

REVIEW

**Alternative Nutrient Cycles for Terrestrial Plants,
Positive Feedbacks through Detrital Processes,
and Nutrient Use Efficiency**

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**육상식물 중심의 영양소 순환 경로와 부식과정에 의한 양성
되먹임과정, 그리고 영양소 이용효율**

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ABSTRACT

Six nutrient cycles involving terrestrial plants are identified and characterized. Plants affect biotic and abiotic cycles through their effects on soil properties. They determine their internal nutritional status and nutrient concentrations in their environment via internal and external cycles. Contributions of organic matter to mycorrhizal, trophic, and detrital mediated external cycles and alterations of nutrient concentrations by plants can promote positive feedbacks leading to increased availability and retention of soil nutrients in open systems. Recognizing alternative cycles through plants leads to a definition of nutrient use efficiency for ecosystems: the ratio of system production to nutrient content of organic matter. A simple graph model to predict changes of nutrient use efficiency during primary succession is then presented.

INTRODUCTION

Ecosystems can be abstracted to a set of three interacting components: autotrophs, heterotrophs, and a detrital pool (O'Neill *et al.*, 1975). As ecosystem processes require energy, autotrophs initiate and power ecosystems. Autotrophic activities are, in turn, regulated and maintained by heterotrophs, such as consumers and decomposers. For example, it is manifest that heterotrophic organisms influence photosynthetic processes

by at least controlling availability of essential limiting elements through recycling processes (Witkamp and Ausmus, 1976). Lastly, a portion of all primary and secondary production is combined and stored in the detrital pool. Functional differentiation of these components through evolution diversifies energy and nutrient element processes in ecosystems.

Here, we first examine and categorize nutrient cycles involving plant and then discuss how they function as positive feedbacks to increase energy fixation (productivity) and storage (biomass) in ecosystems. we focus on plant, because they are the dominant primary producer and a major determinant of decomposition characteristics in terrestrial ecosystems (Grime and Hodgson, 1987). Recognizing these alternative processes highlights potential applications to ecosystem studies, including an alternative definition of nutrient use efficiency that reflects feedback effects on the system as a whole. Finally, a model showing how ecosystem nutrient use efficiencies change during succession is presented.

ALTERNATIVE CYCLE: AUTOTROPH-BASED PROCESSES

Plants exchange energy, nutrients, and water with other components in ecosystem. For example, radiant energy fixed photosynthetically into carbohydrates is maintained inside plants for varying lengths of time, transferred to other ecosystem components, and dissipated ultimately into the environmental heat bath. Because energy fixation is a result of chemical reactions that occur in solution, plants must acquire water as well as the nutrient element reactants. Alternative functions of plants, seen as nodes of global energy flow and nutrient and water cycles, can thus be conceptualized (Fig. 1). This concept implies

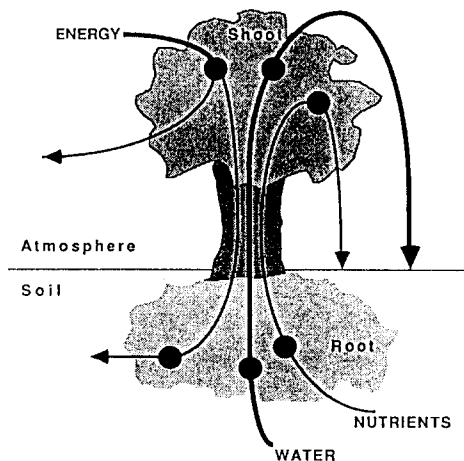


Fig. 1. Conceptualization of plant component in the processings of energy, water, and nutrients in ecosystems.

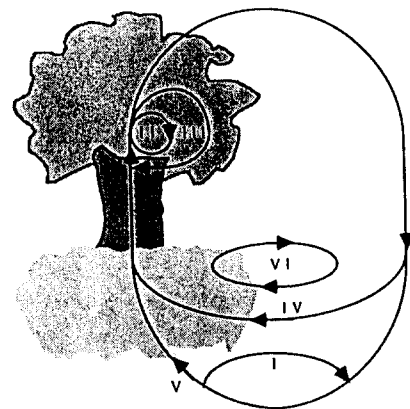


Fig. 2. Alternative nutrient cycles associated with plants(see text for details).

that there are no permanent energy or nutrient sinks or sources in ecosystems; those we recognize are dependent on the time-scale of interest and specified ecosystem boundaries.

