CHAPTER 9

SOIL-PLANT FACTORS AND PROCESSES AFFECTING PRODUCTIVITY IN LEY FARMING

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Introduction

In this work, we will try to summarize the multidisciplinary efforts of the Tropical Pastures Program (TPP) towards a mechanistic understanding of the soil-plant factors and processes affecting productivity in ley farming. We would like to deal with this subject in sections. We will start with a brief introduction, followed by our research efforts to understand the adaptation attributes of forage germplasm, recycling of nutrients, and soil conditions. Then we will use the research data collected on these three aspects to explain the benefits from soil enhancement in pastures. That will be followed by a brief description of our approach to integrate a number of processes related to soil-plant-animal interactions in pastures under grazing. Finally, we will present a few conclusions.

Productivity in nutrient-poor acid soils is influenced by at least three major soil-plant factors in addition to management as described in three other articles in this book (Lascano and Spain, Chapter 3; Fisher et al., Chapter 6; Thomas et al., Chapter 8). These factors include: adaptation attributes of forage germplasm; extent of nutrient recycling; and soil conditions. Each major factor is controlled by a number of key processes. The TPP has begun to identify and elucidate some of these processes in order to: select and characterize germplasm; optimize soil enhancement; and define guidelines for management of a number of the most promising forage grasses and legumes. For the sake of clarity, we will focus in this article on only a few species.

The TPP has developed a research strategy to generate improved forage plants and pasture technology for sustained productivity (Toledo and Nores, 1986). An improved understanding of the above three major soil-plant factors affecting productivity of the most promising species is essential for the development of improved forage plants and pasture technology. The strategy is based on the logic that well-adapted forage species should be able to extract nutrients from infertile

soils and recycle those nutrients within the system effectively and improve soil conditions. Integration of improved germplasm with sound management technologies is essential for the development of viable production systems in different agroecosystems.

Adaptation Attributes

Plants have evolved adaptive mechanisms by which they respond to nutrient-poor acid soil and improve their chances of survival or production of offspring (Foy, 1988; Taylor, 1988; Wright, 1989; Marschner, 1991). Plant adaptation is used to define processes conferred by genetic attributes that serve to "fit" the plant to ambient conditions of light, temperature, and mineral and water availability. In our target environment of nutrient-poor acid soils, plant adaptation responses involve changes in: (1) partitioning of biomass between shoots and roots; (2) root growth and distribution; (3) nutrient acquisition; (4) nutrient transport; and (5) nutrient use efficiency. All these processes are affected by the availability of nutrients and water. Improved understanding of the factors that control these processes will assist our efforts to improve productivity and persistence of forage species.

The size and activity of shoots show a functional equilibrium with root activity (van Noordwijk and de Willigen, 1987). The shoots fix carbon and the roots take up water and nutrients from the soil. Although these functions are separate, both parts of the plant interact to make plant growth possible (Chapin, 1991). Adequate nutrient supply favors shoot growth relative to root growth (Marschner, 1986). Conversely, nutrient stress results in a shift of carbon allocation to roots, leading to decreased shoot growth (Terry and Rao, 1991).

The ability of forage plants to remove nutrients from soil is important both for the use of "natural" nutrients and for the efficiency with which fertilizers are used. As pasture production increases, the demand for nutrients, both total amount and the intensity of supply required, increases. The link between nutrient demand and plant biomass can be modified by changes in the partitioning of assimilates to various parts of the plant, i.e., an increase in relative biomass of shoot will usually increase nutrient demand, while an increase in root will normally reduce relative demand.

Adaptation to low fertility

Under glasshouse conditions at CIAT-Palmira, we have investigated the effect of soil type and fertility on biomass production, dry-matter partitioning between shoots and roots, and nutrient uptake and use efficiency in a number of most promising forage grasses and legumes adapted to acid soils (Rao et al., 1991). The grasses include: *Brachiaria dictyoneura*, *B. brizantha*, *B. humidicola*, *B. decumbens*, *Andropogon gayanus*, *Panicum maximum*, and *Hyparrhenia rufa*. The legumes include: *Arachis pintoi*, *Stylosanthes capitata* CIAT 10280, *S. capitata* CIAT 1315, *S. guianensis*, *S.*

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macrocephala, Centrosema acutifolium, C. brasilianum, C. pubescens, C. macrocarpum, Desmodium ovalifolium, Pueraria phaseoloides, and *Macroptilium gracile.* Results from only a few species will be presented for the sake of clarity. The two soil types used were sandy loam (Alegría) and clay loam (Pista). These soils were collected from an Oxisol at Carimagua (0-20 cm soil profile). These two soils provided contrasting physical and chemical properties (Table 1). Sandy loam soil had 65% sand compared with 18% in clay loam soil. Although both soils are characterized by high acidity and high Al saturation, the sandy loam soil had lower levels of soil organic matter and total nitrogen (Table 1). The low soil fertility treatment was similar to the recommended level of fertility for pasture establishment (kg ha^{-1}: 20 P, 20 K, 48.2 Ca, 14.2 Mg, and 10 S) in which nitrogen and micronutrients were not applied. The high soil fertility treatment was similar to the fertility recommended for crop-pasture rotations (kg ha^{-1}: 40 N, 50 P, 100 K, 103.4 Ca, 28.5 Mg, 20 S, and micronutrients).

A glasshouse study was conducted to evaluate the differences in adaptation to acid soils among three grass + legume associations. The results from a *Brachiaria dictyoneura* + *Arachis pintoi* association are presented. Large plastic containers were used, with 40 kg of soil per container. The two soil types and fertility levels were as described before. Each container was inoculated with mycorrhizae and *Rhizobium*. Grass and legume species were planted in alternate rows with equal distance between the rows.

The differences in biomass production and dry-matter partitioning are shown in Figure 1. There was a clear effect of low fertility on the partitioning of dry matter between shoots and roots in both soils. The proportion of dry matter partitioned in roots under low fertility was higher than that of shoots. In other words, root growth under low fertility increased at the expense of shoot growth. An increase in fertility increased shoot growth more than root growth.

The proportion of legume root biomass in the total root biomass of the associations was determined using the carbon isotope ratio technique. Because of the presence of the C_4 pathway in the grass and the C_3 pathway in the legume, it was possible to quantify the legume root proportion using the differences in ^{13}C to ^{12}C ratio of an association and that of the pure grass or legume (Svejcar and Boutton, 1985). Under low-fertility conditions, the proportion of legume root biomass in an association was 19% in sandy loam soil and 20% in clay loam soil (Table 2). This indicated that the grass could explore more soil volume for nutrients and water than the legume.

Soil type and fertility status affected not only root biomass production but also root length density (Figure 2). Root length density (the length of roots per unit soil volume) was two times higher in the sandy loam soil than in the clay loam soil at both fertility levels. Despite similar root biomass in both soils, this difference in root length density indicates greater fine root production in the sandy loam soil.

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Table 1. Physical and chemical properties of two soil types at Carimagua, Colombia.

| Characteristics	Soil type	
	Sandy loam	Clay loam
Physical		
Clay (%)	17	37
Sand (%)	65	18
Chemical		
Al saturation (%)	77	89
pH	5.1	5.0
Organic matter (%)	0.9	3.4
Total N (ppm)	336	1008
Available P (ppm)	2.0	2.1
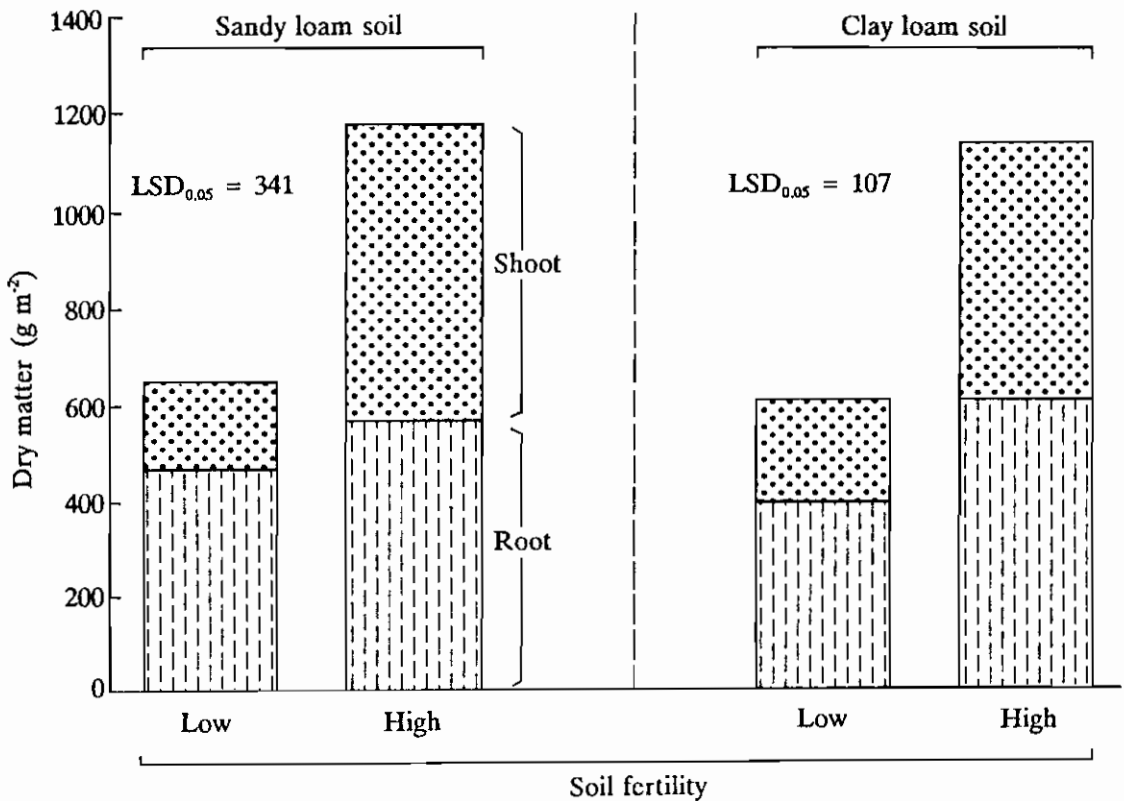
Figure 1. Changes in dry matter partitioning between shoots and roots of a grass + legume association (*B. dictyoneura* + *A. pintoi*) as affected by soil type and fertility status. LSD values at 0.05 probability level are shown for comparison.

