NUTRIENT CYCLING IN TROPICAL PASTURES, WITH SPECIAL REFERENCE TO THE NEOTROPICAL SAVANNAS

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ABSTRACT

We summarize the current information on the pathways of nutrient cycling in tropical pastures and identify areas that are poorly understood. Cycling of N appears to be particularly important, with the balance between the processes of litter breakdown, return through faeces and remobilization critical to understanding. Pure grass pastures commonly degrade in the neotropics, but it is not clear what the causes are. It seems likely that a combination of nutrient deficiencies, possibly of both N and P are responsible, although this conclusion is largely based on anecdotal information. Associative biological fixation of N by obligate endophytic bacteria in grasses could be an important source of N in pure grass pastures. It could be a key factor in preventing pasture degradation, but little is known about how it might be managed or enhanced.

KEYWORDS

Tropical pastures, nutrient cycling, pasture degradation, associative BNF, legume BNF, litter decomposition, net primary productivity, N immobilization.

INTRODUCTION

Cycling of nutrients is a key issue in pastures, and is especially important in tropical pastures. For various reasons, mostly economic and political, actual or hidden subsidies have historically encouraged the application of fertilizer to correct soil deficiencies of nutrients in many grassland production systems in temperate regions. In contrast, in the tropics animal production on grasslands is either based on native grasslands to which no fertilizer is applied, or to introduced grasslands to which, with few exceptions, fertilizer applications are either none or very little. Under these circumstances efficient cycling of plant nutrients is critical to the satisfactory performance of the pasture. Nevertheless, tropical pastures can be managed so that nutrients are cycled between soil, plant and animal pools with minimum loss. By balancing nutrient outputs with strategic inputs, productivity can be sustained at chosen levels. Efficient cycling also minimizes both loss by drainage of excess nutrients, which causes environmental pollution, and depletion of the soil resource.

In this paper we try to bring together the current understanding of nutrient cycling in tropical pasture systems and to focus on its role in pasture stability and its converse, pasture degradation. Because most of our experience is in pasture systems in Latin America, and especially in the neotropical savannas, those systems are emphasized.

THE PASTURE SYSTEMS

Native pastures. In much of the tropics, even in those areas where substantial replacement of the native vegetation with pastures or crops has occurred, native pastures are an important grazing resource and will remain so for the foreseeable future (Fisher et al., 1992). In African savannas there has been little replacement, while in Latin America most replacement has occurred in Brazil, about 47 million ha (Mha) of a total of 205 Mha (Vera et al., 1992; Macedo, 1995). Although the absolute areas of savanna are much less in Venezuela (20 Mha), proportionally more of them have been replaced.

Nutrient cycling in the savannas is a critical component of these systems. Because most of the soils are low to very low in nutrients, remobilization and cycling are very tight with little loss through either leaching or to the atmosphere. At the low levels of utilization of most native pasture systems, mainly because of their low nutritional status, loss to and redistribution by exotic grazing animals is minimal.

Introduced grass pastures. The largest amount of native vegetation replaced by introduced pastures in the tropics is in central Brazil. Of the 205 Mha collectively known as the cerrados, 35 Mha have been replaced by introduced grasses in the last 30 yr (Vera et al., 1992). The majority of the replacement has occurred on lands of the *campo limpo* and *campo sujo*, which occupied some 24% of the total area. These communities were either treeless grasslands or grasslands with a few scattered and stunted trees and shrubs. Some 12 Mha have been converted to cropping, but these were generally the more fertile soils of the *campo cerrado*.

Most of the conversion was to pure grass pastures, principally to one species, *Brachiaria decumbens* (derived from the Australian cultivar, Basilisk), although there are smaller areas sown to *B. humidicola*, *B. brizantha* and *Andropogon gayanus*. In the humid tropics, lands that have been cleared from forest after a few crops are invariably either allowed to revert to bush fallow (*barbecho* or *tururco*), or are sown to pasture, frequently *B. humidicola* or occasionally *B. brizantha*.

Grass/legume associations. A good deal of research has been carried out in the last 20 years or so in Latin America, principally by the Centro Internacional de Agricultura Tropical (CIAT) and its collaborators in the National Agricultural Research Services, who comprised the International Network for the Evaluation of Tropical Pastures (*Red Internacional de Evaluación de Pastos Tropicales* RIEPT). A collection of over 20,000 entries was assembled and evaluated for their suitability to the soils and climates of the region (Maass et al., 1997). A portfolio of grasses and legumes was identified for the range of ecological niches in the region (Miles and Lapointe 1992). Emphasis was placed on grasses and legumes to form productive associations. A number of associations of grasses with legumes have been shown in experiments and farmers' fields to be persistent and productive (Toledo et al., 1989; Schultze-Kraft and Clements, 1990; Lascano, 1991; CIAT, 1992; Kerridge and Hardy, 1994; Miles et al., 1996). Despite this, acceptance by farmers in the neotropics of legume-based pasture technology has been minimal.

THE ROLE OF NUTRIENT CYCLING

General characteristics. In grazed pastures, nutrients are taken up by plant roots and channeled to the shoots, which are either consumed by animals or returned to the soil as litter. The excreta of grazing animals are also returned to the soil, so that the grazing animal plays an important role in nutrient cycling. A simplified model of nutrient cycling is shown in Fig. 1. Shoot and root litter and faeces enter the soil pool through the activities of micro-organisms and soil fauna. These in turn die and contribute residues, which are gradually incorporated into the soil humus complex.

The soil component of the cycle includes nutrients in plant-available form, those held in soil organic matter (SOM), and those in chemically "fixed" forms. Nutrient gains to the cycle occur from rainfall, biological nitrogen fixation (BNF) and the addition of fertilizer. Nutrient losses from the cycle occur through removal in animal

products, leaching, and volatilization as nutrients move through different pathways (Wilkinson and Lowrey, 1973; Till, 1981; Thomas, 1992; Rao et al., 1992; Haynes and Williams, 1993; Thomas and Lascano, 1995; Boddey et al., 1996). Losses may also occur through runoff and soil erosion.