Alternative element cycles that terrestrial plants participate in directly or influence indirectly are depicted in Fig. 2. When an element cycle involves abiotic pools and processes wholly, it is called an abiotic cycle and is depicted as Type I in Fig. 2. For example, H^+ ions may be transferred between an abiotic substrate and its surroundings through redox reactions without requiring biotic influences. These processes are presumed to dominate pre-biotic conditions. Terrestrial plants, through their effects on soil properties, can affect these cycles and in turn, will be affected by nutrient concentrations determined by abiotic cycles. Type I cycles will not be discussed further, except for how they may interact with those cycles involving terrestrial plants.

Circulation of elements inside a single plant is a result of type II and III cycles. These are distinguished by the time scales over which they act; internal reuse of an element may not be considered cycling by some, but whether type II and III cycles are seen as such depends on the spatial and temporal scale of observation. Both relativity and scale-dependency of cycling is discussed by Lee *et al.* (unpublished manuscript). Type II cycles include daily metabolic reuse of nutrient elements in plant biomass during the growing season. Nutrient conservation of evergreenness (Monk, 1966) also belongs to type II cycles. Type III cycles represent resorption and retranslocation, which make nutrient elements conservative within plants themselves on a seasonal time scale. Short-term reuse of a deficient element causes extremely conservative behavior of the element, and enhances nutrient use efficiency as defined by Vitousek (1982) and Birk and Vitousek (1986). Type II and III cycles benefit plants by conserving nutrient elements directly, but do not contribute to nutrient supplies in the environment.

Type IV cycles are those involving movement of nutrient elements out of the plant via litter fall, but with a minimal number of intervening components. These processes are characterized by an intimate association between plants and other organisms. Type IV cycles include direct nutrient uptake by plants from decomposing plant litter (e.g., Herrera *et al.*, 1978; Sanford, 1987) and direct transfer of nutrients between plants connected by mycorrhizae (Newman, 1988). Type IV cycles result in a trade-off of benefits. Unlike cycles II and III, energy (and nutrient) leaves the plant, but this energy supports closely associated microorganisms which may acquire and make available to the plant nutrients from sources otherwise nutrient unavailable, e.g., atmospheric nitrogen and nutrients in soil minerals and structural tissues. Transfer of nutrients from one plant or detritus to another plant via mycorrhizal hyphae is thus an example of a positive feedback on the concentration of available nutrients.

Cycles of type V and VI are those mediated by trophic and detrital processes. In these cycles, plants lose energy and nutrient elements but benefit from indirect mutualistic interactions with organisms that are not in intimate physical relationship with the plants. Type V cycles are formed by trophic relationships among organisms. Advantages to

plants may emerge as the possible nutrient recycling pathways diversify; the number and variety of trophic pathways is enormous (Patten, 1985). Faunal trophic processes have been shown to control nutrient availability and plant community structure (Elliott *et al.*, 1984; Fretwell, 1987; Anderson, 1988; Moore *et al.*, 1988).

Recycling of energy and nutrients through root exudation and sloughing are categorized as cycle VI. Exchanges of organic carbon and nitrogen between legumes and nitrogen fixers are also included here. Type VI cycles are similar to type IV and V cycles, because they are mediated by intimate biological associates or trophic and detrital processes, respectively. But unlike those others, type VI cycles are strictly belowground processes. As a result, they are likely to be intermediate between cycles IV and V in the risk to the plant of its contribution of energy and nutrients in organic matter being lost from the system and in the diversity of possible pathways returning nutrients of plants. Below, we discuss positive feedbacks to plants resulting from detrital processes that close cycles IV, V and VI.

POSITIVE FEEDBACKS THROUGH DETRITAL PROCESSES

Autotrophs' contributions to the detrital pool may be classified into three types based on frequency. A conceptualization of these ideas is depicted in Fig. 3. Root exudation

