Nutrient Use Efficiency and the Management of Degraded Lands

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ABSTRACT

Soil fertility is frequently a limitation to sustainable agriculture and restoration of forests on degraded lands, especially in developing tropical countries. Nutrient use efficiency, which is a an indicator of the effectiveness with which essential elements facilitate productivity, has broad applicability to this problem. A concept that is useful across scales ranging from single leaves to whole plant communities, nutrient use efficiency has been assessed more than a dozen ways, using at least twice that many variables. Despite the variation in method of calculation and underlying assumptions, many indices of nutrient use efficiency share properties across scales of time and size. Thus, they offer promise of cross-scale linkages among them that will be important to land managers. High efficiency of nutrient use can be achieved many ways, ranging from genetic selection for leaf biochemistry that leads to high photosynthetic output, to assembly of communities of plants that fully exploit the soil. By keeping nutrient efficiency high among the criteria for ecosystem design, it should be possible to develop sustainable land use systems that require only enough fertilizer to replace amounts removed in harvest and to restore forests on degraded lands so that they again yield goods and services useful to people.

Key Words : Agriculture, Agroforestry, Fertilizer, Limiting factors, Nitrogen, Nutrient use efficiency, Restoration, Scale, Tropics.

INTRODUCTION

People who have been marginalized economically are forced into environments that have limited agricultural potential. All too often the result is deforestation for non-sustainable agriculture, to be succeeded by more of the same on the next hectare a few years later (Leonard 1989, Ramakrishnan 1992b). In this way, human poverty leads to ecological impoverishment.

How to stop this inexorable trend? One way is to improve the well-being of the rural peoples who are obligated to destroy natural ecosystems in order to earn a livelihood. The design of agro-ecosystems that are economically, socially, politically, and ecologically sustainable is a potent force for conservation. It is, in fact, the only way that society can accommodate growth while conserving its natural heritage.

There is substantial evidence that imitation of forest structure in the design of land use systems can impart desirable ecological traits such as high productivity, resistance and resilience to pest attack, and maintenance of soil fertility (Gliessman et al. 1981, Ewel 1986, Altieri 1995, Ramakrishnan 1992a). The disadvantage of such systems is horti-cultural complexity, making management and marketing arduous tasks. The solution to the design of sustainable land use systems for the humid tropics probably lies somewhere between the unmanageable high diversity of the tropical forest and the dangerous simplicity of annual-crop monocultures.

The fact that vast areas of tropical forest have already been destroyed, coupled with needs for land on which to practice agriculture, signals a tremendous need for restoration. In some cases the goal of restoration should be re-construction of a close facsimile of the original ecosystem – essentially a conservation-based objective; in others the target might be an ecosystem that bears structural resemblance to the original but consists of species useful to people – a sustainable-land-use objective. The two objectives are complementary, for well-conserved natural ecosystems provide the water and soil resources needed by farmers, just as sustainable agro-ecosystems alleviate pressures on natural ecosystems.

One important limitation to sustainable agriculture is the cost of fertilizer. Nutrients removed during crop harvest must be replenished, and the only natural sources are weathering of parent materials, atmospheric deposition as rainfall and dust, and, on flood plains, water-borne deposits. If the amounts removed in harvest exceed the sum of those three sources, then farming is tantamount to nutrient mining; the end result is impoverishment of soil and, ultimately, degraded lands that sustain neither people nor forests.

Nutrient use efficiency is a measure of productivity per unit of nutrient available. Just as the label implies, it is a measure of the efficiency with which elements essential for growth are deployed in plants. The concept is useful at several scales, ranging from single leaves to whole plants to entire plant communities. Although it is most widely used in ecological studies, it is our contention that the concept has equal applicability and, more importantly, utility in agro-ecosystems. Agronomists have long recognized genetic differences in nutrient use efficiency between species, and indeed between cultivars of the same species (Marschner 1995). They have exploited these differences in breeding cultivars that would tolerate deficiencies, particularly of micronutrients, on problem soils (Brown and Jones 1977), and to select for cultivars with a high uptake efficiency in order to better utilize applied fertilizer in intensive cropping systems (Schenk and Barber 1979, Mengel 1983). There is now a growing awareness of the need to select for cultivars that would have a high efficiency of nutrient uptake and use even under low-input conditions (Gabelman and Gerloff 1983, Dambroth and El Bassam 1990, Sauerbeck and Helal 1990). Farmers who are able to manage plant nutrients in ways that are conservative, effective, and efficient have a greater likelihood of sustaining their efforts than those whose use of limiting nutrients is wasteful, ineffective, and

inefficient. The applicability of nutrient use efficiency may be of greatest value in tropical countries, where manufactured fertilizers are disproportionately expensive and where degraded lands are often the starting point for agricultural development.