The time taken for a nutrient molecule to complete a cycle varies considerably. Transfers involving micro-organisms are measured in hours to days, while acquisition by, and growth of plants is measured in months. Intake and growth of animals is measured in years, while transfers involving the physical environments, e.g. from atmosphere to land and sea and the formation of rocks is measured in thousands or million of years. Thus, the time scale of any nutrient cycle under study must be carefully defined. Any measurement at an instant in time usually neglects some other aspects of the dynamic nature of nutrient cycling (Agboola and Kintomo, 1995).

Soil N, P or C contents must be split into functional pools, and the fluxes between them quantified to assess realistically the degree of nutrient cycling efficiency, to monitor input and output relationships, and to develop nutrient management strategies. There are models available (e.g. Parton et al., 1994), but the methodologies for measuring pool size and the magnitude of fluxes are not well developed or tested (Woomer et al., 1994; Gijsman et al., 1996). If the soil cannot meet the nutrient requirements of the pasture plants, irrespective of whether they come from the primary soil minerals, fertilizer or recycling, or in the case of nitrogen from BNF, plant performance and hence animal production will be reduced. In extreme cases the pasture will degrade and must be recuperated if animal performance is to be restored. Clearly, if no fertilizer is applied, and particularly if the ability of the soil to supply nutrients is limited, then recycling becomes crucially important.

Level of nutrient stress. In many cases, the soil is able to supply many of the macro- and micro-nutrients required by pasture plants as long as the level of animal production is in balance with the ability of the system to support it. Obviously in the case of many native grassland communities, where levels of utilization are low, the combination of recycling and supply of nutrients from the primary soil minerals is sufficient to maintain the system. Moreover, for whatever reason, usually low quality of the herbage, many of these systems are self-protecting, at least at the broader scale, in that exotic grazers will die before the pasture resource is put at risk. When the degree of utilization is increased, as for example in providing nutrient supplements or feed supplements that overcome the primary limitation of the pasture, the system becomes stressed by changing the patterns of recycling. As the stress increases and the patterns of recycling become more and more disturbed, the system becomes potentially more unstable.

Net primary productivity. Net primary productivity (NPP) of tropical pasture systems is as much as 5-10 times higher than commonly supposed (Long et al., 1989; 1992). The reason for this is that in most studies of yield of tropical pastures, including those of the IBP in the 1960's, turnover by senescence and death both in tops and roots was ignored. However, in a series of careful experiments, Long et al. (1989; 1992) estimated losses due to senescence and death in both tops and roots to 15 cm in five contrasting native pasture communities in the tropics (Table 1). Despite this, even they may have underestimated the amount of root turnover by restricting their measurements of roots to 15 cm. It has recently been shown that introduced pastures in the eastern plains of Colombia accumulate substantial amounts of C as SOM, 75-95% of it at depths below 20 cm (Fisher et al., 1994; 1997).

PATHWAYS OF NUTRIENT CYCLING

Nutrient cycling through above-ground litter. The balance of the processes of recycling then is a major issue. Levels of utilization of even introduced pastures in the tropics are commonly low, and rarely more than 30% of NPP above-ground (Fisher et al., 1997). As a consequence there is rarely less than 70% of above-ground NPP recycled through litter.

The decomposition of above-ground litter from tropical forage grasses and legumes has been shown to be very variable and species dependent. Litter half lives range from 26 to over 170 days during the wet season on the Colombian eastern plains (Thomas and Asakawa, 1993). Little or no decomposition occurs during the dry season. Patterns of nutrient release (disappearance of nutrients from litter) also vary with N and P behaving similarly but K disappearing much more rapidly. These and other reported studies are carried out mainly using litter bags over short time scales. There are few reports on the fate of nutrients released from litter in tropical pastures. This is a clear knowledge gap, with important implications for understanding nutrient cycling in tropical pasture-based systems.

Lignin:N, lignin + poylphenol:N and C:N ratios together with rainfall can predict the rate of litter decomposition reasonably well (Palm and Sanchez, 1991; Thomas and Asakawa, 1993). The decomposition sub-model for tropical forages of the CENTURY model also predicts rates of decomposition reasonably well (R.J. Thomas, unpublished data). However, CENTURY appears to require adjustments to the P sub-model for tropical soils low in available P (Gijsman et al., 1996).

Recoveries of ^{15}N from labeled above-ground litter of *B. dictyoneura* and the legumes *Arachis pintoi* and *Centrosema acutifolium* during 92-120 days of regrowth of *B. dictyoneura* under both field and controlled conditions in the glasshouse were only 1-14 % (M. Rondon and R.J. Thomas unpublished data). Total recovery of ^{15}N in both plants and soil ranged from 50-85% in the glasshouse. This implies that, as leaching did not occur, losses of N through volatilization could be important in tropical pastures. There are few reports on N losses by volatilization from pastures of the sub-tropical and tropical zones. Moore (1974) measured losses of 10% of ^{15}N from litter of *Chloris gayana*, possibly as ammonia. Further studies are needed using litters of different quality to determine the extent of gaseous N losses.

These data also imply that recycling of nutrients through plant litter would not be sufficient for further pasture growth. Moreover, it would probably result in immobilization of N as reported by Robbins et al. (1987). To overcome the effects of this potential immobilization and continue to grow at high rates, a pasture would require large inputs from either fertilizer-N or a legume content in the pasture of greater than 30% (estimated from Thomas, 1992). The role of associative BNF to meet this requirement is discussed below.

The reason for low returns of nutrients via litter is the very efficient remobilization of nutrients as the tissues senesce, so that the nutrients acquired from the soil are efficiently used for growth. From an ecological viewpoint, less nutrients cycling through the soil gives the established plants a powerful competitive edge by denying nutrients to potential invaders. Many of the introduced grasses and legumes have strong vegetative reproduction in which nutrients are directly transferred to the daughter plants. It is possible that this is why well-managed pastures of many *Brachiaria* spp have remarkably few invading weeds. It also makes the formulation of grass-legume associations more difficult unless the legumes have characteristics such as superior nutrient-uptake efficiency to compete with

aggressive grasses (Rao et al., 1993).

Nutrient cycling through animal excreta. The proportion of the pasture consumed that is returned as faeces will depend on the digestibility of the material that the grazers consume. Only in exceptional cases in tropical pastures is digestibility more than 65% and more frequently it is as low as 50% or less (Fisher et al., 1996). In the case of native grasslands of low digestibility the proportion of the forage consumed that is returned will be even higher. Animals return 60-90% of the nutrients they consume in the form of faeces and urine (Barrow, 1987; Haynes and Williams, 1993). Moreover, because of their grazing habits and behaviour, grazing animals can cause spatial variability in the concentration of nutrients, e.g. elevated levels around watering points and stock camps.