Table 2. Proportion of legume shoot and root dry matter in a grass + legume association
of *B. dictyoneura* + *A. pintoi*.

Soil and fertility	Proportion of dry matter	
	Shoot	Root
	(%)	
Sandy loam		
Low fertility	59	19
High fertility	25	8
Clay loam		
Low fertility	57	20
High fertility	42	16
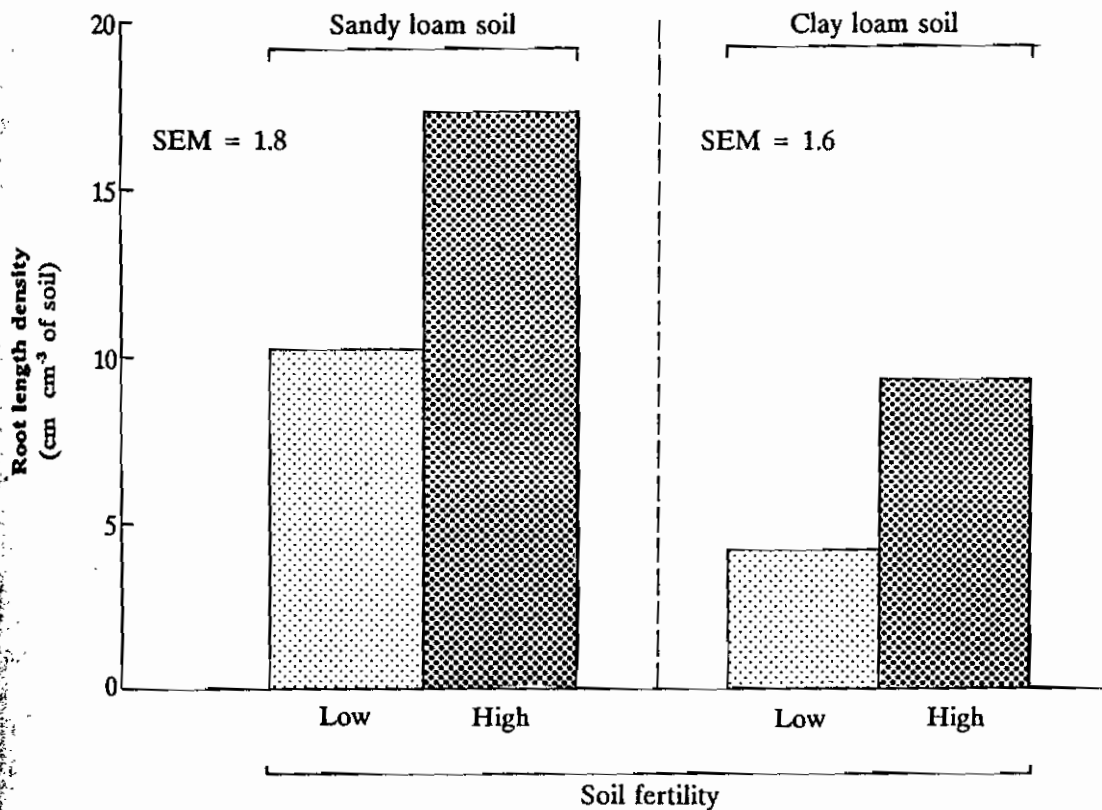
Figure 2. Changes in root length density of a grass + legume association (*B. dictyoneura* + *A. pintoi*) as
affected by soil type and fertility status. Each value represents the average rooting density
over a 0-15 cm depth of soil profile. Standard error mean values are shown for comparison.

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Maintaining photosynthetic activity is essential for guaranteeing the productivity of a grass + legume association in nutrient-poor acid soils. Photosynthetic measurements on intact grass leaves indicated that because they have a C_4 photosynthetic pathway, their net photosynthetic rates were higher than those of the legume with a C_3 photosynthetic pathway (Figure 3). An important observation was that low fertility did not reduce the rate of net photosynthesis in the leaves of either the grass or legume in the association. These results indicate that grass-legume associations adapt to low-fertility acid soils by maintaining their photosynthetic activity per unit leaf area and allocating a higher proportion of fixed carbon to root growth and production.

Responses to change in phosphorus supply

Phosphorus deficiency in forage species is a function of both the supply of phosphorus to the plant and the plant's demand for phosphorus. Phosphorus availability in the soil limits productivity in acid, infertile soils (Sánchez and Salinas, 1981; Salinas and Saif, 1990; Salinas et al., 1990). Therefore, another glasshouse study was conducted to determine how the supply of P in the soil affects biomass production, dry-matter partitioning, and uptake and utilization of P by three different legumes when grown alone (monoculture) or in combination with a grass (association). The trial was conducted in two soil types as described before, but results from a clay loam soil are presented for the sake of clarity. The mineral nutrients added to the soil were the same as for high fertility in the previous experiment except for the element P. The four rates of P used were 0, 10, 20, and 50 kg ha^{-1} supplied as triple-superphosphate. All containers received mycorrhizae and legumes received inoculation with effective *Rhizobium* strains. The results from *B. dictyoneura* and *A. pintoi* as monocultures as well as associations are presented.

The response to P of the shoot biomass per unit soil surface area is shown in Figure 4. In the monoculture, the response to P was greater with the grass than the legume at all P rates except when there was no P supply to the soil. Furthermore, the grass responded to increased P supply enormously when compared with the legume. The legume responded only up to 20 kg ha^{-1}. The differences in shoot biomass production became larger as the supply of P increased in the soil.

The response of root biomass production to increased P supply is shown in Figure 5. Root biomass production in the grass and the association increased with the increase in P supply, while the increase was very small with legume alone. The legume root proportion in the association was determined by the carbon isotope ratio technique. Because of the presence of a C_4 photosynthetic pathway in the grass and a C_3 pathway in the legume, it was possible to quantify legume root proportion in an association. An increase in P supply in soil increased grass root biomass, while the increase was small in legume roots (Figure 6). This dramatic difference in root production between the grass and the legume helps the grass to be very aggressive and dominate the legume in order to explore the soil volume for the uptake of nutrients
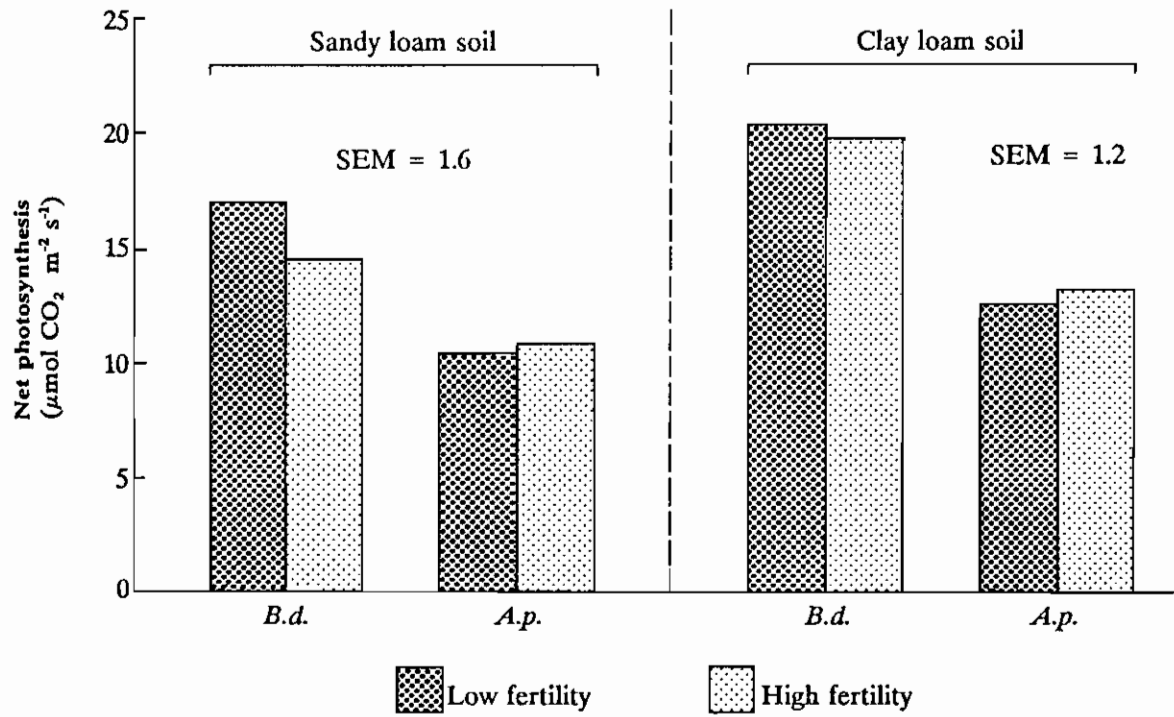
Figure 3. Changes in net photosynthesis of leaves of a grass + legume association (*B. dictyoneura* + *A. pintoi*) as affected by soil type and fertility status.
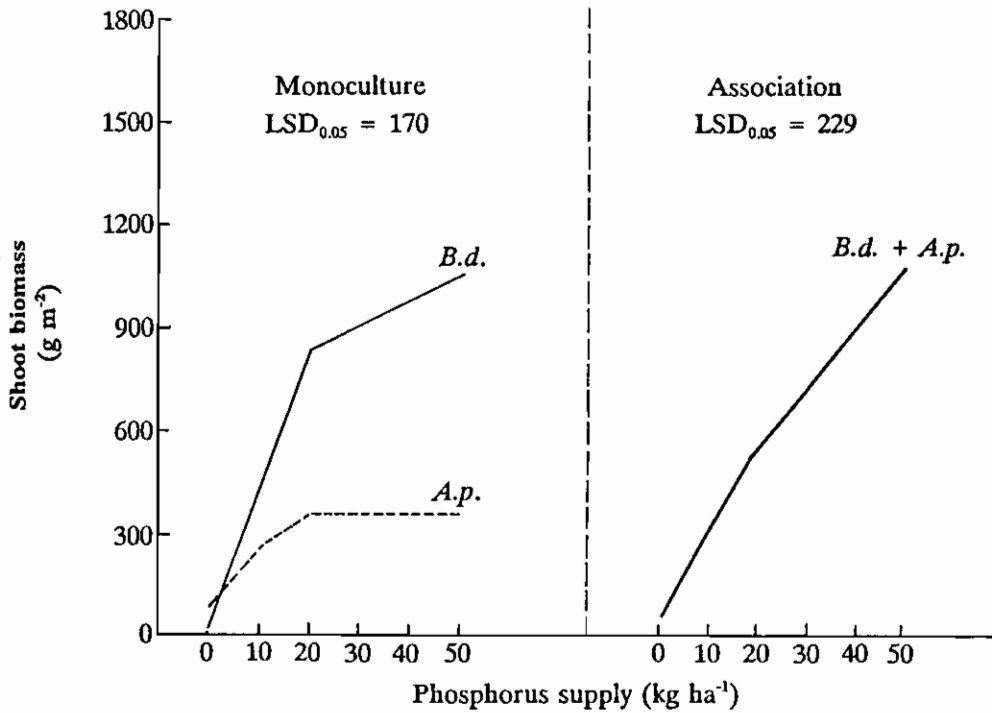