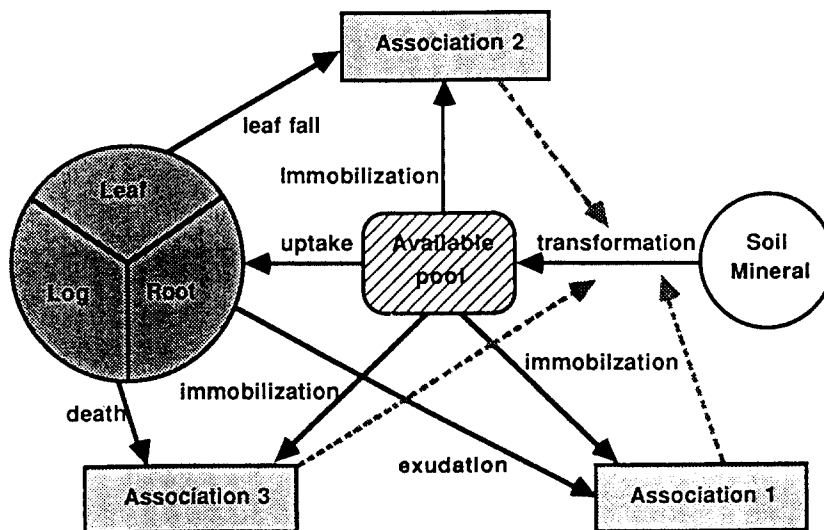


Fig. 3. Positive feedbacks leading to enhanced nutrient availability and biotic and abiotic immobilization of nutrients through organic matter processing initiated and differentiated by woody plants. Here immobilization includes physical retention in standing water, chemical adsorption, and biological uptake. Direct transfers of energy and nutrients are indicated by solid arrows, controls by faded arrows.

operates typically on a daily time scale during the growing season and would therefore mediate relatively rapid ecosystem processes (Cycle VI) in the soil subsystem. Leaf fall, a component of Cycles IV and V, has intermediate frequency and impacts on heterotrophic ecosystem components. Death of woody plants, which occurs on a relatively low frequency, exerts persistent influences on the components of cycles IV and V. Temporally and spatially differentiated associations of organisms can be generated through these processes operating at various rates, resulting in compartmentalization of ecosystem functions (McGill and Myers, 1987; Anderson, 1988). Compartmentalization is a fundamental requirement for mutualisms via positive feedbacks (Post *et al.*, 1985).

A positive feedback to plants and other ecosystem components forming type VI cycles occurs when organic exudates from roots contribute to increased nutrient concentrations through the solubilization of primary minerals and subsequently, increased system productivity (Richards, 1974). This idea was recently extended to include trophic processes (Naiman, 1988; Pastor *et al.*, 1988). Plants do not need to be conservative if the production and transfer of organic matter to other ecosystem components results subsequently in increased availability to plants of nutrient elements in the atmosphere and soil. The result is a positive feedback, whereby the plant improves its nutritional environment by being less conservative.

Nutrient cycles mediated by detrital organic matter (cycles IV, V and VI) also may act as positive feedbacks to primary producers by enhancing nutrient availability and nutrient retention. Organic matter can increase the availability of inorganic nutrients originating from soil minerals, especially phosphorus (Lee unpublished manuscript). Hydrogen ions and organic acids derived from decomposing organic matter accelerate the weathering of soil minerals and the release of nutrient elements (Adams and Boyle, 1979). Organic anions block anion adsorption sites on aluminum and iron, thus keeping nutrient elements in dissolved or labile forms (Lee *et al.*, 1990). Organic acids also prevent crystallization of Fe and Al compounds (Kodama and Schnitzer, 1977, 1980) and thus increase the reactivity of Al and Fe cations for adsorbing dissolved anions (Huang and Violante, 1986); hence, organo-aluminum complexes in many soils adsorb and thus retain phosphate and sulfate (Bloom, 1981; Fuller *et al.*, 1985). This is also exemplified by soil incubation experiments where glucose treatment enhanced the phosphorus fraction extracted by 0.1 M NaOH (Lee *et al.*, 1990). A large portion of cation exchange capacity in soil systems to retain larger quantities of nutrient elements, and increases water-holding capacity (Elliott, 1986). Organic matter also feeds microorganisms, which are important nutrient carriers preventing leaching loss in soil systems (Bowden, 1987; Vitousek and Walker, 1987).

The enhanced chemical and physical retention and biological (microbial) immobilization of nutrients made possible by the above mechanisms can further promote the solubilization of soil minerals by depleting dissolved concentrations. Gradual release of nutrients coincident with plant requirements would lead to higher primary production than if nutrients were not retained in the system. For example, during the growing season root exudates

disrupt soil macroaggregates and dissociate organo-metal complexes thereby releasing nutrients for primary production (Reid *et al.*, 1982). Different mechanisms for increasing availability of other types of elements, such as those originating only in the atmosphere, e. g., nitrogen, are discussed in the following section. Contribution of organic matter by plants can thus promote during succession and maintain in the steady state nutrient retention and availability in soil components. Moreover, these mechanisms are additional to and perhaps complement the positive feedbacks promoting new growth during secondary succession that were identified by Gutierrez and Fey (1976).

