L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. *Quart. Rev. Biol.* 51: 137-154.
- Pickett, S.T.A., S.L. Collins, and J.J. Armesto. 1987. Models, mechanisms and pathways of succession. *Bot. Rev.* 53: 335-371.
- Redfield, A.C. 1958. The biological control of chemical factors in the environment. *Am. Sci.* 46: 205-221.
- Reiners, W.A. 1986. Complementary models for ecosystems. *Am. Nat.* 127: 59-73.
- Rich, P.H. 1984. Trophic-detrital interactions: vestiges of ecosystem evolution. *Am. Nat.* 123: 20-29.
- Salisbury, E.J. 1929. The biological equipment of species in relation to competition. *J. Ecol.* 17: 197-122.
- Sibanda, H.M. and S.D. Young. In Press. The effect of humus acids and soil heating on the availability of phosphate in oxide-rich tropical soils. *J. Ecology*.
- Smeck, N.E. 1985. Phosphorus dynamics in soils and landscapes. *Geoderma* 36: 185-199.
- Stewart, J.W.B., C.V. Cole, and D.G. Maynard. 1983. Interactions of biogeochemical cycles in grassland ecosystems: Pages 247-269 in B. Bolin and R. B. Cook eds. *The Major Biogeochemical Cycles and Their Interactions*. SCOPE 21. Wiley, Chichester, England.
- Stewart, J.W.B. and A.N. Sharpley. 1987. Controls on dynamics of soil and fertilizer phosphorus and sulfur. pages 101-121 in *Soil Fertility and Organic matter as Critical Components of Production Systems*. Soil Sci. Soc. Amer. Pub. NO.19. Amer. Soc. Agronomy, Madison, Wis.
- Swift, M.J., O.W. Heal, and J.M. Anderson. 1979. *Decomposition in Terrestrial Ecosystems*. Univ. of Cal. Press. Berkeley.
- Tate, K.R. 1984. The biological transformation of P in soil. *Plant and Soil* 26: 245-256.
- Thomas, G.V., M.V. Shantaram, and N. Saraswathy. 1985. Occurrence and activity of phosphate-solubilizing fungi from coconut plantation soils. *Plant and Soil* 87: 357-364.
- Tilman, D. 1985. The resource-ratio hypothesis of plant succession. *Am. Nat.* 125: 827-852.

- Tilman, D. 1986. Evolution and differentiation in terrestrial plant communities: the importance of the soil resource: light gradient. Pages 359-380 in J. Diamond and T.J. Case, eds. *Community Ecology*. Harper and Row, N. Y.
- Tribe, H.T. 1960. Aspects of decomposition of cellulose in Canadian soils. I. Observations with the microscope. *Can. J. Microbiology* 6: 309-323.
- Uehara, G. and G. Gillman. 1981. *The Mineralogy, Chemistry, and Physics of Tropical Soils with Variable Charge Clays*. Westview Press, Boulder, Colorado.
- Uhl, C. 1987. Factors controlling succession following slash and burn agriculture in Amazonia. *J. Ecology* 75: 377-407.
- Vitousek, P.M. 1985. Community turnover and ecosystem nutrient dynamics. Pages 325-333 in S.T.A. Pickett and P.S. White eds. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Orlando.
- Vitousek, P.M. and P.S. White. 1981. Process studies in succession. pages 267-276 in D.C. West, H.H. Shugart, and D.B. Botkin eds. *Forest Succession, Concepts and Application*. Springer-Verlag, N. Y.
- Walker, L.R. and F.S. Chapin. 1987. Interactions among processes controlling successional change. *Oikos* 50: 131-135.
- Walker, T.W. 1965. The significance of phosphorus in pedogenesis. Pages 295-315 in E.G. Hallworth and D.V. Crawford eds. *Experimental Pedology*. Buftterworths, London.
- Walker, T.W. and A.F.R. Adams. 1958. Studies on soil organic matter: I. Influence of phosphorus content of parent materials on accumulations of carbon, nitrogen, sulfur, and organic phosphorus in grassland soils. *Soil Sci.* 85: 307-318.
- Wiens, J.A. 1977. On competition and variable environments. *Am. Sci.* 65: 590-597.
- Young, S.D. and B.W. Bauch. 1985. Aluminium-organic complexation: formation constants and a speciation model for the soil solution. *J. Soil Science* 36: 261-269.