The effectiveness of nutrients returned in the excreta in stimulating pasture production depends on: (i) the proportion of the pasture affected by excreta; (ii) the rate at which the nutrient was returned; and (iii) the extent of recovery of that nutrient by the pasture. The amount of nutrients returned to the soil in faeces and urine varies widely between farming systems (Haynes and Williams, 1993). Some nutrients such as K are excreted predominantly in urine while others such as P, Ca, Mg, Cu, Zn, Fe and Mn are excreted mainly in faeces. Nitrogen, S, Na, and Cl are excreted in both faeces and urine and the partitioning between them varies depending on the nutrient content of the diet (Barrow, 1987).

Recycling of nutrients from excreta to soil and back to pasture plants occurs where the urine and faeces are deposited (Haynes and Williams, 1993). Faeces and urine of cattle decay three times faster than freshly-fallen litter of *B. decumbens* (Buschbacher, 1987), so that excreta stimulate pasture growth. Although excreta patches may cover only 30-40% of the pasture surface annually, the high nutrient input stimulates plant growth that may represent 70% of the annual pasture production (Saunders, 1984). Moreover, recycled nutrients are returned to small volumes of soil in quantities that generally exceed the immediate requirements of pasture plants. Rates of urine application can be in the vicinity of 100 kg K ha^{-1} and 500 kg N ha^{-1} (Saunders, 1984). Consequently, nutrient losses in the form of leaching and volatilization occur in these small areas of pasture (Haynes and Williams, 1993). These losses are the major reason that maintenance fertilizer applications are required to sustain pasture production.

Cattle fed on diets low in protein (7 to 11%), such as the *Brachiaria* spp., excrete about equal amounts of N in urine and faeces (Boddey et al., 1996). Since N in faeces is largely organic, and only 20-25% is water soluble (Haynes and Williams, 1993), total N losses are much smaller in low-protein pastures. Even at high temperatures in the tropics, N losses from cattle faeces are minor (Boddey et al., 1996). Losses of N from urine under tropical conditions are probably considerably higher (Vallis et al., 1985) than under temperate conditions (Haynes and Williams, 1993). Field experiments conducted in the eastern plains of Colombia, using ^{15}N- labeled cattle urine, indicated a subsequent recovery of urine-N by *B. dictyoneura* plants of only 10% (R.J. Thomas and M. Rondon, unpublished data).

In field studies on *B. decumbens* pastures on the Colombian eastern plains, doubling the stocking rate from 1 to 2 head of cattle ha^{-1} in a rotational grazing experiment doubled the number of faecal pats (R. Santiago, M. Ayarza and I.M. Rao, unpublished data). At 1 head ha^{-1} faeces were deposited more at the sides of the paddock, while they were more evenly distributed at 2 head ha^{-1}, presumably reflecting differences in animal behaviour with stocking rate Dung

beetles increased the individual area of the faecal pats from 310 cm^2 at excretion to 675 cm^2 two weeks later, and incorporated the faeces 20 cm into the soil. In a pasture of *B. decumbens* alone there were an average of 17 dung beetles in each pat, while in a pasture of *B. decumbens* with the legume *C. acutifolium* there were 35, and more of the pasture was covered by the (degraded) pats.

Major nutrient transformations and movements that occur in the urine patch have been documented (Doak, 1952; Hogg, 1981; Steele and Vallis, 1988; Williams et al., 1989). The plant nutrients in urine are either in a form that is immediately available to plants or are rapidly converted into an available form. Immediately after an animal urinates, some of the urine flows down through the soil through the macropores created by plant roots, earthworms and soil cracks. If the urine moves in this way beyond the plant rooting depth then the nutrients it contains are lost from the pasture (Williams et al., 1989).

In contrast to nutrients in urine, nutrients in dung must be physically incorporated into the soil before they become available for plant uptake. Dung can be incorporated into the soil through physical breakdown by soil macrofauna (earthworms and dung beetles), rainfall and the invasion of plant root into the dung material. The release of nutrients from dung has been investigated by Haynes and Williams (1993). They showed that K and Na is released rapidly whereas Ca, Mg and P, which are present in less soluble forms, are released more slowly. Physical degradation of dung pats is the major factor controling nutrient release in moist humid environments. In dryland conditions, leaching of nutrients from pats is the major mechanism of release.

Nutrient cycling through below-ground litter. Roots take up nutrients and water, and their ability to extract available soil resources increases with increasing root length (Davidson, 1978). When plant growth was uninhibited by environmental stresses or plant competition, root systems have been reported to achieve lengths of up to 71 km plant^{-1} (Pavlychenko, 1937). Studies of root dynamics have generally not been included in investigations of nutrient cycling in agroecosystems (Persson, 1990). This is mainly due to (i) lack of good methods; (ii) the large amounts of processing time involved and (iii) an assumption that roots contain less carbon and nutrients than the above-ground biomass. Moreover, many agroecosystems have a fairly complicated structure impossible to describe accurately, even when considering just the above-ground biomass. Root structure is even more difficult.

Nevertheless, root growth and turnover are two key components of nutrient cycling in pastures and carbon sequestration in soils (Deinum, 1985; Rao et al., 1992; Veldkamp, 1993; Fisher et al., 1994; Cadisch et al., 1994; Jackson et al., 1996; Rao et al., 1997). Estimates of production below-ground in natural grass ecosystems in the tropics, only to a depth of 15 cm, ranged from 0.61 to 5.68 Mg ha^{-1}. Annual turnover of biomass below-ground in the same ecosystems, estimated as production divided by mean biomass, were between 1.7 and 4.0 (Long et al., 1989).