The above mechanisms are basically those dealing with organic carbon processing; additional indirect mechanisms may be possible whereby decomposing organic residues facilitate the supply of one nutrient element, which in turn, accelerates the availability and accumulation in organic matter of other more limiting nutrients. It is conceivable that increased phosphorus concentration due to organic matter decomposition will promote nitrogen fixation, which requires much phosphorous (Vitousek and Walker, 1987). Because incorporation rates of nutrient elements into organic fractions are controlled by limiting laws and the stoichiometry of biomass (William, 1987; Lee unpublished manuscript), interactions between environmental availability and biological requirements. This can result in a condition of balance between organic elements in the climax (steady) state.

The positive feedbacks discussed here, mechanisms by which organic matter accelerates further accumulation of organic matter via enhanced nutrient supplies in ecosystems, contrast with proposals by other researchers. Vitousek (1982) and Shaver and Melillo (1984) presented, as an example of positive feedbacks with negative effects on soil nutrient concentration and therefore organic matter production, the case where nutrient-poor forest return leaf litter with a higher ratio of carbon to nutrients. This can be a result of increased nutrient use and resorption (Cycles II and III). Processing of litter leads to further decreases in nutrient availability in soil due to enhanced microbial immobilization. Vitousek and Matson (1988) recently proposed a similar idea, that under cool climate slow decomposition causes nutrient limitation due to greater microbial immobilization and slower release of nutrients from organic litter. Both contrasting positive feedbacks, those promoting and those inhibiting nutrient concentrations, are theoretically possible (DeAngelis *et al.*, 1986; Vitousek and Walker, 1987). The question is under what conditions are each important.

The two contrasting positive feedbacks are compared in Fig. 4. Elements X and Y represent nutrients with relatively small available pools and Z a nutrient with a large available pool. It is assumed that growth of biomass is only possible with incorporation of elements from the environment. Element rates of incorporation and release of elements. Incorporation of nutrient element Y during time interval Δt is compared in systems (a) and (b). It should be noted that the proportion of limiting element in biomass is reduced in many cases merely by the diluting effect of incorporation of other readily available elements. This reduction is possible, even for currently nonlimiting nutrients, whenever

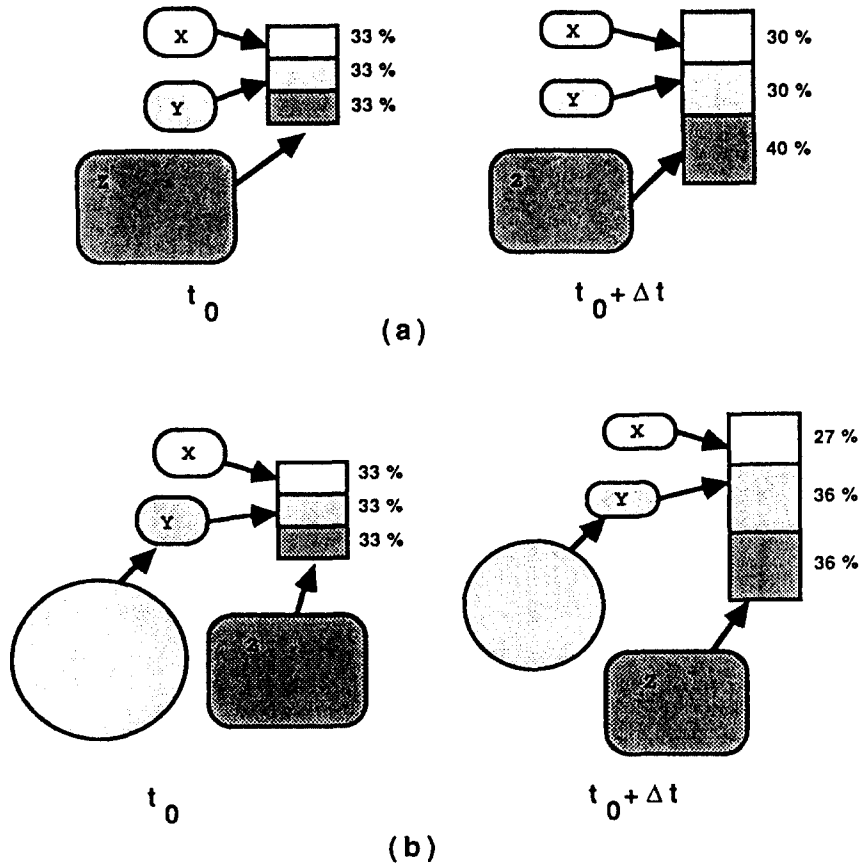


Fig. 4. Comparison of conditions favoring the two contrasting positive feedbacks on nutrient ratios and concentrations in ecosystems where available pool of an essential element is restricted; a) case where there is no alternative source or refilling rate is very slow; b) case with alternative sources refilling available pool. Elements in biomass and in pools relatively available and unavailable to plants are represented by rectangles, rounded rectangles, and circles, respectively.

the biological incorporation rate of an element is lower than those of other essential elements. This is especially true for carbon during ecosystem succession.