Figure 4. Changes in shoot biomass production per unit soil surface area for a grass (*B. dictyoneura*) or a legume (*A. pintoi*) when grown as a monoculture or as an association (*B. dictyoneura* + *A. pintoi*), as affected by phosphorus supply in a clay loam soil.
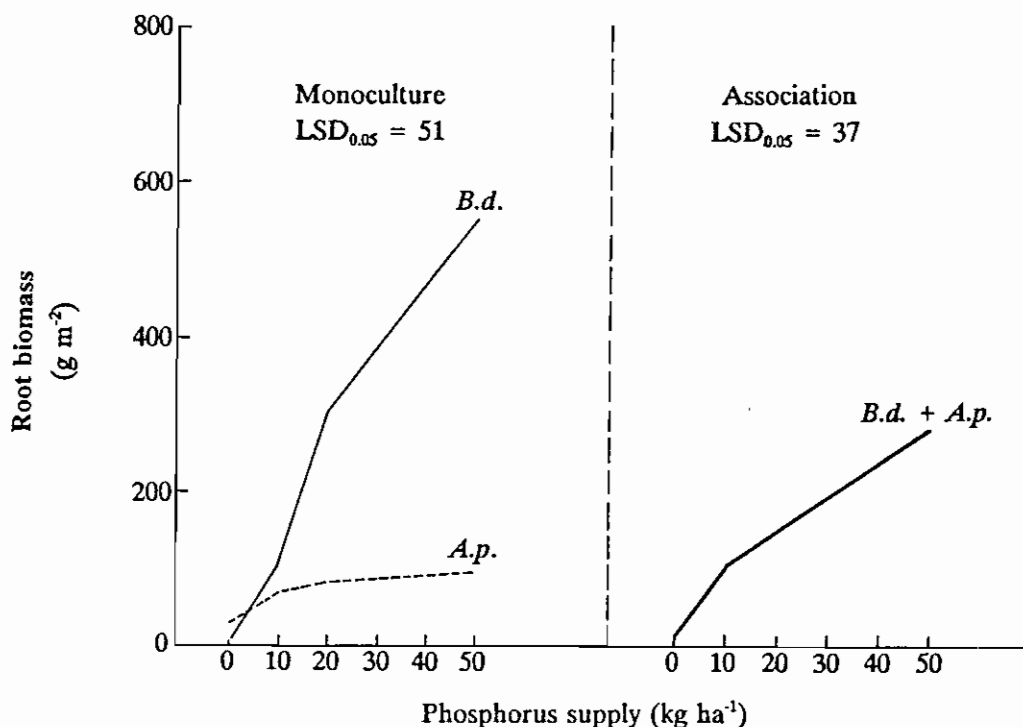
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Figure 5. Changes in root biomass production per unit soil surface area for a grass (*B. dictyoneura*) or a legume (*A. pintoi*) when grown as a monoculture or as an association (*B. dictyoneura* + *A. pintoi*), as affected by phosphorus supply in a clay loam soil.
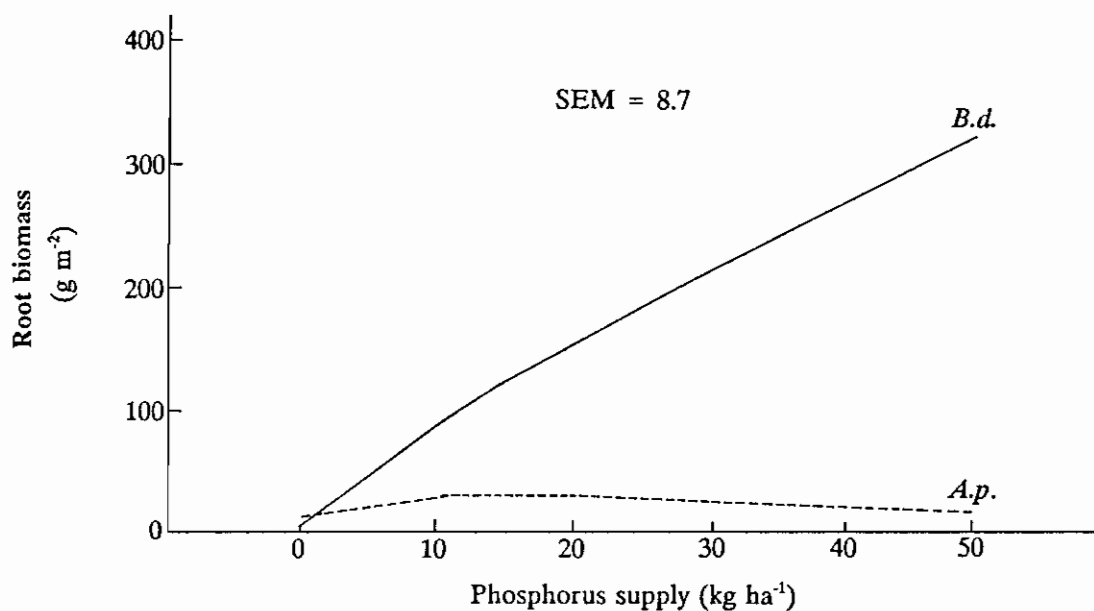

Figure 6. Root biomass production of a grass (*B. dictyoneura*) and a legume (*A. pintoi*) in an association as affected by phosphorus supply in a clay loam soil. The relative proportion of root biomass was estimated based on stable carbon isotope analysis.

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and water. This competitive ability of the grass in root growth together with the presence of a C_4 photosynthetic pathway helps the grass to produce markedly higher shoot biomass (forage yield) than the legume (Toledo and Fisher, 1990).

Total P uptake (per unit soil surface area) of the legume with its smaller root biomass was better than for the grass at all levels of P supply (Figure 7). At 50 kg ha^{-1} of P, the total P uptake of the association was significantly higher than that of the grass-alone treatment. The increase in total P uptake of the legume was achieved through higher P uptake efficiency (P uptake in shoot biomass per unit root weight), which was several times higher than that of the grass (Figure 8). The P uptake efficiency of the legume increased with the increase in P supply, while for the grass it either remained the same or even decreased. This is simply because the grass responded to increased P supply by increasing the root biomass so that P uptake efficiency per unit root weight remained the same.

Vesicular-arbuscular mycorrhizae are important for phosphorus supply to forage grasses and legumes in tropical Oxisols (Salinas et al., 1985). The superior P uptake efficiency in the legume could be due to more efficient mycorrhizae and/or increased root phosphatase activity in addition to other factors such as superior uptake kinetics, longer roots, and longer root hairs. We tested mycorrhizal root infection in both species and found that there was a higher infection level in grass than in legume (Figure 9). The percentage of root length mycorrhizal decreased with the increase in P supply to both species. However, the activity of root acid phosphatase was several times higher in the legume at higher levels of P supply in monoculture as well as in association (Figure 10). When there was no external supply of P, the root acid phosphatase activity of the grass was even higher than that of the legume. These results indicate that the mechanisms of P acquisition between the grass and the legume are different.

Phosphorus use efficiency (g of forage produced for g of P uptake in shoots) of the grass was several times higher than that of the legume (Figure 11). The highest P use efficiency of the grass was observed at the recommended level of pasture fertility, i.e., 20 kg ha^{-1} of P supply. In addition to P use efficiency, N use efficiency of the grass was also higher than that of the legume, especially at higher levels of P supply (Figure 12).