NUTRIENT USE EFFICIENCY

The efficiency with which elements essential for growth are deployed in plants can, in the simplest sense, be expressed as the ratio of plant biomass to plant nutrient content (Chapin and Van Cleve 1989). This is equivalent to the inverse of plant nutrient concentration. In the case of perennials, however, this measure is complicated by tissue and nutrient losses over a plant's lifetime due to leaf abscission, herbivory, and foliar leaching. Nutrient use efficiency estimated in this manner neglects nutrients that are taken up and used to produce biomass but are subsequently lost, due either to leaching from foliage or to leaf abscission, thereby *over-estimating* nutrient use efficiency. Conversely, this measure disregards the proportion of nutrients in the plant that comes from internal recycling, for instance due to resorption at the time of leaf abscission, thereby *under-estimating* nutrient use efficiency. In perennials, therefore, resource utility, which is the ratio of the total rate of biomass production to the total rate of nutrient uptake, is a better measure of nutrient use efficiency (Hirose 1975). Total nutrient uptake can be determined by adjusting net uptake (measured as nutrient content at the time of sampling) for nutrient resorption and nutrient losses via litterfall and foliar leaching.

Historically, numerous indices have been used to estimate plant nutrient use efficiency (Table 1). These range from estimates at the individual leaf level to estimates at the level of the whole community. In addition, the indices encompass a range of time scales, from instantaneous measures to measures that integrate across processes occurring over many years. Direct comparisons among the indices are precluded because determinations of productivity and nutrient availability vary greatly. Taking the plant-level indices as an example, productivity is estimated variously as total plant biomass (Chapin 1980, Shaver and Melillo 1984), annual foliage production (Ågren 1983), and wood and leaf mass produced (Boerner 1984). Similarly, taking the community-level indices as an example, nutrients available for biomass production are estimated as the total amount of nutrients lost from plants or the rate at which they are stored within plants (which is equivalent to nutrient uptake; Vitousek 1982, Waring and Schlesinger 1985), annual nutrient return to the soil (Gray 1983), and nutrients available to plants from resorption and mineralization (Lennon et al. 1985).

What, then, are appropriate measures of nutrient use efficiency at several scales that would allow a comparison of parallel physiological and ecological processes occurring at these scales? We suggest that nutrient use efficiency be measured as the ratio of total productivity to total nutrients available for achieving that productivity. Thus, at the leaf level, nutrient use efficiency is the potential maximum photosynthetic rate for a certain leaf nutrient content (Field and Mooney 1986); at the plant level nutrient use efficiency is the ratio of biomass produced to total nutrients taken up (Hirose 1975); and at the community level nutrient use efficiency is the ratio of total biomass production to total nutrients available for uptake from the soil.

Table 1. Indices of nutrient use efficiency at various scales. Adapted and modified from Grubb (1989).

Measurement Scale	Index	Definition	References
Leaf	Photosynthetic production	saturation net photosynthetic rate × leaf duration × nitrogen retention fraction	Small (1972)
	Potential photosynthetic nutrient use efficiency	$\dfrac{\text{maximum photosynthetic rate}}{\text{foliar nutrient content}}$	Field and Mooney (1986)
Plant	Resource Utility	$\dfrac{\text{net dry matter production}}{\text{amount of resource absorbed}}$	Hirose (19750
	Nutrient use efficiency	$\dfrac{1}{\text{tissue nutrient concentration}}$	Chapin (1980)
	Nitrogen productivity	$\dfrac{\text{annual yield of foliage}}{\text{unit of nitrogen in the foliage}}$	Agren (1983)
	Nitrogen and phosphorus growth efficiency	$\dfrac{\text{wood and leaf mass produced}}{\text{nitrogen or phosphorus lost in litterfall}}$	Boerner (1984)
	Uptake efficiency	$\dfrac{\text{increase in plant N or P mass}}{\text{N or P mass available}}$	Shaver and Melillo (1984)
	Recovery efficiency	$\dfrac{\text{(N or P mass per unit area mature leaves)} - \text{(N or P mass per unit area of dead leaves)}}{\text{(N or P mass per unit area of mature leaves)}}$	Shaver and Melillo (1984)