Fig. 4(a) represents systems where availability of an essential element, Y, is restricted, and there is no other source or the refilling rate of the pool of available nutrient is very low. In the case, repetitive production and decomposition of organic matter enhances biotic and abiotic immobilization, due to increased organic carbon supply, thereby reducing the availability of nutrients to plants. Thus, relative unavailability of the element becomes severely limiting to plant production (Vitousek, 1982; Vitousek and Matson, 1988). This

view is implicitly based upon the assumption that pool size of the nutrient of interest is restricted. In addition, it focuses on microorganisms as competitors of plants for nutrients and litter fall as a waste of plant metabolism, and leads accordingly to the conclusion that plants should reduce nutrient concentrations in these putative wastes.

Biological systems with mechanisms, such as those described earlier, to make unavailable forms of essential elements more readily available and thus remedy the deficiency to some extent, should have an advantage over those without. If such mechanisms cause a rapid refilling of available pools of nutrients (Fig. 4b), they may facilitate rapid plant uptake despite small available-pool size. During organic matter recycling under these two contrasting conditions, the alternative positive feedbacks will emerge, and the concentration of element Y in organic matter will either decrease, respectively (Fig. 4a or 4b).

Positive feedbacks in the natural world are usually, if not always, coupled to negative feedbacks (Odum, 1971). Unless there are negative controls, or constraints, positive actions will drive systems without limitation. For example, organic matter with high ratio of carbon/nutrients can lead to microbial immobilization of essential elements and cause lower nutrient availability in soils (Vitousek, 1982). But, a sequence of lower plant production and lower supply of energy for microbial activities follows necessarily. Microbial activities may be suppressed eventually and competition for plant nutrients can be at least partially reduced. An ensuing surplus of organic carbon can enhance nutrient elements in biomass and labile forms in soils (Lee unpublished manuscripts). Elliott *et al.* (1984) explain how plant nutrient availability can be enhanced by root loss of soluble carbon through microfauna increasing [rhizosphere] bacterial turnover and accelerating C, N, and P mineralization rates. Additionally, nutrient elements in excess may enlarge labile pools of other essential elements through repetitive assimilation and mineralization. Nevertheless, positive influences of organic matter on nutrient availability will be restricted eventually by negative counteractions, environmental constraints, or both. In this respect, each of the positive feedbacks is recognized as a possible constraint on the other.

The positive feedback of Fig. 4a is more likely in closed systems, the other (Fig. 4b) in open systems. The conditions where ecosystems are open to nutrient inputs during later successional stages or climax conditions must be identified to determine the relative importance of these contrasting positive feedbacks. If nutrient cycles become closed during ecological succession (Odum, 1971), as a result of decreased nitrogen fixation for example, then growth and replacement of components in ecosystems, which is facilitated by positive feedbacks during earlier successional stages, will be eventually constrained during later successional stages by different positive or negative feedbacks. Future models for ecosystem succession incorporating the interactions of positive and negative controls on nutrients could build on those of Gutierrez and Fey (1975) and Connell and Slayter (1977).

NUTRIENT CYCLING AND USE EFFICIENCY DURING SUCCESSION

Nutrient use efficiency has been defined for plants as the amount of organic matter fixed per unit of nutrient uptake (Vitousek, 1982). Warning and Schlesinger (1985) suggest a similar definition: net primary production per unit of nutrient lost from vegetation. Birk and Vitousek (1986) reported that high nutrient use efficiency, *sensu* Vitousek (1982), is related to internal metabolic efficiency rather than plant uptake and retranslocation. This explains to some degree why there is no conclusive correlation between soil nutrient availability and nutrient resorption efficiency of plants. Lajtha and Klein (1988) found that N and P use efficiency, defined as the ratio of plant biomass to plant N or P mass, was negatively related to N and P availability, but could not observe a predictable response of N and P resorption efficiency to varying levels of nutrient availability.