It is generally believed that larger root systems with greater surface area, typical of tropical grasses, may be better for acquiring P per unit soil surface area than the smaller ones that are typical of tropical legumes. Larger root systems are often associated with plants that are better competitors, such as tropical grasses, and that trait may competitively exclude companion species such as legumes. However, legumes with smaller root systems may have evolved a greater capacity to rapidly take up P than grasses with larger root systems. The higher uptake of P in the legume *A. pintoi* than in the grass *B. dictyoneura* per unit soil surface area may be attributed to the ability of the legume root system to modify the chemistry of the rhizosphere by
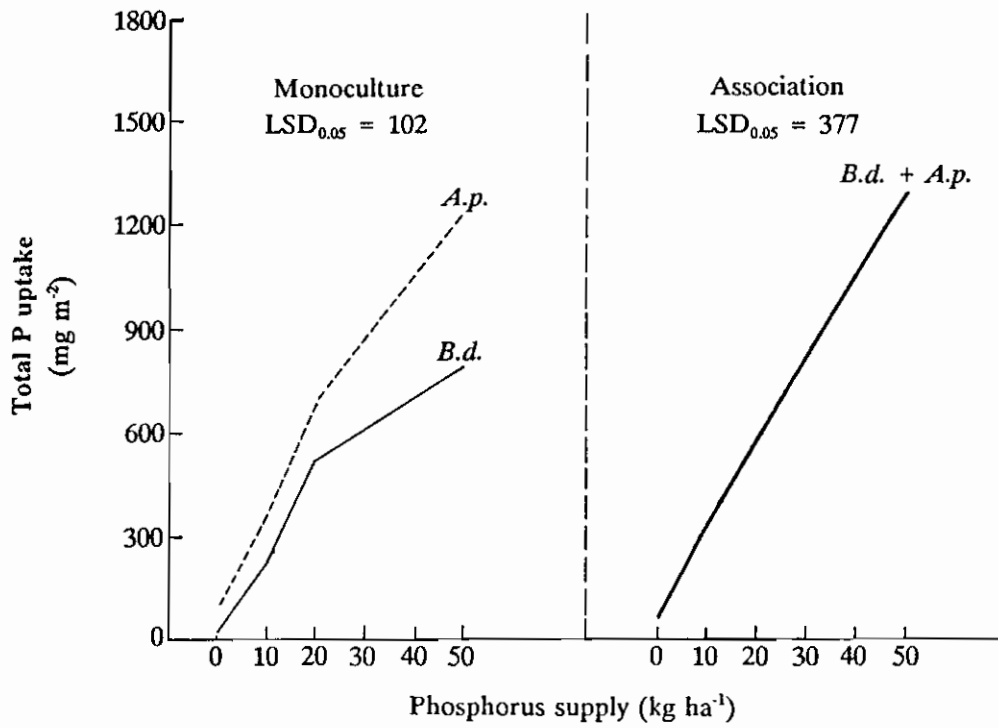
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Figure 7. Changes in total P uptake per unit soil surface area for a grass (*B. dictyoneura*) and a legume (*A. pintoi*) when grown as a monoculture or as an association (*B. dictyoneura* + *A. pintoi*), as affected by phosphorus supply in a clay loam soil.
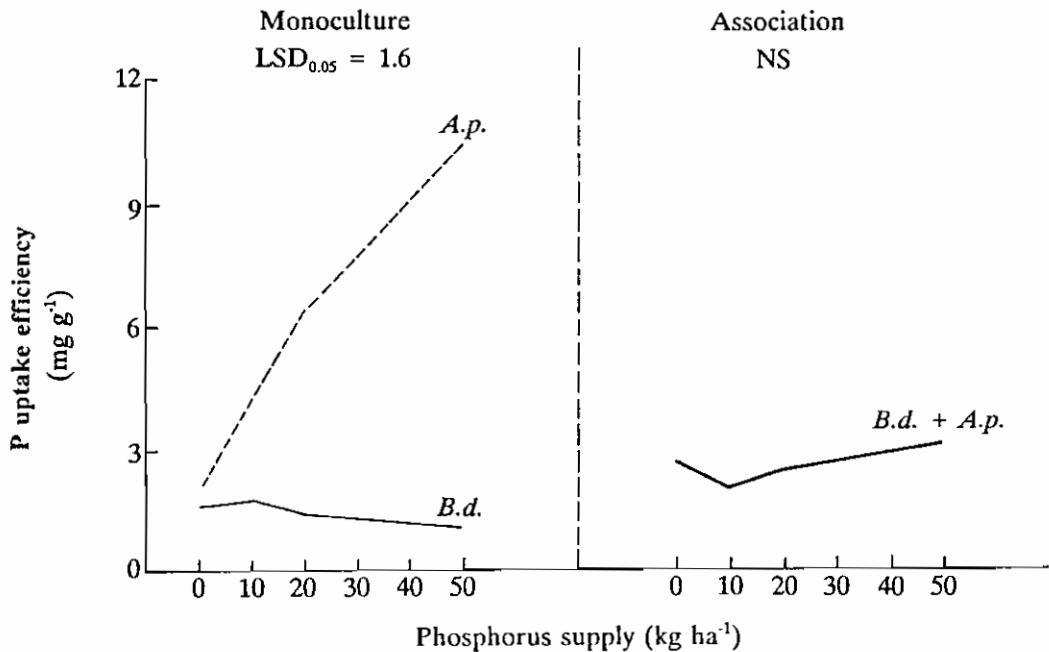

Figure 8. Changes in P uptake efficiency for a grass (*B. dictyoneura*) or a legume (*A. pintoi*) when grown as a monoculture (*B. dictyoneura*) or as an association (*B. dictyoneura* + *A. pintoi*), as affected by phosphorus supply in a clay loam soil. NS = not significant.
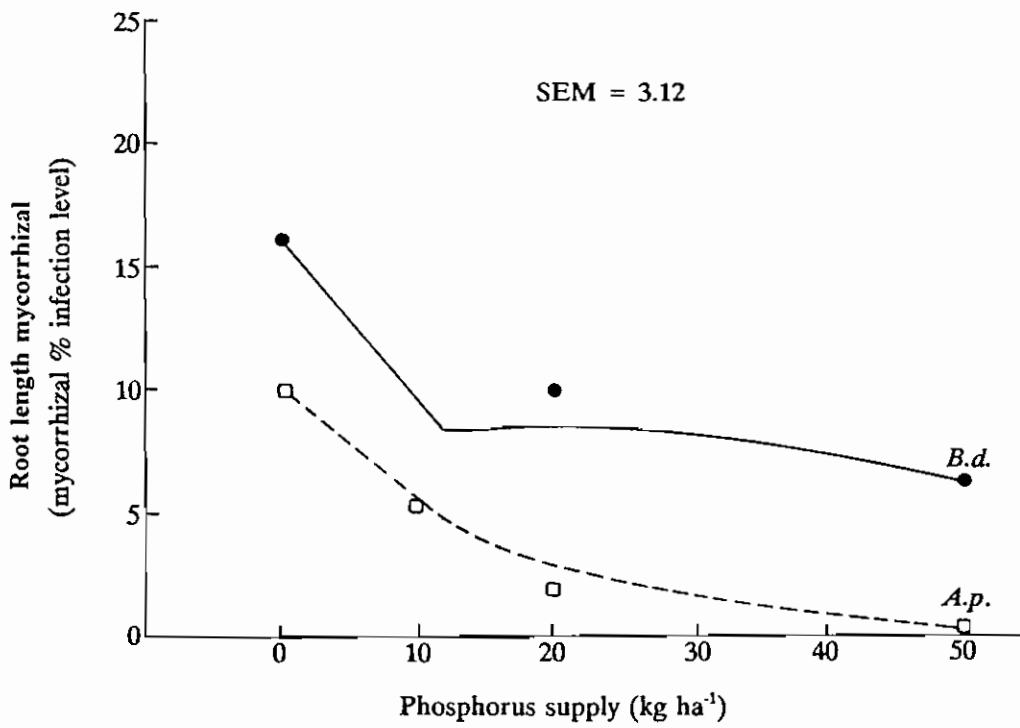
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Figure 9. Changes in root length mycorrhizal (% infection) for a grass (*B. dictyoneura*) or a legume (*A. pintoi*) in a monoculture, as affected by phosphorus supply in a clay loam soil.
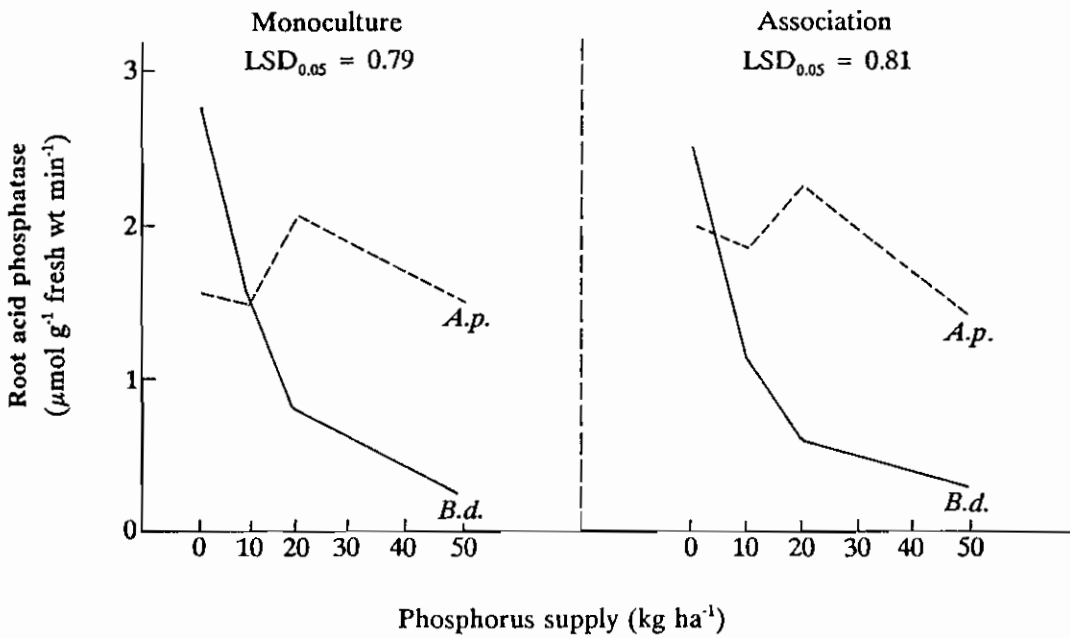