Roots of introduced pastures have been recorded as penetrating soil as deep as 8 m (Nepstad et al., 1994). However, the greater part of the root biomass and root length is found in the top 30 cm of the soil profile (Goedert et al., 1985; Spain and Couto, 1990; Rao et al., 1992; Cadisch et al., 1994). It is here that most nutrients available to plants are located as a result of nutrient cycling and soil biological activity (Haynes and Williams, 1993; Rao et al., 1994; Thomas et al., 1995; Boddey et al., 1996). The deep root systems of many tropical grasses and legumes are efficient in extracting nutrients from depth and

recycling them throughout the whole plant (Rao et al., 1992). In doing so they concentrate nutrients in the surface layers of the soil and in addition can contribute to carbon sequestration deep in the soil (Fisher et al., 1994).

Rao et al. (1997) compared the performance of root systems of introduced tropical pastures with that of native savanna pasture in the eastern plains of Colombia. They measured the distribution of root yield and length over four consecutive growing seasons, at 10, 15, 19, 22, 27, 32, 35 and 47 months after sowing. They found that the mean 'standing' biomass of live roots (and root length) over 0-80 cm soil depth of *Brachiaria dictyoneura* alone was 5.7 Mg ha^{-1} (21.5 km m^{-2}) compared to *B. dictyoneura* with the legume *Centrosema acutifolium* of 3.8 Mg ha^{-1} (13.8 km m^{-2}). In contrast, the native savanna pastures had only 1.4 Mg roots ha^{-1} (9.5 km m^{-2}).

Rao et al. (1997) also estimated differences in rooting strategies of introduced and native pastures and found that both native savanna grasses and introduced pastures were deep rooted. The native pasture was relatively the most deep rooted with higher specific root length (root length per unit weight, a measure of fineness of the roots). These root attributes of native savanna may form part of an adaptive strategy to infertile soil conditions.

The larger amounts of standing live roots of introduced pastures contribute to greater cycling of nutrients upon root death and decomposition (Rao et al., 1997). In contrast, a lower contribution would be expected from the native savanna grasses because of their low root biomass. Roots of the introduced pastures contained as much as 18 kg N ha^{-1}, whereas the roots of the native savanna pasture contained a maximum of about 6 kg N ha^{-1}. Roots of introduced pastures also contained as much as nine times more P than those of the native savanna.

Roots are not normally consumed by higher animals, so that for all practical purposes below-ground NPP recycles through their consumption by soil macro- and micro-organisms. However, information on decomposition of roots of tropical forage species is very limited. Preliminary studies using litter bags in soil showed that legume roots decomposed faster than grass roots. These differences were mainly attributed to initial per cent lignin and/or the lignin:N ratio (A. Celis and R.J. Thomas, unpublished data).

Soil texture was found to be important in determining the rate of root decomposition in highly weathered acid soils (Gijsman et al., 1997). Furthermore, roots are likely to decompose faster in fine-textured soils compared with coarse-textured soils, since the latter will generally be drier. Low P concentration in roots (C:P ratio up to 1700) and low availability of soil mineral-P to the microbial decomposers may make P a major limitation in root decomposition in strongly P-fixing soils in the tropics.

Conditions that favor the activity of soil biota will stimulate decomposition of dead roots. In the acid soils of the Colombian eastern plains, a *B. decumbens* pasture had 5 times more earthworms than the native savanna. A pasture of *B. decumbens* with the legume *Pueraria phaseoloides* had 10 times more than the savanna (up to 51 g m^{-2} liveweight and 139 individuals per m^2, Decaens et al., 1994). It is noteworthy that this liveweight is equivalent to that of 1.6 standard cattle ha^{-1}. Depending on their biomass, earthworms can contribute considerably to nutrient cycling and can transfer soil organic carbon from the surface to deeper soil layers (Fisher et al., 1997). It is also of interest that the biodiversity of the earthworm populations was unaffected, although the majority of the increase

was in a species of *Martiodrillus*, the adult individuals of which weigh 30 g and are up to 30 cm long (Fisher et al., 1995).

SPECIFIC NUTRIENT CYCLES

Nitrogen. Nitrogen cycling in pastures has been thoroughly reviewed recently (e.g., Steele and Vallis, 1988; Peoples et al., 1995; Thomas, 1995) and only a few pertinent points are addressed here. Although N off-take in grazed pastures is small compared with cropping systems, tropical pastures are frequently N-limited (Humphreys, 1994). In the absence of the availability of, or accessibility to N-fertilizers, inputs of nitrogen to balance the N cycle must come from BNF, either legume or associative fixation (associative fixation is discussed in more detail below). The amounts of N needed to maintain the N balance of the pasture are 15-158 kg N ha^{-1} yr^{-1} for tropical pastures, depending on the total biomass production and utilization (the proportion of NPP consumed by grazing animals, Thomas, 1992). Forage legumes have the potential to provide sufficient N for pastures by symbiotic BNF, but moderately-utilized pastures require legume contents of 20-30% of above-ground dry matter (Thomas, 1992; Peoples et al., 1995). Legume contents as high as this are seldom either achieved or maintained over significant periods of time in tropical or even most temperate pastures (Thomas, 1995).

For example, Boddey et al. (1996) estimated the pool sizes and the fluxes between them for pastures of *B. humidicola* alone and with the legume *Desmodium ovalifolium* grazed by cattle at 2, 3 and 4 head ha^{-1} at a humid site in Itabela in Bahia state of Brazil (Fig. 2). Yearly above- ground NPP was estimated at 19.7 and 22.8 t ha^{-1} in the pure grass and the association respectively. Animal consumption of the pure grass pasture was estimated at 28% of the dry matter (DM) produced and at 24% in the association.

Boddey et al. (1996) concluded, "In the grass-legume sward, almost no net loss or gain occurred to [soil organic matter (SOM)] (-5 kg ha^{-1} yr^{-1}), and in the pure *Brachiaria* pasture a small loss of N (-30 kg ha^{-1} yr^{-1}) occurred. As the contribution of BNF associated with the *B. humidicola* has not been investigated, it was assumed to be negligible, but if a credible contribution of 30 kg N ha^{-1} yr^{-1} is assumed, then both pastures at this stocking rate experienced a neutral or slightly positive N balance." *D. ovalifolium* was stated to persist in pastures at this site for more than 10 yr, and in this experiment contributed 16% of pasture DM at a stocking rate of 3 head ha^{-1}.

Even though the amounts fixed by rhizobium BNF appear to be sufficient, it is the low efficiency of transfer of this N to the associated grass that may limit the N cycle (Peoples et al., 1995). As mentioned earlier this process is mediated by the soil microbial biomass. Research efforts should now be concentrated on determining if it is feasible to manipulate microbial processes and populations to increase the efficiency and rate of N cycling (discussed further below).