	Use efficiency	$\dfrac{\text{plant biomass}}{\text{plant N or P mass}}$	Shaver and Melillo (1984)
	Nitrogen use efficiency	nitrogen productivity × mean residence time of nitrogen in the plant	Berendse and Aerts (1987)
Community	Litterfall nutrient use efficiency	$\dfrac{\text{total biomass lost from plants or stored within plants}}{\text{total nutrients lost from plants or stored within plants}}$	Vitousek (1982)
	Nutrient use efficiency quotient	$\dfrac{\text{annual canopy production of dry matter}}{\text{annual nutrient return to the soil}}$	Gray (1983)
	Production efficiency	$\dfrac{\text{aboveground biomass production}}{\text{nutirent uptake}}$	Waring and Schlesinger (1985)
	Nitrogen use efficiency	$\dfrac{\text{aboveground biomass production}}{\text{nutirent available (resorption and mineralization)}}$	Lennon et al. (1985)

Leaf Nutrient Use Efficiency

The potential maximum photosynthetic rate attainable for a given leaf nutrient content is a measure of nutrient use efficiency at the leaf level. Potential maximum photosynthetic rate increases linearly with leaf nutrient content (Field and Mooney 1986). The large interspecific variation in the potential maximum photosynthetic rate for a certain leaf nutrient content could arise from differences in the partitioning of nitrogen into RuBP carboxylase and thylakoid proteins – the explanation being that it may not always be necessary to maximize photosynthetic capacity for a given leaf nutrient content (e.g., plants in low irradiance environments; Evans 1989).

High maximum photosynthetic rates have been associated with short leaf life spans (Reich et al. 1992). Rapid leaf turnover is necessary to avoid self shading and to maintain high photosynthetic rates (Field 1983, Field and Mooney 1986, Schmid and Bazzaz 1994). On the other hand, greater leaf longevity may compensate for low rates of maximum photosynthesis, by leading to high cumulative carbon gain per unit of leaf nutrient over the life span of a leaf (see Chabot and Hicks 1982).

Plant Nutrient Use Efficiency

Nutrient use efficiency at the plant level is the ratio of total biomass production to total nutrient uptake (Hirose 1975). This depends on the efficiency with which plants use nutrients that they have taken up and the efficiency with which nutrients taken up are conserved within the plant. A more formal statement of this idea is provided by Berendse and Aerts (1987), who propose that nutrient use efficiency be considered as the product of nutrient productivity and mean residence time of nutrients in the plant. Nutrient productivity is biomass produced per unit nutrient per unit time. Mean residence time is related to longevity – whether of the plant as a whole, or of a particular plant part – and to the efficiency with which nutrients are retained in the plant at the time of tissue abscission (Shaver and Melillo 1984, Birk and Vitousek 1986).

There may be evolutionary tradeoffs between selection for traits that lead to higher nutrient productivity and those that lead to longer nutrient residence times (Aerts 1990). Thus, the same nutrient use efficiency may be achieved in more than one manner. It has been suggested that high fertility environments select for higher nutrient productivity (Aerts 1990); in low fertility environments, in contrast, longer mean residence times may be of greater advantage, even though plants with higher nutrient productivity show more rapid initial growth (Aerts and van der Peijl 1993).

Community-level Nutrient Use Efficiency

The most commonly used index of community-level, or ecosystem, nutrient use efficiency is the ratio of litterfall mass to litterfall nutrient content (Vitousek 1982), which assumes that litterfall mass is equivalent to net productivity and litterfall nutrient content reflects net uptake. This measure has been related to the tightness with which nutrients are cycled through the system (Vitousek 1984), the suggestion being that a larger ratio of litterfall mass to litterfall nutrient content causes more conservative nutrient use and less potential loss from the system (e.g., by leaching). Comparisons

between ecosystems using this index have shown a tendency for greater efficiency in the use of nutrients that are less available for plant uptake (Vitousek 1982, 1984, Cuevas and Medina 1986, Silver 1994, Bridgham et al. 1995).