Figure 10. Changes in acid phosphatase activity in root extracts for a grass (*B. dictyoneura*) or a legume (*A. pintoi*) when grown as a monoculture or as an association, as affected by phosphorus supply in a clay loam soil.
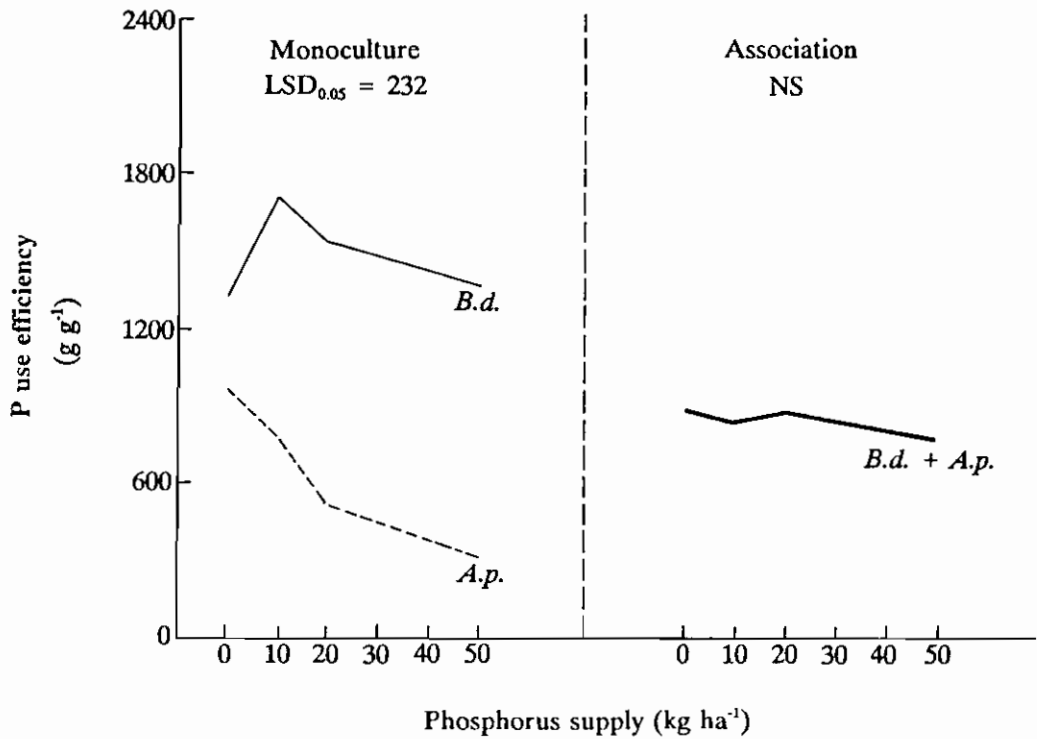
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Figure 11. Changes in P use efficiency for a grass (*B. dictyoneura*) or a legume (*A. pintoi*) when grown as a monoculture or as an association (*B. dictyoneura* + *A. pintoi*), as affected by phosphorus supply in a clay loam soil. NS = not significant.
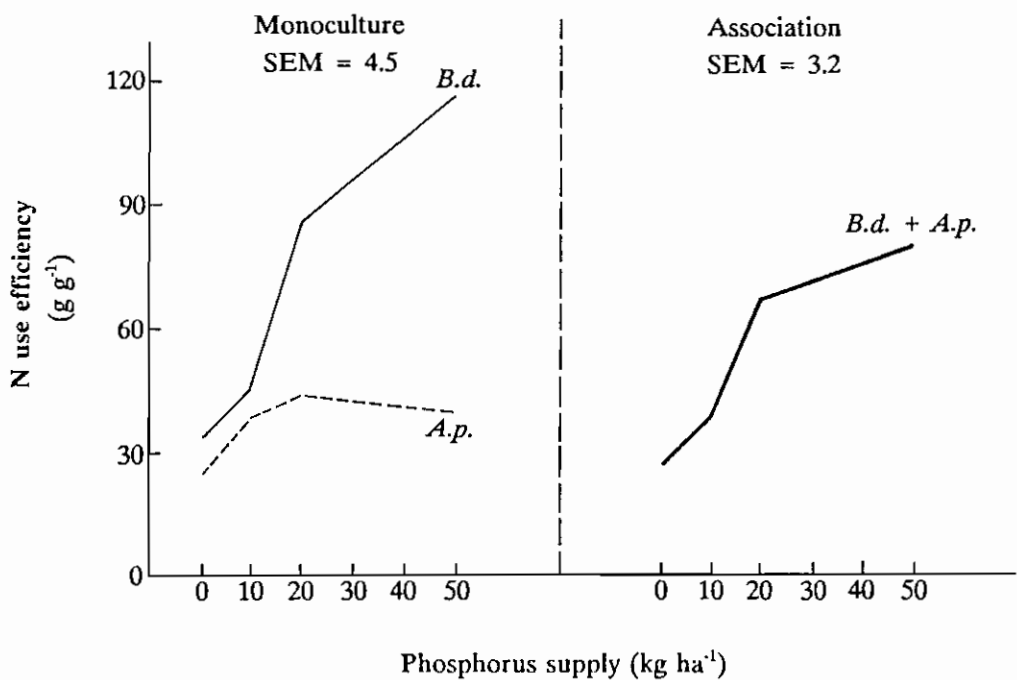

Figure 12. Changes in N use efficiency for a grass (*B. dictyoneura*) or a legume (*A. pintoi*) when grown as a monoculture or as an association (*B. dictyoneura* + *A. pintoi*), as affected by phosphorus supply in a clay loam soil.

exuding organic acids, Al- and Fe- chelators, reducing agents, or enzymes such as phosphatases.

Response to water deficits in soil

Seasonal drought is a dominant feature of the savanna environment, so that adapted forage species must be able to tolerate considerable soil water deficits (Cochrane et al., 1985; Baruch and Fisher, 1991). Research conducted in the TPP before this review period indicated that a number of most promising forage grasses, including *Brachiaria* spp., *Andropogon gayanus*, and *Panicum maximum*, are tolerant of seasonal droughts (CIAT, 1978). Recently, the ability of a range of forage legume species to tolerate water stress was evaluated (Table 3). The data presented are for the minimum water potential measured, and the number of weeks to achieve it. Water potential is a measure of physiological water deficit in plant tissue (Hsiao, 1973). Well-watered plants have leaf water potentials around 0 to -5 bars. Most crop plants tolerate water deficits up to -20 bars in leaves. When we compare tropical forage legumes to most field crops, they seem to tolerate much lower water potentials. Both *S. capitata* and *D. ovalifolium* were outstandingly tolerant of water stress. In contrast, *C. brasilianum* maintained its water potential relatively high (less negative value). A time-dependent decrease in leaf water potentials for *A. pintoi* and *C. brasilianum* is shown in Figure 13. Tolerance of soil water deficits in *A. pintoi* was better than in *C. brasilianum*. These two species may have contrasting physiological mechanisms to tolerate (*A. pintoi*) or avoid (*C. brasilianum*) water deficits in soil. These data indicate a broad range of adaptation to water stress in the forage species tested.

Recycling of Nutrients

In grazed pastures, nutrients cycle from the soil to pasture plants and then back to the soil, either through the death of plant tissue or via the excreta of grazing animals as shown in Figure 14. Nutrient gains to the cycle occur from rainfall and the addition of fertilizers. Nutrient losses from the cycle occur via removal in animal products, leaching, and volatilization as nutrients move through different pathways (Wilkinson and Lowrey, 1973).

The soil compartment includes plant and animal residues, available soil nutrients, and unavailable soil nutrients. The plant compartment includes the whole plant (tops + live roots). The available plant nutrient compartment involves those nutrients in solution in soil water as well as elements from the soil's labile pool of nutrients. The unavailable soil-plant nutrient compartment lumps together all sources of unavailable plant nutrients. Nutrients may be released from this compartment by processes of weathering, by mineralization of organic forms of the nutrient, or by solubilization, and may be rendered unavailable by the processes of immobilization and chemical fixation. The fertilizer compartment is shown with mineral flow to the soil's available plant nutrients.

Table 3.   Water stress tolerance of forage legumes.

Legume species	Minimum water potential (bars)	Time to reach minimum water potential (weeks)
Stylosanthes capitata	- 65.9	21.5
Desmodium ovalifolium	- 65.7	14.8
Arachis pintoi	- 61.9	13.3
Centrosema acutifolium	- 60.8	13.2
Centrosema brasilianum	- 28.9	16.8
Standard error of means	5.4***	1.0***

*** $P < 0.001$.

Animals retain only a small proportion, about 20%, of the nutrients that they ingest, and the rest are returned to the soil through excreta. The expected "buildup" in soil fertility in a grass-legume pasture under grazing could result from a more rapid cycling and greater proportion of nutrients in a plant-available form.

For purposes of illustration, a pasture ecosystem from Carimagua is used as a basis for demonstrating the extent of nutrient recycling in pastures. The pastures consist of several most promising forage species, but for the sake of clarity one grass and one legume species are selected.