In the absence of either this knowledge or the availability of N fertilizer, efforts should be made to produce simple guidelines that carefully match pasture production to carrying capacity of the pasture to avoid placing undue stress on the soil-plant system. Knowledge of the inputs, outputs and losses of nutrients from grazed pastures is required in addition to knowledge of the effects of grazing on plant population dynamics.

Phosphorus. Cycling of P in grazed pastures is different than N because P is relatively less mobile in soil, which reduces the risk of leaching losses from the system. P cycles through both inorganic (ortho-P) and organic-P (Po) pools of soil, plants, decomposers (microorganisms) and herbivores (invertebrates and vertebrates) in

grazed pastures as shown in Fig. 3 (Jeffrey, 1988). The plant-mycorrhizal system takes up P from the soil solution, which contains only a minute fraction of total soil P, but which is constantly replenished by the hydrolysis of labile ortho-P or mineralization of Po.

Labile ortho-P fractions, in turn, are exchanged with more stable inorganic-P compounds (Fe-P, Al-P, Ca-P) through slow reactions. Thus the P supply to the plant-mycorrhizal system depends on quantities of labile ortho-P, the rates of transformation between labile and more stable inorganic P, and the size and the rates of transformation of the mineralizable Po pool in the system (Tiessen et al., 1994; Gijsman et al., 1996). Invertebrate predators may be of great importance in transferring P to the food web, whilst vertebrates accumulate P as skeletal apatite. Both plant and animal residues returning to the soil make a major contribution to P-availability in soil. Fire may lead to a massive short circuit in the cycle of Po to ortho-P (Cook, 1994).

Efficient use of applied P fertilizer in grazed pastures depends on the extent of excretal transfer loss to stock camps, leaching losses, surface run-off, mineralization of soil Po, and the immobilization of applied P (Blair et al., 1977; Barrow, 1987). Various New Zealand and Australian researchers have constructed mass-balance models of P for pastures (Karlovsky, 1982; Lewis et al., 1987; Saggar et al., 1990; Nguyen and Goh, 1992). In addition to the application of P fertilizer, the process of mineralization of SOM contributes to a major portion of available P in pastures. Over 77% of P in above-ground litter and 79% of P in dead roots can become available for pasture growth and productivity (Jones and Woodmansee, 1979).

Export of P in animal products has generally been assumed to approximate 10% of animal P intake (Karlovsky, 1982). Although the proportion of P returned by animals is similar to that of N, almost all P recycled is in the form of faeces. The proportion of inorganic P in faeces is dependent on P concentration of the forage (Barrow, 1987). The loss of P in excretal transfer may be reduced by management practices that involve rotational grazing at high stocking rates (Nguyen and Goh, 1992).

Phosphorus is one of the most limiting nutrients for pasture production in the neotropical savannas (Rao et al., 1993). P deficiency in livestock grazing on native savanna is widespread, affecting especially reproductive performance (Fisher et al., 1992). Improved tropical forage and legume germplasm cannot be established without additions of fertilizer P because there are insufficient amounts available in the unamended oxisols to improve P cycling (Thomas et al., 1995).

A recent study examined P transformations in 15-year-old pastures of the introduced grass *B. decumbens* (cv. Basilisk) and *B. decumbens* with the legume *P. phaseoloides* compared with a native savanna in an oxisol on the Colombian eastern plains (Oberson et al., 1997; A. Oberson, D. K. Friesen, H. Tiessen and C. Morel, unpublished data). Sequential chemical P-fractionation was used to assess the significance of P transformations. Integrated consideration of P availability, P fractions, total soil P, and P budget showed that the grass-legume association cycles P more efficiently than either the grass alone pasture or the savanna.

Potassium. The recycling processes of K in grazed pastures are similar to those of N and P. Soil K can be divided in three fractions: K as a structural element of soil minerals, K^+ adsorbed in exchangeable form to soil colloids such as clay minerals and organic

matter, and K^+ present in the soil solution. The infertile acid soils with a predominance of low activity clays, and low cation retention capacity, are considered highly susceptible to leaching of applied K. Knowledge of the rate of movement and the magnitude of leaching of applied K to tropical pastures is limited.

A study was conducted in Yurimaguas, Peru to determine K dynamics in grazed pastures of a pasture of *B. humidicola* and *Desmodium ovalifolium* in association (Castilla et al., 1995). The uptake of K corresponded closely to the amounts returned through the above- and below-ground litter together with faeces, urine, rain and fertilizer. The standing residual forage constituted the largest sink for K, but only 40% of the calculated urine flux was accounted for.

The K budget of the pasture indicated that recycling of K through plants is extraordinarily efficient. However animals, by urine redistribution, disrupted rather than enhanced K cycling in the system. Leaching was found to be a major pathway of K loss from the system with concentration of K in urine patches as high as 465 kg K ha^{-1}. Because of this process, a net K extraction occurs from most of the grazed area and the pasture would require maintenance K fertilizer to sustain animal production.

MANAGEMENT

Grazing Management. Increase in stocking rate accelerates the rates of nutrient flow between pools (Haynes and Williams, 1993; Castilla et al., 1995). Except at excessively high stocking rates, a higher level of forage utilization increases the total nutrients of the animal biomass and the rate of product output. The greater partitioning of plant nutrients to animal excreta rather than to the more slowly-available litter pathway increases nutrient availability in soil (Barrow, 1987). However, the increase in stocking rate could increase spatial transfer of nutrients and losses from volatilization and leaching (Haynes and Williams, 1993). If external fertilizer inputs could meet these losses of nutrients, high stocking rates could increase nutrient availability in pastures. High stocking rates could also decrease root production and thereby reduce the amount of nutrients immobilized in roots.

Fertilizer. Application of fertilizers to tropical pastures has important implications for the rest of the nutrient recycling and loss processes. Fertilizer application in low amounts (kg ha^{-1}: 20 P, 20 K, 50 Ca, 12 Mg, 10 S and micronutrients) is needed for establishment of improved tropical grasses and legumes in the acid soils of low fertility of the neo-tropics (Rao et al., 1993; Thomas et al., 1995). These species respond to additional application of nutrients when sown in association with crops (Vera et al., 1992). For sustained animal production through efficient nutrient cycling, maintenance fertilizer applied once every two years (at half of the establishment levels) appears to be needed. These applications of maintenance fertilizer help to compensate nutrient losses through the actions of grazing animals as mentioned above (Haynes and Williams, 1993).