A disadvantage of this measure is that it neither accounts for nutrient losses via canopy leaching, nor considers differences in proportional allocation to leaf and stem tissue under varying conditions of nutrient availability (Grubb 1989). Species' differences in root-shoot allocation are also neglected by this measure (Aerts and Caluwe 1994). As an alternative, community-level nutrient use efficiency can be characterized as the ratio of total biomass production to total nutrient supply. This depends on the efficiency with which the individual species comprising the community use nutrients that they take up, and the efficiency with which the community as a whole takes up available nutrients from the soil.

CROSS-SCALE LINKAGES IN NUTRIENT USE EFFICIENCY

Are there linkages between nutrient use efficiency at several scales? It has been suggested (Holling 1992) that ecological systems are characterized by hierarchies of organization governed by processes operating at distinct spatial and temporal scales – in particular, that processes at higher scales operate independently of those at smaller scales. Others contend that physiological processes operating at the scale of the organism feed into larger scale processes such as biogeochemical cycling (Field and Ehleringer 1993), and that bottom-up scaling is necessary to understand the mechanisms controlling processes at higher scales (Dawson and Chapin 1993). To a great extent, nutrient use efficiency at the leaf, plant, and community scales is a function of processes operating at those scales (Figure 1). But, as we illustrate below, there also may be linkages between nutrient use efficiency at several scales.
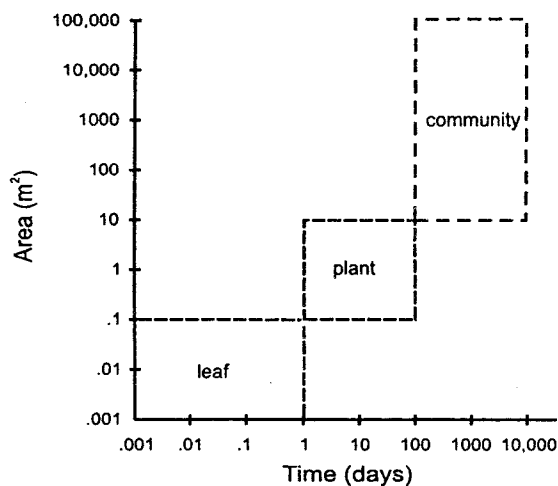

Figure 1. Cross-scale relationships in nutrient use efficiency at the level of the leaf, the plant, and the plant community.

From Leaf to Plant

Photosynthetic nutrient use efficiency was defined earlier as the potential maximum photosynthetic rate that could be achieved for a certain leaf nutrient content. This measure by no means scales directly to nutrient productivity at the level of the whole plant. The factors affecting photosynthetic rate vary continuously, and there are changes in photo-synthetic capacity over a leaf's lifetime (Field and Mooney 1983, Harrington et al. 1989, Ackerly and Bazzaz 1995). In addition, patterns of allocating photosynthate vary from species to species, and this affects whole plant carbon gain. For a given photo-synthetic production, a plant that invests proportionally more photosynthate (consequently nutrients) in leaf tissue is likely to have greater carbon return per unit nutrient invested at the whole plant level than one that invests more photosynthate in root tissue (Bloom et al. 1985, Chapin et al. 1987). Nonetheless, the maximum photosynthesis that can be achieved per unit of nutrient in a leaf, in conjunction with the life span of that leaf, serves as an indicator of the potential efficiency with which nutrients invested in leaves are used for biomass production (see Small 1972, Harrington et al. 1989).

Leaf characteristics, in addition to being linked with nutrient productivity at the plant level, can have a bearing on nutrient retention within plants. Long-lived leaves are associated with reduced rates of nutrient losses from plants (Escudero et al. 1992, Aerts 1995), a proposed explanation for the dominance of evergreens in low fertility environments (Aerts 1995). Greater within-plant nutrient retention may also be achieved by more efficient nutrient resorption at the time of leaf abscission (Shaver and Melillo 1984, Birk and Vitousek 1986). There is some evidence for more efficient resorption in nutrient-poor habitats (Miller et al. 1976, Turner 1977, Boerner 1984, Vera and Cavelier 1994), although the evidence is confounded by there being species differences between habitats; there is some evidence for the opposite phenomenon as well (Lennon et al. 1985, Birk and Vitousek 1986, Chapin and Moilanen 1991, Nambiar and Fife 1991).