Biomass production

The above- and below-ground biomass pools for a grass alone (*B. dictyoneura*) and a grass + legume (*B. dictyoneura* + *C. acutifolium*) pasture were quantified eleven months after planting and just before grazing on a sandy loam soil. There was a visual difference between the pastures. The grass-alone pasture was apparently nitrogen-deficient. These pastures received recommended fertility for establishment, which did not include nitrogen. Although the grass-alone pasture looked chlorotic, it had almost an equal amount of above-ground biomass (Table 4). However, the below-ground biomass production in the grass-alone pasture was 44% higher than in the association. These data indicate that, in the absence of the legume, the grass explores a greater volume of soil in search of the limiting nutrient nitrogen.
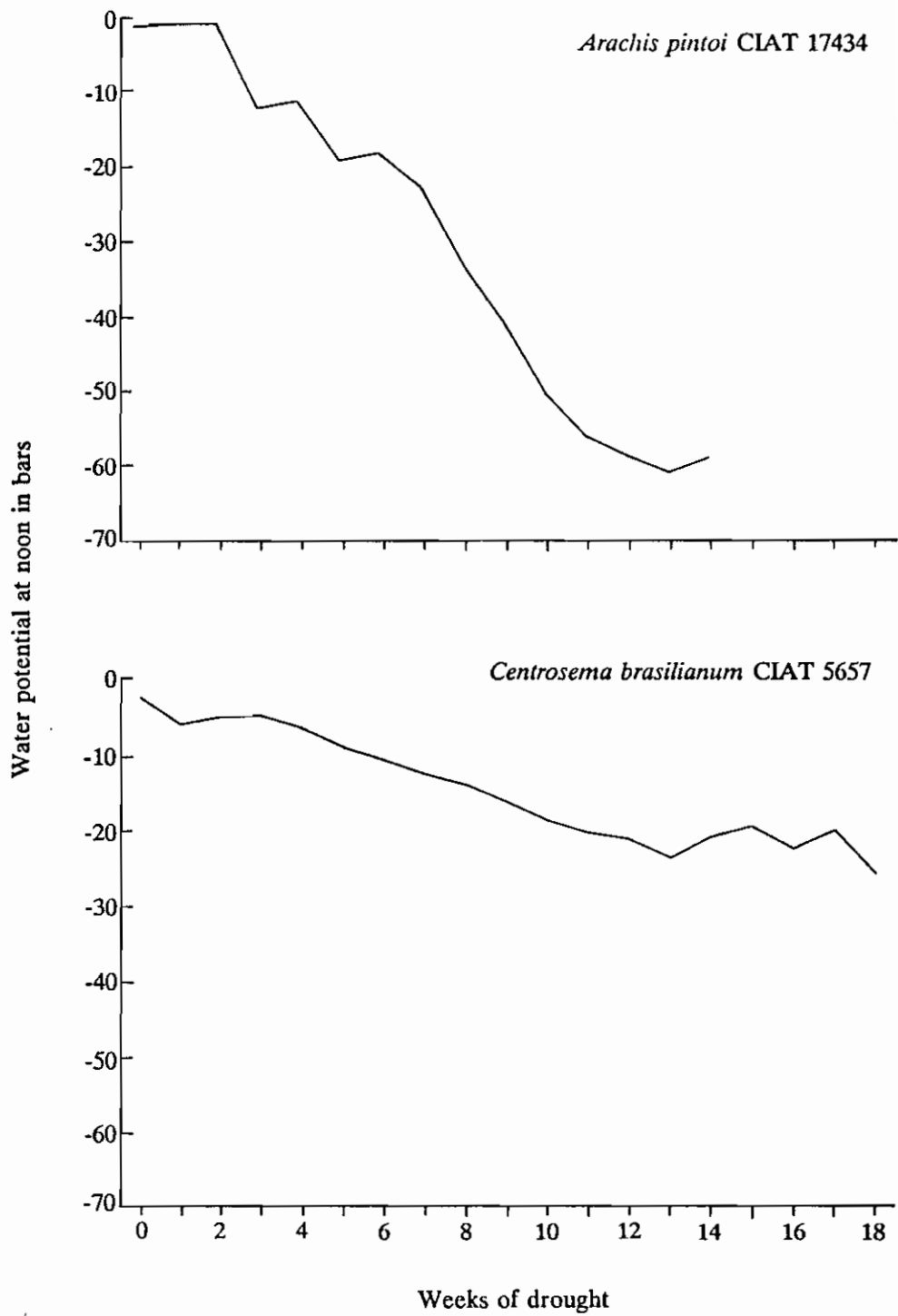
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Figure 13. Changes in leaf water potential during drought.
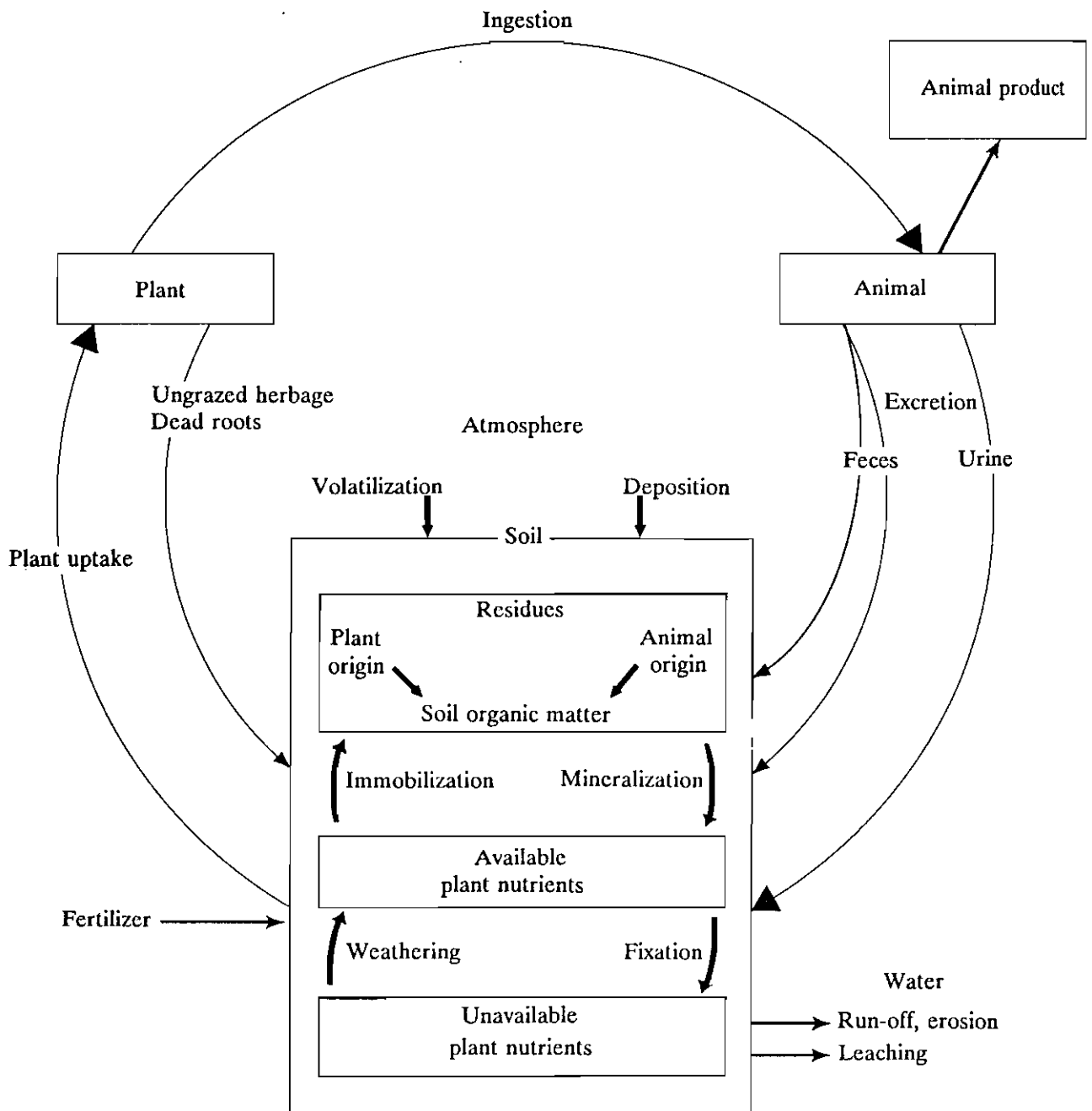
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Figure 14.   Simplified cycle of nutrients in grazed pasture.   (After Wilkinson and Lowrey, 1973.)

Table 4. Distribution of above- and below-ground biomass (g m⁻²) in 11-month-old pastures in a sandy loam soil prior to grazing.

Dry matter	Grass alone (*B. dictyoneura*)	Association (*B. dictyoneura* + *C. acutifolium*)	
Above-ground			
Standing live	213	173	79
Dead	149	109	39
Below-ground			
Roots	418 ± 156	291 ± 101	
Total	780	691	

± S.E.

Root distribution across the soil profile for the same pastures is shown in Figure 15. There was more root biomass in the top 20 cm of soil profile in the grass-alone pasture than in the association. The legume root proportion in the association was estimated using a $^{13}C/^{12}C$ ratio and found to be less than 20% across the soil profile. Also, the greater distribution of roots in the topsoil layers is important for nutrient conservation because the distance between the site where nutrients are released by plant residues and organic matter and the site where they are absorbed by the plant is very short. Therefore, nutrients are not leached before being used by the plant. It is important to note that a considerable amount of root biomass was distributed in the deeper layers of the soil profile.

Plant residues

The above-ground litter decomposition over time as a percentage of organic matter remaining for *B. dictyoneura* and *A. pintoi* was determined using litter-bag techniques (Figure 16). It is clear that decomposition was faster for the legume than for the grass. The half-life of grass litter was 116 days compared with only 50 days for legume litter. The extent of release of N from the legume litter was also markedly higher than that of the grass (Figure 17). The legume litter released almost four times more nitrogen than the grass. The legume litter also released P and K (Figure 18). The pattern of release of P was similar to that of N, but 80% of K was released very rapidly within two weeks.

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Grass alone

Total root biomass 4.2 t ha^{-1}
S.E. = 0.15

Total root length = 31 km m^{-2}

B.d.

Association

Total root biomass 2.9 t ha^{-1}
S.E. = 0.1
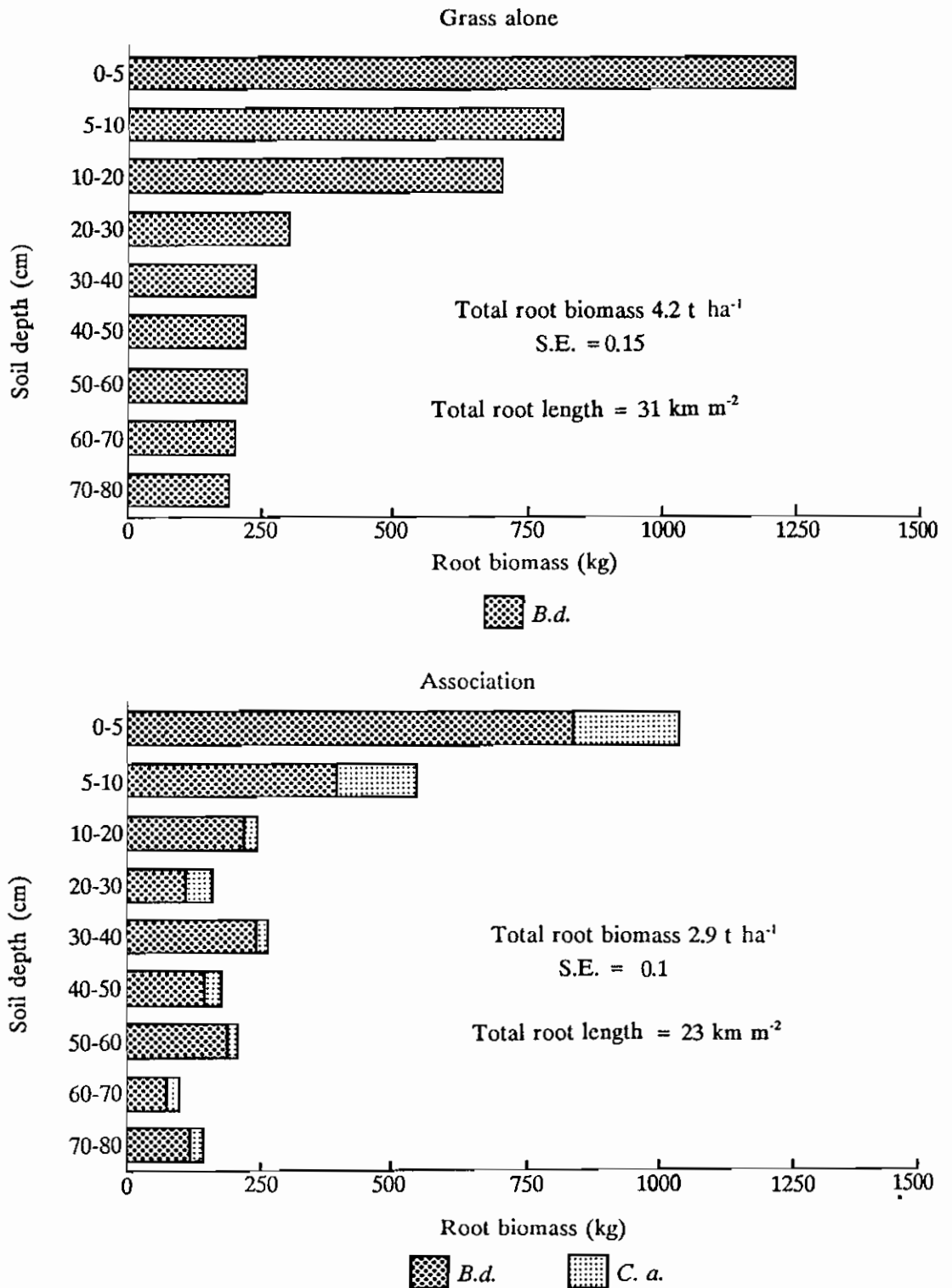
Total root length = 23 km m^{-2}