Models of Nutrient Cycling and Their Use for Nutrient Management. Models have many current and potential uses for answering questions in research, decision making in production systems, and policy analysis (Thornley and Johnson, 1990; Boote et al., 1996). There are two principal types of models that quantitatively describe nutrient cycles: mass-balance and dynamic models (Haynes and Williams, 1993).

Mass-balance models are balance sheets of the amounts of nutrients within various compartments, or pools, of the system and the amounts entering and leaving the system. Dynamic models differ from these simple mass-balance models in that they include equations describing

the feedback control mechanisms that affect nutrient transformations. Models are extremely powerful tools from the stand-point of farm management and fertilizer advice and for developing management options to maximize cycling, minimize losses and develop more sustainable pasture systems.

Because of their potential usefulness, there is a long history of attempts to model nutrient cycling. The N cycle is relatively well understood (Thornley and Verberne, 1989; Thomas, 1992; Haynes and Williams, 1993), but cycling of other nutrients, even P and K, in tropical systems is not. Other nutrients such as Ca and Mg are scarcely understood at all in these systems, even where deficiencies are known to occur. Key issues are the nature, size and fluxes between the various pools. In many tropical soils, these aspects need much further study before they are understood well enough to allow the construction of adequate models. At present, there is little understood of the residual values of applied fertilizer and their relation with the different soil mineralogies encountered in many tropical soils. For these reasons, it is not possible to make satisfactory predictions of nutrient management in many, if not most, tropical systems.

Microbial biomass. Decomposition of plant material in soil is mediated by the soil microbial biomass (SMB). Any efforts to manage SMB requires knowledge of the relevant processes. However, land management decisions are not usually based on knowledge of the underlying processes (McGill et al., 1993). For tropical pastures, knowledge of decomposition at the microbial level is so meagre that it is unlikely that meaningful options to manage SMB will be generated in the near future. Therefore the selection of plant material, and hence litter quality (e.g. lower lignin contents), and aspects of soil management, such as mechanical disturbance and burial of litter, appear to be the main options for the land user to modify nutrient cycling by decomposition processes.

PASTURE DEGRADATION
Degradation, usually defined as a decline in both individual animal production and carrying capacity, is common in pastures of pure introduced grasses in much of the neotropics. Introduced pastures in the savannas that degrade are often reclaimed by cultivation and reseeding, either alone or sown under a crop. This is not a traditional ley system where a crop is introduced to take advantage of the fertility accumulated under a legume-based pasture, but rather the reverse. In this case the pasture probably takes advantage of the residual nutrients from the fertilizer required to produce satisfactory crop yields (e.g. the Barreirão system developed in Brazil, Kluthcouski et al., 1991.)

It appears that pasture degradation is a complex process involving interactions between P, N and possibly other nutrients and BNF whether from legumes or associative fixation. At the CNI-Carimagua research station on the Colombian eastern plains, pastures that receive maintenance P do not commonly degrade. Some of them are as much as 17 yr old. Although some of them are on relatively heavy soils with slow drainage, this is by no means universal.

Robbins et al. (1989) found that N release from litter of green panic (*Panicum maximum* var. *trichoglume*) in sub-tropical south-east Queensland was much slower than the loss of dry matter. They concluded that "a major cause of declining productivity in sown grass pastures is the immobilization of N in decomposing litter." Putting a somewhat different viewpoint, Myers and Robbins (1991) thought that the flush of growth after initial seeding, or renovation, was a "run-up" due to the release of protected soil N during cultivation. The process, commonly thought of as "run-down", was merely a

return to a base level of productivity controlled by the lesser amount of N available.

Surveys of farms on the eastern plains of Colombia (Moya, 1991; R.R. Vera, personal communication) have shown that farmers disk their pastures roughly every four years and about a quarter of them apply P fertilizer at this time. However, fertilizer application does not decrease the frequency of renovation. A small number of on-farm small plot experiments were established across a range of soil textures in degraded pastures with typically low vigor and slow regrowth together with decreased ground cover of the sown species. Without exception, the addition of P, K and/or micronutrients either alone or in factorial combinations, with and without disking, made very little difference in terms of rates of regrowth above ground. In all cases it was obvious that N was limiting (N fertilizer was not applied).

Another group of on-farm experiments (R.R. Vera, personal communication) has clearly shown that degraded *B. dictyoneura* pastures can be reclaimed by resting them at the beginning of the rainy season and by applying N and S fertilizer for seed production. This combination of grazing for several years followed by seed production (with fertilizer) in the third year appears to result in pastures that do not degrade. These results appear to confirm the key role of N in maintaining productive pastures, although it is not known whether these pastures have associative BNF (see below), nor what its role might be. Future work on the processes of pasture degradation and reclamation should look carefully at both nutrient balances and ratios as well as the role of soil biota.

ROLE OF ASSOCIATIVE N FIXATION
There are free-living N-fixing bacteria in the rhizosphere that mostly live on the exudates from plant roots, but they have to compete with other rhizosphere organisms for their share of them. They then must die and pass through mineralization processes before the N becomes available to higher plants (Gibson et al., 1988). Moreover, the plants have to compete for the N released in mineralization with all the other organisms in the rhizosphere, so, as far as the plant is concerned, it is an inefficient system.

Some years ago, it was discovered that sugar-cane has bacteria that live in the xylem and which fix N (Döbereiner et al., 1988). First it was thought that they were only in the roots, but recently several new species have been found in stem and leaf and in both xylem and phloem (Döbereiner et al., 1995). In contrast to the rhizosphere N-fixers, the associative organisms live inside the plant, get their metabolites directly from the host, and liberate N directly to it. The amount of N fixed in the case of sugar-cane can be as high as180 kg ha^{-1} yr^{-1}.