From Plant to Community

Nutrient use efficiency at the community level – the ratio of total biomass production to total nutrient supplied by the soil – is really a composite of two indices, the efficiency with which nutrients taken up by the component species are utilized for biomass production, and the efficiency with which available nutrients are taken up, and are thereby prevented from being leached from the system (see also Bridgham et al. 1995):

$$\frac{\text{Biomass Production}}{\text{Nutrient Supply}} = \frac{\text{Biomass Production}}{\text{Nutrient Uptake}} \times \frac{\text{Nutrient Uptake}}{\text{Nutrient Supply}}$$

It follows that increased community-level nutrient use efficiency is possible under one of three scenarios (or some combination of the three). First, if the component species have high plant-level nutrient use efficiencies (i.e., large amount of biomass produced per unit of nutrient taken up), then the ratio of total biomass production to total nutrient uptake by the community would be greater than by a community of species with low nutrient use efficiencies. This, then, would be a direct relationship between nutrient use efficiency at the plant and community scales.

A second way in which high community-level nutrient use efficiency could be achieved is if the community as a whole had a high nutrient uptake efficiency. The ability of plants to take up available nutrients depends on root architecture and the extent to which roots explore the soil volume (Caldwell and Richards 1986). In addition, a mixture of species may have greater resource uptake than a species grown alone if (i) species are temporally separated in their peak demand for resources (Rao 1986, Fukai and Trenbath 1993), (ii) there is spatial separation in species' root systems (Huck 1983), and (iii) species take up resources in different proportions (e.g., mixtures of legumes and non-legumes; Martin and Snaydon 1982).

The third possible situation under which there can be higher community-level nutrient use efficiency is if high productivity is achieved in spite of decreased nutrient availability. This could occur in communities comprising species that resorb a large propor-tion of nutrients before leaf abscission, or in communities comprising species with long-lived leaves. High within-plant nutrient retention leads to poor quality litter and therefore low rates of decomposition and nutrient supply (Schlesinger 1991). Greater leaf longevity has been related to low rates of litter decomposition (Gower and Son 1992). Long-lived leaves tend to be sclerophyllous, possibly to provide greater protection over an individual leaf's life span (Turner 1994). Such leaves make tough litter that breaks down slowly, leading to reduced rates of nutrient supply (Aber and Melillo 1982, Melillo et al. 1982).

Thus, nutrient use efficiency at the leaf, plant, and community scales may be subject to variation in factors operating independently of one another. For instance, leaf nutrient use efficiency may change from minute-to-minute as light and humidity vary, without that having any bearing on growth and productivity at the plant and community levels, respectively. Similarly, seasonal variation in temperature and rainfall may influence rates of litter breakdown, consequently soil nutrient supply, but have little direct effect on leaf nutrient use efficiency. Nevertheless, there should be linkages between nutrient use efficiency across scales, as we have discussed. A better understanding of these linkages would enable us to manage for a high efficiency of nutrient use at several scales.

MANAGING NUTRIENT USE EFFICIENCY

The land manager might strive for several objectives regarding nutrient use efficiency. First and foremost, there are the benefits to be derived from having high primary productivity per unit of nutrient available. As illustrated above, this can be achieved at scales as small as a leaf and as large as an ecosystem. The important point is that conversion efficiency must be kept in mind at all levels of endeavor. This includes selection and manipulation of genotypes (including breeding programs), choice of species, and the spatial and temporal configuration of species in communities.

In addition to high efficiency of conversion, the manager is concerned with retention of those nutrients that are available, and here again the issue can be addressed at various scales: leaf, plant, community. There is evidence that high within-plant retention is related to high within-system retention (Hobbie 1992, Aerts 1995, van Breemen 1995), so management practices that enhance one aspect are likely to reinforce the other.

High efficiency of conversion, when coupled with effective nutrient retention, alleviates risk of nutrient loss (Vitousek 1984). Risk avoidance is a critical aspect of sustainable land use, especially on marginal lands, and the concept pertains as much to unforeseen loss of soil fertility as it does to crop failure (Alcorn 1984, Clawson 1985). The goal of minimum dependency upon subsidies of fossil-fuel derived fertilizers can only be approached by keeping nutrient use efficiency and nutrient retention firmly in mind when managing agro-ecosystems. In combination these factors lower the risk of soil degradation and, if successfully deployed, they not only sustain fertility but lead to enhancement of site quality.