B.d. *C. a.*

Figure 15. Root biomass distribution in a grass alone (*B. dictyoneura*) or grass + legume (*B. dictyoneura* + *C. acutifolium*) pasture at 11 months after establishment. The legume root biomass in an association was determined by stable isotope analysis.
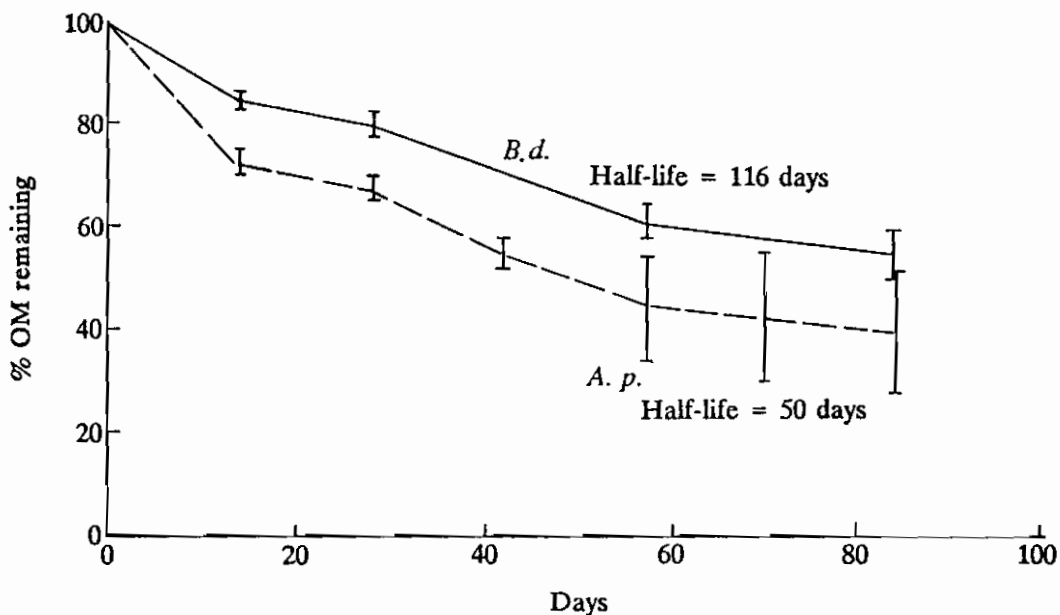
Figure 16. Decomposition of a grass (*B. dictyoneura*) or a legume (*A. pintoi*) litter over time as determined by % of organic matter remaining in the litter bag. Values are mean ± S.E. for 5 replications.
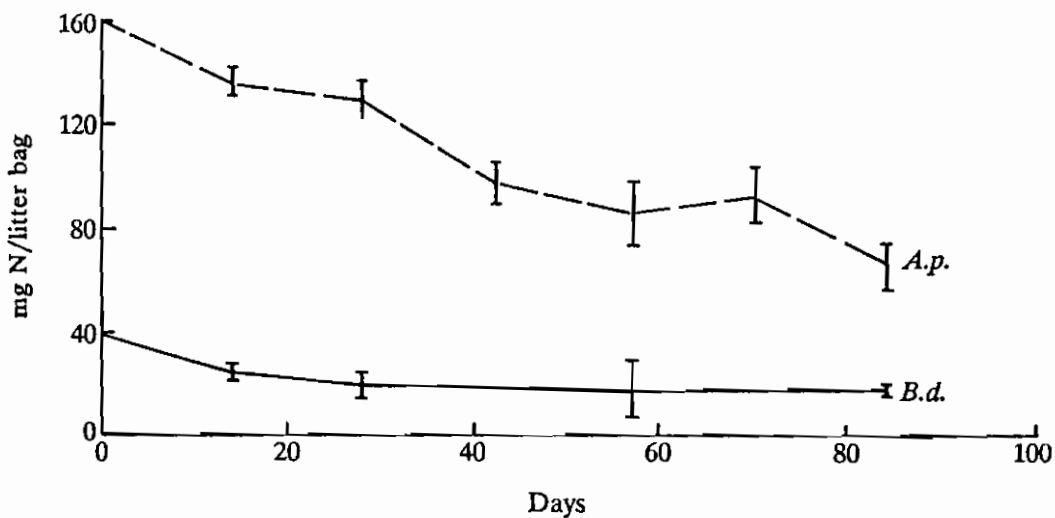

Figure 17. Release of N from litter bag for a grass (*B. dictyoneura*) or a legume (*A. pintoi*) over time. Values are mean ± S.E. for 5 replications.
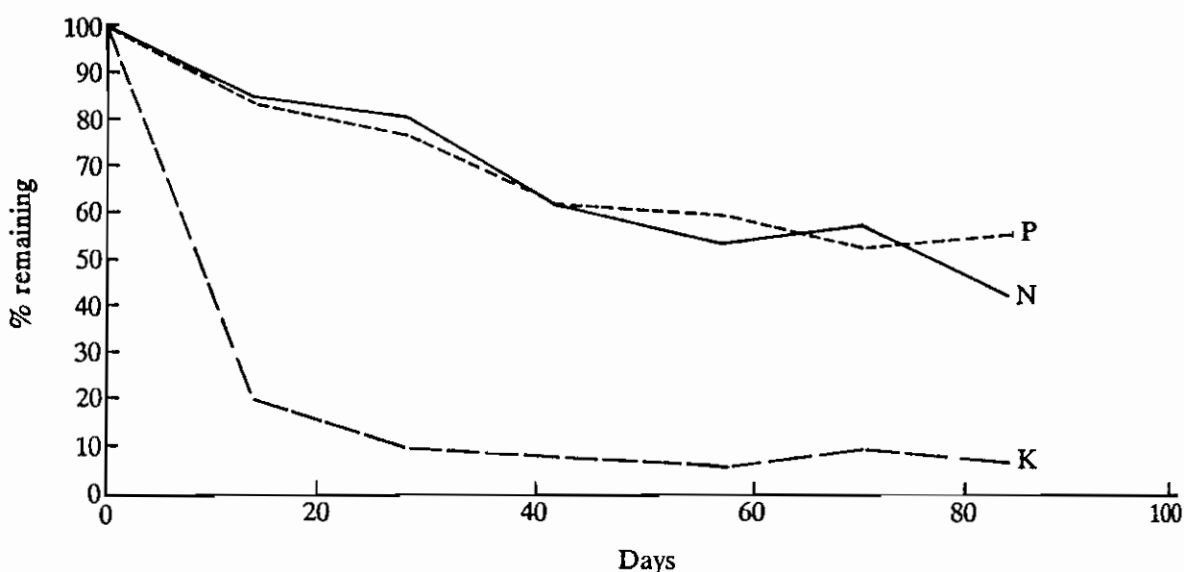
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Figure 18.   Release of N, P, and K from a legume (*A. pintoi*) litter over time as determined by % of nutrient remaining in the litter bag.

Animal residues

Compared with the nutrient composition of above-ground litter, the animal dung pats had a higher concentration of several key nutrients (Table 5). The levels of N, K, and S are high in the urine. Since the animal in the system is mobile, cycling of nutrients from animal residues will be a function of that mobility, whereas cycling of mineral nutrients from plant residues is not complicated by mobility factors. The mapping of feces distribution in a grass + legume pasture at two stocking rates indicated that dung pats tended to be randomly distributed across the paddock and the number of dung pats increased with the increase in stocking rate.

Organic matter quality and turnover

Plant and animal residues contribute to the overall soil organic matter quality and turnover. This was assessed in long-term pastures (12 years old) of grass alone (*B. decumbens*), grass + legume (*B. decumbens* + *Pueraria phaseoloides*), and legume alone (*P. phaseoloides*) using principles of isotopic dilution. In collaboration with scientists from CSIRO (J. Skjemstad and R. LeFeuvre), Australia, we have used the technique of ^{13}C natural abundance in soil organic matter (Skjemstad et al., 1990; Vitorello et al., 1989) in order to identify carbon sources in soil and to determine the changes that occur in soil organic matter when a native savanna vegetation (C_4) is substituted by grass (C_4) or grass + legume (C_3) pastures.

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Table 5. Nutrient composition of above-ground litter and dung pats of animals.

Source	Nutrient composition				
	N	P	K	Ca	Mg
			(% of dry wt)		
Grass litter (*B.d.*)	0.50	0.04	0.09	0.27	0.06
Legume litter (*A.p.*)	1.79	0.07	0.40	1.92	0.12
Dung pats	1.40	0.61	0.56	1.41	0.50

The differences in vertical distribution of total carbon and $\delta\,^{13}C$ values for each pasture at different soil depths are shown in Figure 19. The total carbon content in grass-alone and grass + legume pastures was very similar at different soil depths (Figure 19A). However, when $\delta\,^{13}C$ values of the two pastures were compared, there were marked differences between the two pastures. Using these $\delta\,^{13}C$ values, the percent carbon derived from the legume was calculated at 2-cm intervals for the top 10 cm of the soil profile. These values are shown in parentheses for the grass + legume pasture. Based on these calculations, the contribution of the legume carbon was estimated to be up to 29% of the total carbon of the association at 0-2 cm soil depth, and its contribution decreased gradually through the soil profile (7% at 8-10 cm depth) (Figure 19B).

Soil Conditions

Well-adapted, well-managed, legume-based tropical pasture systems have low levels of soil nutrient extraction because most of the output is high-quality energy and protein that is primarily made of freely available C, N, H, and O and small amounts of P, K, Ca, and Mg from soil. As shown before, such pastures also maintain high above-ground production (Thomas et al., Chapter 8) coupled with profuse and vigorous root systems for minimizing leaching of nutrients and soil erosion while improving soil structure and fertility status.