It is hypothesized that the reason for the success of associative BNF in sugar-cane in Brazil is because it has been grown for centuries on soils low in N (Döbereiner et al., 1995). Elsewhere in sugar-cane, when N supply is ample, the same organisms cause a sub-lethal leaf mottling, which is not seen in Brazilian cultivars. At least some of the grasses sown on the 35 Mha of the Brazilian cerrados exhibit associative BNF. But what is the relation between effective associative BNF in grasses and old sugar-cane sites in Brazil? Did the infection of grasses originate from cane?

Associative BNF appears to have much untapped potential. The amounts seem to be a maximum of 40 kg/ha/yr (Boddey and Victoria, 1986; Miranda et al., 1990), but for most tropical pastures at the common levels of utilization of 30%, this should be enough to keep

the system in balance for N. The unknown is the relation between adequate nutrition of the host to allow associative BNF to be expressed, and what is its potential to avoid pasture degradation.

It is possible that any marginal (or worse) deficiency apart from N could mask the expression of associative BNF. Moreover, there do not appear to be data about the effectiveness of the associative BNF as affected by grass species, although there are cultivar differences in sugar cane (Döbereiner, 1992). Nor has effectiveness of associative BNF been related to the presence or absence of particular species of the associative organisms. Although these questions suggest complex interactions, forty years ago legume-rhizobium interactions were also thought to be complex. A fraction of the effort put into understanding the latter applied to associative BNF could yield outstanding results.

Associative BNF has been found in a number of other grass crops, including rice, and the bacteria seem to be seed transmitted (Döbereiner, 1992). The potential is that no one so far has looked for strains of the bacteria with superior fixing ability, not in cane and certainly not in grasses. If they were to be identified, could they be successfully inoculated into plants in the field, and would they survive from generation to generation? The density of BNF organisms in the soil declines rapidly to the level where they cannot be detected (Olivares et al., 1996). Bacteriologically sterile sorghum plants placed in the soil at this stage soon became infected, leading to the inference that the organisms are able to survive at low numbers in the soil. But, is their distribution affected by soil type, climate or other factors?

Does *B. decumbens* cv Basilisk generally have effective associative symbiosis? Olivares et al. (1996) isolated *Herbaspirillum seropedicae* but not *H. rubrisubalbicans* from *B. decumbens*. Although they give no information about the collection site(s), they were not old sugar cane fields (R.M. Boddey, personal communication). Nor do they give information about effectiveness, which is different from presence or absence of the organisms. Does the associative BNF occur in farmers' fields of the Colombian eastern plains where Vera (personal communication, see above) made his observations? If not, what are the prospects for introducing it? Is it the reason why at least some of the pastures at the Carimagua station have not degraded after as long as 17 yr? Associative BNF organisms have been found in vesicular-arbuscular mycorrhizae (VAM) (Döbereiner et al., 1995), which could be a delivery mechanism (although VAM inoculation of pastures has not been an unqualified success, Salinas et al., 1995).

Clearly at present there are no answers to most of these questions. However the possibilities for a major impact on sustainability of pure grass pastures makes them important topics for further research. This research certainly would not be "demand driven" from the point of view of small farmers, few of whom would know what an endophytic bacterium is. Doubtless, however, they would find the prospect of sustainable pastures attractive, even if they did not know how it might be achieved.

THE WAY FORWARD
Compared with temperate pastures, nutrient cycling in tropical pastures is poorly understood. In this paper we have tried to identify the priority areas to overcome this lack of knowledge. The processes of pasture degradation, common in introduced pastures in much of the neotropics, and conversely those involved in the recuperation of degraded pastures, are clear priorities, as is the potential contribution of associative BNF to pasture sustainability.

Unfortunately, the whole future of understanding in tropical pasture research presently lies at a cross-roads. There are wide-spread problems in the public funding of research, which in much of the tropics has few other sources to tap. The political agendas have also shown a marked trend away from understanding of bio-physical functioning towards social and economic problems and issues such as preservation of biodiversity. Because of these changes, many institutions that were making important contributions to the understanding of nutrient cycling in tropical pasture-based systems have shifted their attentions to other areas.

Nevertheless, we believe that production systems in the tropics, and probably elsewhere as well, have their main chance of sustainability if they are based on pastures. Although agronomists are devising cropping systems that are less damaging environmentally, they usually require fundamental changes in the management of residues. In many low input systems, as in the tropics, a pasture phase, as in the ley-based systems of the temperate regions, may be the easiest and most efficient way to achieve sustainability (Mohammed Saleem and Fisher 1992; Thomas et al. 1995). As Fisher et al. (1994) stated 'far from being environmentally degrading, improved pastures can fulfill the restorative role in tropical systems that was recognized in pre-Roman times for Mediterranean systems.'