Efficiency of Uptake

How can the farmer or manager take good advantage of these concepts? One tactic is to use plants with high uptake efficiency. This in fact is the approach that has led to dramatic increases in grain production in recent decades, as plant breeders produced genotypes capable of taking up (and using) large quantities of limiting nutrients, particularly nitrogen. The danger of focusing on high uptake efficiency in a plant breeding program is that productivity is then dependent upon a large supply of nutrient to be taken up, so land use systems that depend upon such plants are extremely vulnerable to nutrient shortages and fertilizer costs.

But high uptake efficiency need not necessarily equate to a requirement for a vast supply, and many traditional cultivars are efficient at uptake of nutrients from relatively nutrient-poor soils. Such plants often achieve efficient uptake by having a root system that thoroughly exploits a large volume of soil. It is the overall architecture of the root system that makes exploitation of deep soil and distant nutrient hot-spots possible, particularly of highly mobile nutrients such as inorganic nitrogen. Uptake efficiency is further enhanced by mycorrhizae. The roots of almost all tropical plants are symbiotic with fungi, and the root-fungus symbiosis, the mycorrhizae, facilitate the thorough exploitation of soil aggregates, which is imperative for the effective exploitation of immobile nutrients such as phosphorus (Alexander 1989, Bolan 1991).

Efficiency of Use

Another strategy, one that is certainly not in conflict with the first, is to use plants having high nutrient use efficiency. For example, by selecting species having long-lived leaves that are effective at resorbing nutrients as they senesce, the manager gains some insurance against loss (Vitousek 1984, Hobbie 1992, Aerts 1995). Gains that are even more direct are achieved when species that take up different chemical species of the same element, such as nitrate or ammonium (e.g., Fredeen and Field 1992), are combined in polyculture.

Substantial benefit is to be gained by combining plants that partition nutrient uptake spatially or temporally. Nevertheless, the determination of spatial partitioning of below-ground resource use is fraught with pitfalls. For example, the observation that the root systems of two plant species growing together occupy different soil strata is not convincing evidence of partitioning because the spatial separation may have been induced by competition between the two species. Such observations do not constitute

evidence that one species, if given the site to itself, would not have exploited the soil as completely as the two-species combination.

Temporal partitioning tends to be more straightforward. This is accomplished by combining plants that differ in phenology, such that uptake by at least one component occurs at all times: a molecule that is taken up by a plant is a molecule that is protected from loss through leaching. For example, at a site in the humid lowlands of Costa Rica, we found that monocultures of a deciduous tree were extremely susceptible to leaching losses when a dry-season rain storm occurred. Adjacent stands that were under-planted with evergreen monocots, in contrast, lost almost no nutrients during the same storm because of uptake by the fully functional understory (Figure 2).
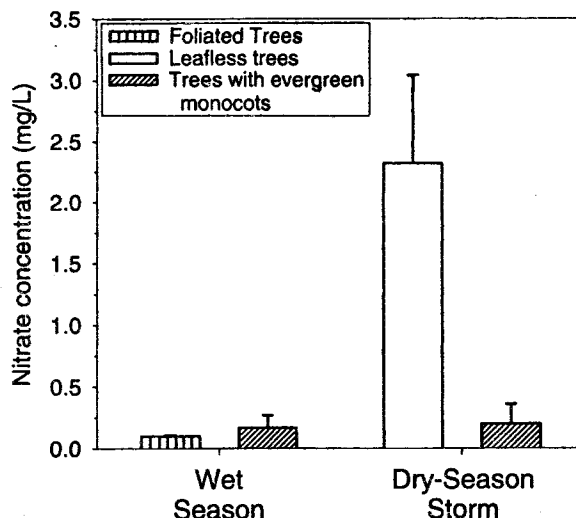

Figure 2. Nitrate in capillary soil water, vulnerable to loss via leaching. During the rainy season, when all plants had leaves, nitrate was taken up by plants and prevented from leaching. During a dry-season rain storm, the evergreen monocots sustained nutrient uptake in polycultures, but losses were extremely high beneath the leafless trees. The tree was *Cedrela odorata* and monocotyledons were a palm (*Euterpe oleracea*) and a giant, perennial herb (*Heliconia imbricata*).