Recognizing alternative cycles through plants leads to a definition of nutrient use efficiency for ecosystems. At the ecosystem level, nutrient cycling can increase, *i.e.*, systems can become more efficient, by both conservation within plant (high internal reuse) and rapid uptake by plants of nutrients mobilized from biomass (Vitousek, 1984). The contribution of rapid recycling to ecosystem nutrient use efficiency is not included in the definitions of Vitousek (1982) and Waring and Schlesinger (1985) because these definitions were meant initially to characterize only plants or primary producers. Under these definitions, rapid external recycling causes a decline of plant nutrient use efficiency, because it increases the denominator, the uptake or loss of nutrient element. A definition of nutrient use efficiency for the ecosystem, on the other hand, must include the enhanced use efficiency made possible by all the cycle types (Fig. 2). A simple ratio of annual ecosystem production (gross or net) to the concentration of nutrient element existing in plant or total biomass, or total organic matter, are alternatives for an index of ecosystem nutrient use efficiency.

Ecosystem nutrient use efficiency, defined as the ratio of system production to nutrient content, is closely related to Margalef's (1968) index of successional "maturity", the ratio of biomass to primary production (units of time), based on ecosystem energy processing. Maturity is an estimate of the residence time of carbon or energy fixed in organic matter; ecosystem nutrient use efficiency (units of inverse time) is an estimate of the turnover rate of nutrients. They are actual inverses if the amount of nutrient required for a unit of carbon fixation (primary production) is equal to the amount of nutrient per unit biomass carbon. If production is measured over a fixed time interval both efficiency indices are unitless ratios. Just as Margalef (1968) used "maturity" to compare the successional status of two ecosystems, ecosystem nutrient use efficiency may also be used to describe and compare spatial and temporal characteristics of different nutrient elements during succession (Lee unpublished manuscript).

Changes during primary succession in nutrient use efficiency of two hypothetical essential elements, A and B, which can be obtained, respectively, with ease and difficulty by biological components, are compared in Fig. 5. For instance, N and P in highly weathered soils can be so categorized. It is assumed that A is incorporated into biomass relatively rapidly and reaches steady state earlier than B, and that ecosystem production is largely controlled by the element that is relatively most inaccessible or unavailable. The result is shown in Fig. 5a, where organic elements A and B and annual ecosystem gross production are standardized to their steady state values.

An index of ecosystem nutrient use efficiency can then be defined as annual gross ecosystem production per unit of nutrient element in organic form. A standardized nutrient use efficiency is calculated by dividing gross production by the value of each element at a given time, resulting in curves A and B of Fig. 5b. These suggest that during developing stages of ecosystems both elements are largely assimilated into organic form and thus ecosystem nutrient use efficiencies for these two elements decrease. Nevertheless, the incorporation rate is different due to different availability in soils. Because ecosystem production is largely dependent on B, its use efficiency is less variable than A. Use efficiency of B reaches its nadir after that of A, due to the relatively slower accumulation of B in organic form (Lee unpublished manuscript).

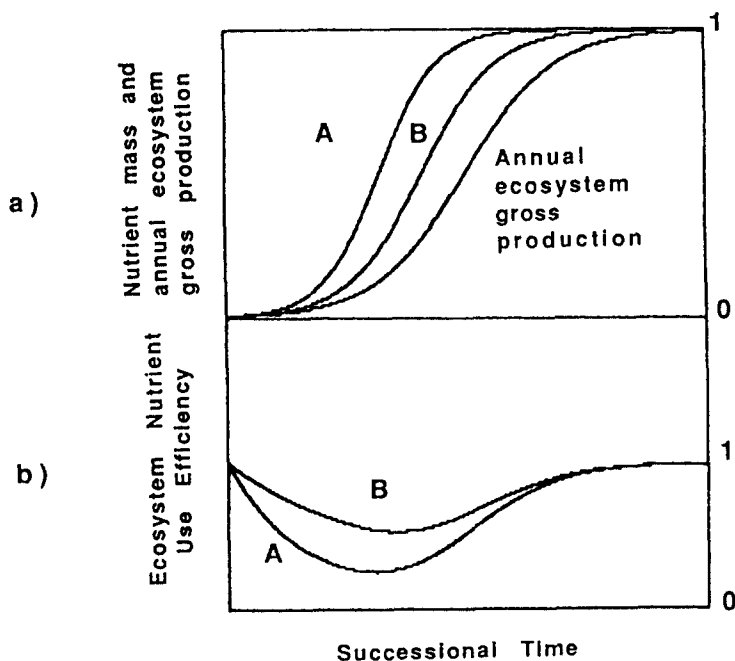


Fig. 5. Hypothetical model of ecological succession showing variations in a) element mass in organic forms and annual ecosystem gross production; b) the ecosystem nutrient use efficiencies of elements relatively (A) easy and (B) hard to obtain by biological processes. Note that the curves are standardized to steady-state values.