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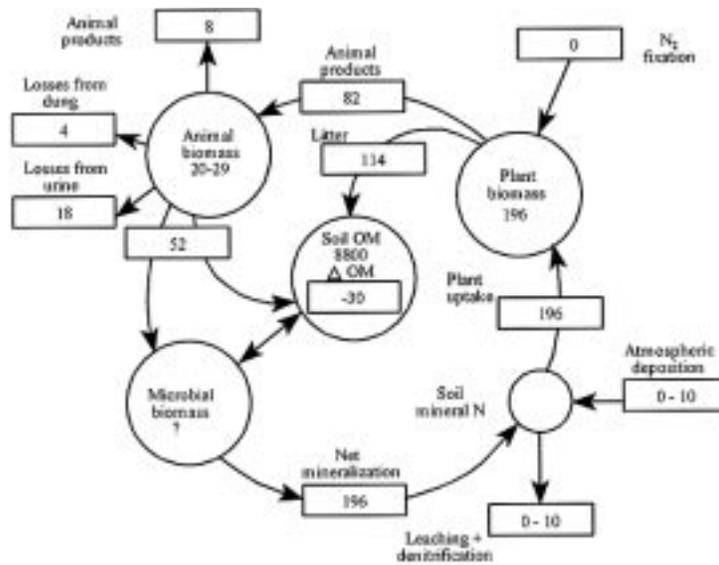
Figure 1
Simplified nutrient cycle for grazed pasture ecosystems (adapted from Haynes and Williams, 1993). The letters A-J indicate the order followed by the processes.
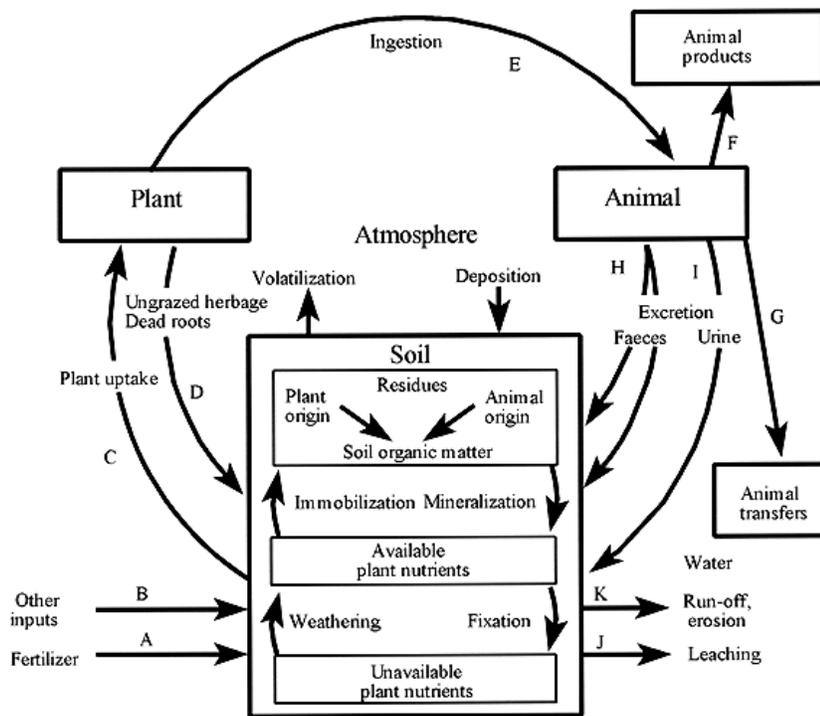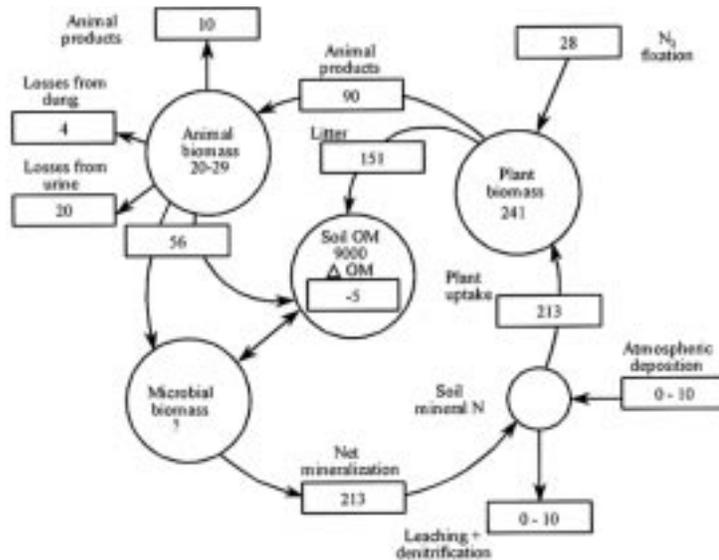
Figure 2

Nitrogen cycling in grazed pastures of (A) *Brachiaria humidicola* and (B) *B. humidicola* with the legume *Desmodium ovalifolium* at Itabela, Bahia state, Brazil. Boxes represent fluxes and circles represent pools. The numbers are kg ha^{-1} of N, and for a stocking rate of 3 cattle ha^{-1}. Assumptions were that 90% of the N in animal intake was returned to the soil as excreta, equally divided between urine and faeces, and that deposition of N from the atmosphere was equal to gaseous and leaching losses, except those from excreta. Itabela has a humid tropical lowland climate (1300 mm annual rainfall, evenly distributed throughout the year). (From Boddey et al., 1996.)
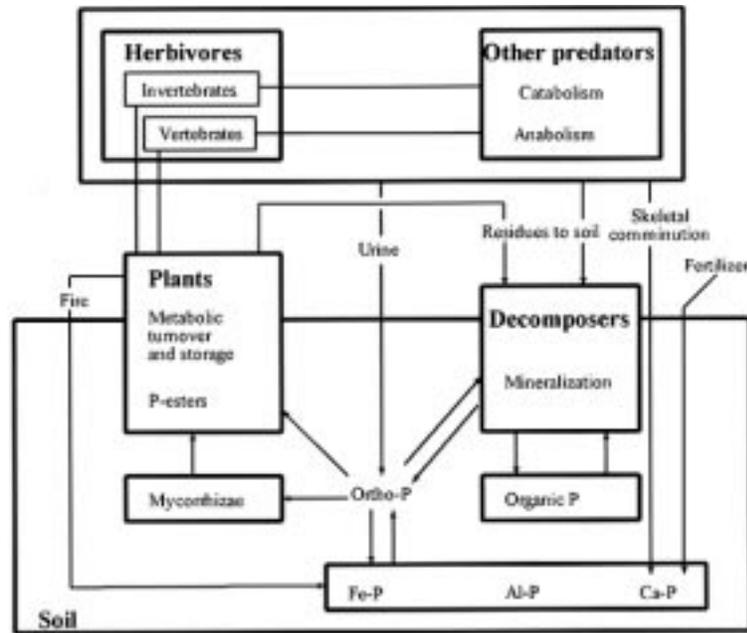
Figure 2a

Figure 2b

Figure 3

Flow diagram illustrating the phosphorus cycle for grazed pastures (adapted from Jeffrey, 1988).

Table 1

A comparison of estimates of net primary production (NPP) taking account of losses through death and below-ground production to 15 cm with estimates from biomass change alone (Long *et al*. 1989).

Net primary production (g m^{-2} yr^{-1})	Montecillos, Mexico	Nairobi, Kenya	Klong Hoi Kong, Thailand
Accounting for mortality (including below-ground organs)	1741	1242	2220
Accounting for mortality (above- ground only)	1063 (39%)*	811 (35%)	1595 (28%)
IBP standard method (including below-ground organs)	740 (56%)	663 (47%)	663 (74%)
Maximum biomass (above- ground only)	430 (75%)	337 (75%)	442 (80%)

* The figures in parentheses are the underestimation of productivity as a percentage of NPP over   the 12 months.