Relay cropping is another tactic by which high efficiency of nutrient use can be achieved. In relay cropping schemes, one species follows another in the same field, the second often being planted before the first senesces. This ensures that ground cover, nutrient uptake, and production are uninterrupted. To achieve maximum retention of nutrients, which is a key to high use efficiency, the manager might employ a sequence of crops that imitates a successional sere, in which annual plants are followed by increasingly long-lived species (Holdridge 1959, Hart 1980, Denevan et al. 1984, Subler 1993). Permanence is a strong guarantee of nutrient retention, and it is when sites are bared following harvest that soil nutrients are most vulnerable to loss through erosion and leaching.

Still another pathway to the sound management of nutrient use efficiency involves manipulation of nutrient interactions. Sometimes this can be achieved by selection of species to fulfill a certain need. For example, many trees that are symbiotic with nitrogen-fixing microbes have low nitrogen use efficiency, presumably because the symbiont provides them with adequate amounts. As a result, they tend to be ineffective at nitrogen resorption, and large quantities of this crucial nutrient are dropped to the soil surface when leaves abscise. Some of this discarded nitrogen may be taken up by the nitrogen-fixing tree itself, but some of it enhances decomposition (which is often a nitrogen-limited process), and some of it is taken up by other species in the community. In this way a relatively low nitrogen use efficiency by one species can enhance nitrogen use efficiency (and productivity) of the whole ecosystem (Binkley et al. 1992).

Nitrogen fixation is not the only way that use efficiency of a limiting nutrient can be enhanced. Despite the fact that independence from fertilizers is an important and laudable management objective, there are situations when a modest amount of judiciously chosen fertilizer is exactly what is needed. A classic example is the priming effect of nitrogen on nitrogen fixation (McConnell and Bond 1957, Russell 1973). Fixation rates are very low on sites with abundant nitrogen, but they are equally low on sites with almost no nitrogen, and it is modest additions of nitrogen fertilizer to the latter that can launch the process, often obviating the need for further additions. This strategy is not restricted to additions of nitrogen. It has been demonstrated, for example, that where an imbalance in nutrient availability exists due to a critically low amount of a particular element, additions of that most-limiting nutrient can lead to greater overall use efficiency (de Wit 1992, Crews 1993).

Benefits and Pitfalls

By managing for efficient uptake and use of nutrients, several objectives can be reached. One of these, mentioned above, is reduced dependency on (but not complete freedom from) fossil-fuel-derived nutrient subsidies. This comes about for two reasons. First, there is the inherently greater capability of some species to use nutrients more efficiently than others. Where marginal lands are involved, whether for low-input agriculture or for ecosystem restoration, such plants are the logical choice, and they should be identified and used preferentially. In addition to the immediate benefits to be derived from the growth and productivity of efficient plants themselves, there are added benefits, most notably the buildup of soil organic matter. Soil organic matter has many well documented attributes of ecological and agronomic benefit, one of which is that it constitutes a reservoir of nutrients itself (Sanchez 1976, Jordan 1985). Some of those nutrients are chemical constituents of the mineralizable compounds of which the organic matter is composed, while others are bound to electrostatic exchange surfaces. Both of these organic sources of nutrients can serve as important buffers against nutrient shortage, and as such they play an important role in risk aversion (Tiessen et al. 1994).

An ancillary benefit of constructing ecosystems characterized by high nutrient use efficiency may be resistance to herbivore attack. Leaf longevity and palatability are inversely correlated (Coley 1988, Turner 1994), as long-lived leaves tend to be well defended, chemically and physically, against potential consumers.

Is there a dark side to an emphasis on the use of leaves, plants, and ecosystems exhibiting high nutrient use efficiency? Sadly, there may be, and that concerns a variable of crucial importance to many — agronomic yield. The ultimate in efficiency is zero "waste," a state that can be achieved only with zero output (Odum and Pinkerton 1955, Odum 1995). The key to success is identification of that point at which inputs are compensated by yield: If output is too low, the system, however efficient, is of no interest to the farmer; if inputs are too high the system is likely to be unaffordable.

It is through use of a judicious combination of efficient components coupled with modest but catalytic inputs, that sustainable solutions will be found. The optimum prescription for any site will be unique, but there is no doubt that, on soils that have been degraded through ill-advised human use, it is wise to err on the side of high efficiency. To continue to exploit such soils toward the single goal of high yield is ecologically short-sighted, and the end result can only be further degradation of the resource.

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