Ecosystem nutrient use efficiency may increase during later successional stages because further production is possible after accumulation of both elements in organic matter reaches steady state. It will, however, level off because ecosystem production is limited eventually by light availability, or by other constraints such as those discussed above. For each nutrient element, the point at which ecosystem nutrient use efficiency is at minimum (Fig. 5b) occurs when positive feedbacks enhancing nutrient availability via detrital processes are constrained by positive feedbacks decreasing nutrient availability. After this point, the latter processes dominate, leading to increases in ecosystem nutrient use efficiency.

Relative contributions of alternative cycle types to nutrient use efficiency will depend on plant species and nutrient status. Conservative species may have advantages in nutrient-deficient areas, e. g., evergreens (Monk, 1966). It is hypothesized that cycles IV, V, and VI of Fig. 2 are active in ecosystems where availability of nutrient elements is unbalanced with biotic requirements, especially during earlier stages of succession. The questions arise, how ecosystems overcome unbalanced ratios of available nutrient elements and how organic matter influences nutrient ratios during successional time?

The quality of organic matter, which can be indexed by ratios of organic carbon to nutrient elements, also alters nutrient resource ratios by influencing solubilization rate and availability of phosphate compounds, nitrogen fixation, and other transformations, e.g., mineralization, nitrification, denitrification. Altered nutrient resource ratios, in turn, affect rates of succession. Because nitrogen-fixers require much available phosphorus, organic matter additions may accelerate accumulation of organic nitrogen in terrestrial ecosystems. Little attention has been paid to the effects of organic matter on nitrogen fixation through sulfur chemistry, although enzymes catalyze nitrogen-fixation. Sulfur is an essential element of enzymes, so nitrogen fixation should be mediated through its chemistry. Turner *et al.* (1979) reported that nitrogen fertilization led to increasing requirement of sulfur in Douglas-fir forests, in Washington and Oregon. Binkley *et al.* (1984) demonstrates that addition of Sitka Alder to Douglas-fir forest near British Columbia caused higher foliar nitrogen content, but induced potential phosphorus and sulfur deficiencies, as indicated by reducing foliar concentrations of those elements.

These examples suggest that dynamics of nitrogen, sulfur, and most probably other nutrient elements in ecosystem are coupled. Once an ecosystem's components retain an abundance of one nutrient element for metabolic needs, they may encounter limitation by another element due to these couplings: this is perhaps an extension of Leibig's Law of the Minimum to ecosystems. It follows that ecosystems should possess mechanisms to overcome each new limitation, either as traits of components or through their interactions. In this context, detrital plant residues can be seen as a significant site of nitrogen fixation in forest ecosystems, since nitrogen fixers can extract the necessary energy and nutrients from organic materials, the surrounding atmosphere, and soil (Cornaby and Waide, 1973; Roskoski, 1980; Silvester *et al.*, 1982; Harmon *et al.*, 1986). It is hypothesized that

ecosystems will succeed toward stabilization of nutrient ratios through exchange of excesses between components.

During developing stages of ecosystems, nutrient elements are intensively incorporated into biomass so nutrients may be in short supply with only recycling of organic matter. In this case, the positive feedbacks discussed previously are obviously important to overcome shortages by taking advantage of atmospheric and soil element sources. As there is usually a shortage of available phosphorus, the chemistry of aluminum, iron, and calcium cannot be neglected. These elements are major factors controlling phosphorus availability in soil systems. In alkaline soils, where calcium phosphate is the major phosphorus source and sink, increasing size and turnover rate of the easily available phosphorus pool are initiated as organic matter dissociates calcium from major phosphorus compounds. In acid soils, most phosphorus is fixed by aluminum and iron, which are in turn bound by organic matter resulting in increased phosphorus availability. Accumulation of other organic elements also depends on phosphorus availability (Walker and Adams, 1985; Walker and Syers, 1976).

In general, nitrogen-fixing organisms often initiate succession by providing substantial amounts of nitrogen. Since substantial phosphorus-associated processes govern nitrogen fixation, nitrogen-fixers should use phosphorus efficiently (Vitousek and Walker 1987). On the other hand, early successional stages are frequently colonized by organisms that are not associated with nitrogen-fixation (Grubb, 1986; Walker *et al.*, 1986). Tilman (1986) demonstrated that these early successional species are largely dependent on their ability to compete for available soil nitrogen. Despite the lack of generalizations about early colonizers during succession, there have been no attempts to identify major controlling factors.

Predictions about the plant species dominating an ecosystem at any point during succession or about the evolutionary fitness of different plant traits resulting in different cycle types depend on the perspective one takes on nutrient use efficiency. Looking at plant nutrient use efficiency, one might predict that the most efficient plants will outcompete inefficient forms under limiting conditions, resulting in a predominance of Cycles II and III. But, even if plants are able to capture and internally recycle nutrients, the increasingly lower nutrient concentrations in soils should suppress recruitment locally. This trait will thus only enhance the fitness of plants with effective dispersal mechanisms.

Different predictions are suggested when ecosystem nutrient use efficiency is considered. Plants that are less efficient internally or less conservative may outcompete more efficient nutrient users by enhancing the flow of energy and nutrients through other ecosystem components, resulting in Type IV, V and VI cycles. These other components perform work on the environment that can result in increased stability and size of nutrient supplies and subsequently, plant productivity and local population recruitment and growth. Ecosystems with high nutrient use efficiency might therefore be more resistant than less efficient ecosystems to perturbations which can move the ecosystem to different and per-

haps earlier successional states.

Other questions remain to be answered, such as how do early successional species that are unable to fix nitrogen meet nitrogen requirements; how do nitrogen-fixers metabolize phosphorus; do they have mechanisms to promote external supplies or enhance internal use efficiency? While these are being empirically addressed, we must continue to improve the theoretical basis for understanding complex interactions among ecosystem components.

CONCLUSIONS

Several alternative nutrient-element cycles were illustrated with a focus on plants, the dominant terrestrial primary producer. Through these alternative cycles, plants control their internal nutritional status and determine partially nutrient concentrations in their environment. Internal metabolic reuse of a nutrient element enhances the nutrient use efficiency of plants and conserves the nutrient within plants, but does not improve environmental nutrient availability.

Partial or temporary losses of organic matter may benefit plants through several positive feedbacks. Losses to herbivory and detritus may increase the concentration of nutrients, at least during early stages of succession. Even if the positive feedbacks discussed here are not the main cause of herbivory and detritus production, rather fortuitously beneficial indirect effects, these traits could be adaptive for terrestrial plants otherwise unable to reduce energy and nutrient losses. Contribution of organic matter by plants can, however, promote nutrient retention and availability in soils during succession and maintain it during steady state (climax).

By considering alternative cycles and potential positive feedbacks, an index of ecosystem nutrient use efficiency was suggested: annual gross ecosystem production per unit of nutrient element in organic form. Temporal trends during ecosystem development can be measured and compared using this ecosystem-level variable. Ecosystem nutrient use efficiency may decline during early phases of succession when the rate of organic carbon fixation. Later, it may increase until the system reaches steady state, as gross production is enhanced by increasing nutrient availability.

적 요

육상식물을 중심으로 일어나는 영양소 순환경로들을 그 특징에 따라 6 가지로 구분할 수 있다. 식물은 토양특성에 영향을 줌으로써 생물적 비생물적 순환경로에 영향을 주게 된다. 식물은 내부순환과 외부순환을 통하여 자신의 영양상태와 환경에서 영양소 농도를 결정하게 된다. 식물에 의한 영양소 농도 변화와 균근, 영양단계, 부식과정을 매개로 외부순환에 작용하는 유기물질에

의한 농도변화는 열린계에서 양성 퇴적과정에서 유발시켜 토양의 영양소 이용도와 보유능력을 증가시킨다. 식물을 중심으로 일어나는 여러 경로의 영양소 순환을 인식함으로써 생태계 영양소 이용효율이라는 개념을 다음과 같이 제안하게 되었다: 생태계 영양소 이용효율 = 생태계 생산성 / 유기물질의 영양소 농도. 그리하여 일차천이 동안 일어나는 생태계 영양소 이용효율 변화를 예측하는 그래프모형을 제시했다.

ACKNOWLEDGEMENTS

We thank F. B. Golley, B. C. Patten, G. Bataminian, D. L. DeAngelis, and two anonymous Koreans for constructive comments on earlier drafts. D. L. was supported by grants from the National Science Foundation and U.S. Environmental Protection Agency while this paper was prepared.

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(Received December 9, 1992)