Fertility

Changes in soil organic matter content and total nitrogen status at different soil depths for long-term pastures of grass alone, grass + legume, and legume alone are shown in Figure 20. Although the soil organic matter content of the topsoil for grass-alone and grass + legume pastures was similar (Figure 20A), and because of the contribution of the legume residues which had higher nitrogen status, the total
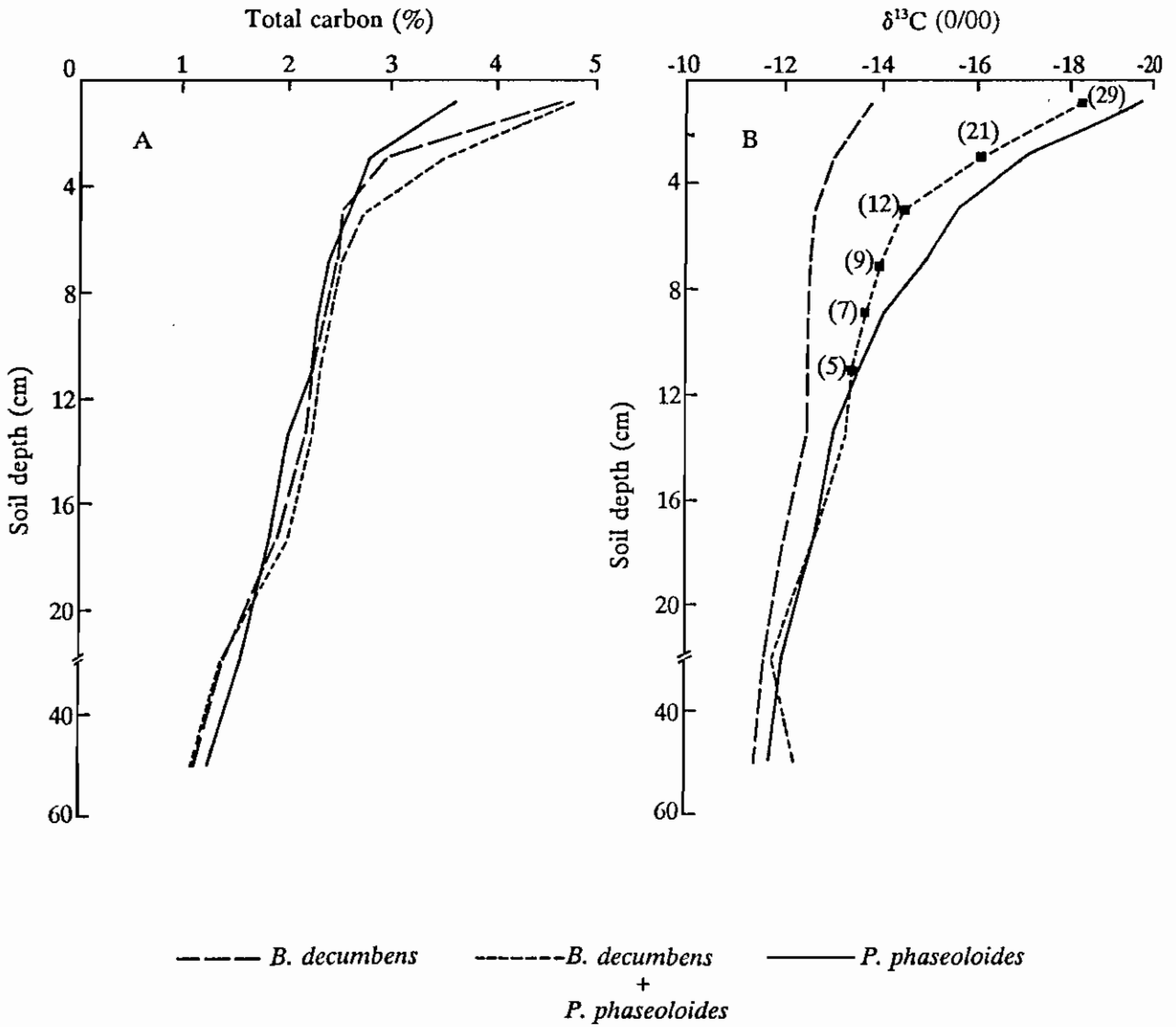
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Figure 19. Distribution of total carbon content and ^{13}C natural abundance in relation to soil depth in different pastures. Values in parentheses represent % of carbon derived from legume in a grass + legume association.
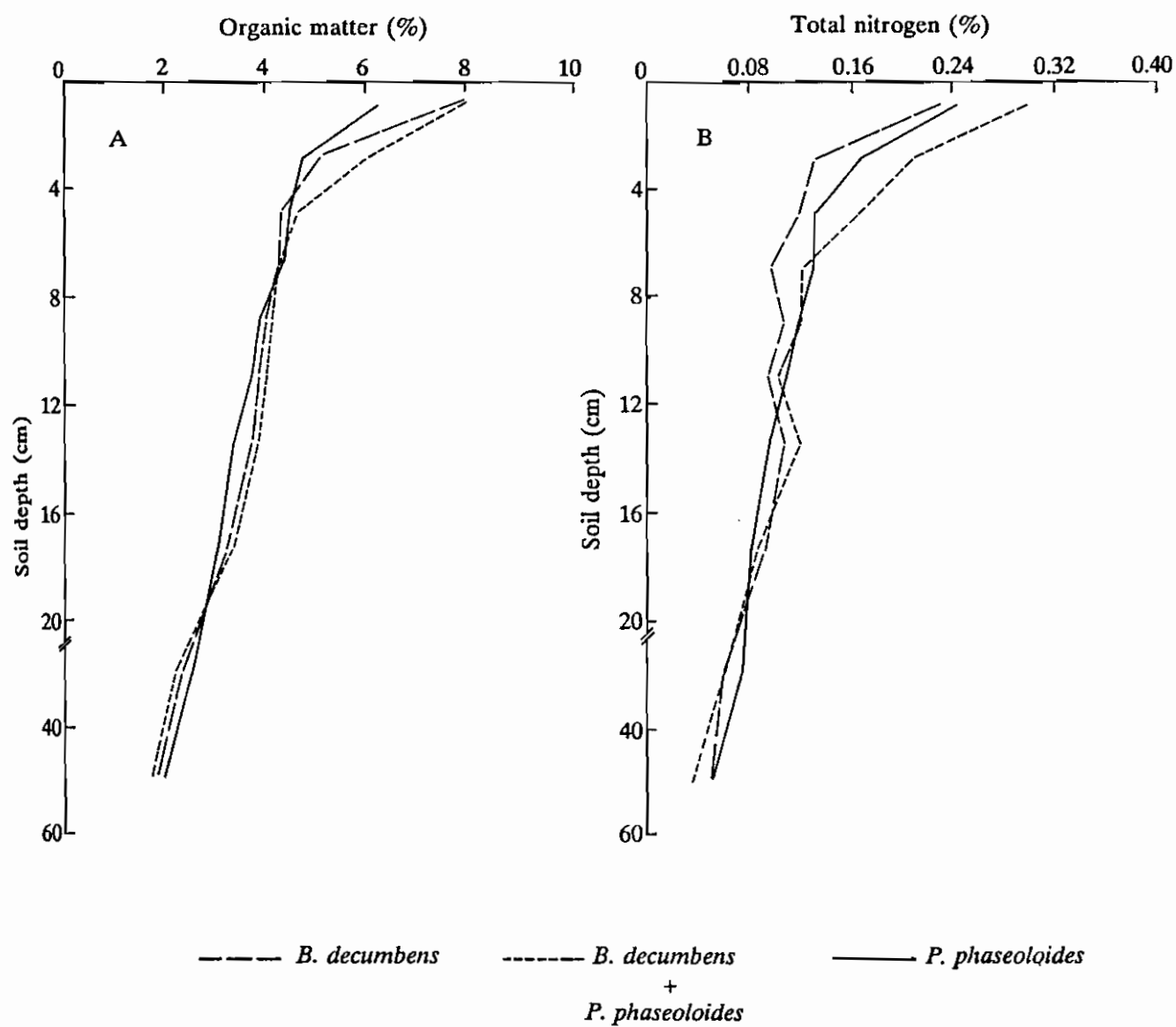
Figure 20. Distribution of soil organic matter and total nitrogen in relation to soil depth in different pastures.

nitrogen content of the 0-10 cm depth of the profile was higher in the grass + legume pasture (Figure 20B). The potential N mineralization rates (as assessed by two different methods) of soil from grass + legume pastures were substantially higher than that of the grass-alone pastures (Table 6).

Soil organic P level as a percent of total P was estimated in native savanna, improved grass, and grass + legume pastures (Figure 21). Legume-based pasture had twice as much organic P as the native savanna. In the case of exchangeable levels of K, Ca, and Mg, the legume-based pastures within two years pumped more Ca and Mg from deeper layers of soil profile while K availability was not much affected (Figure 22).

Structure

In order to estimate soil structural changes in different pastures, we have determined soil aggregate size and water infiltration rates. Compared with native savanna pastures, legume-based leys improve soil structure by increasing soil aggregates and water infiltration (Table 7).

Biological activity

Compared with native savanna, the biological activity of the improved pastures, in terms of the population of nitrifying bacteria (TPP annual report, 1985) and mycorrhizal spores and percent of mycorrhizal root infection (Dodd et al., 1990), was markedly higher (Table 8). The activity of earthworms increased threefold in the improved pastures. This increased biological activity is beneficial to soil properties such as mineralization, humification, texture, porosity, water infiltration, and retention. Soil characteristics are both a determinant and the consequence of earthworm activities, since these macro-organisms greatly influence the functioning of the soil system. They build and maintain the soil structure and take an active part in energy and nutrient cycling through the selective activation of both mineralization and humification processes (Lavelle, 1988).

Benefits from Soil Enhancement

The contribution of legume residues to soil organic matter quality and turnover together with improved soil fertility, soil structure, and biological activity were associated with a 1.7 t ha^{-1} yield increase in a rice crop following 10-year-old grass + legume plots that did not require any N fertilizer when compared with rice following a grass-alone pasture of the same age (Figure 23). These yield differences indicate that the technique of ^{13}C natural abundance in soil organic matter may prove to be a valuable aid in predicting the likely beneficial effects of a forage legume for subsequent production of pastures and/or field crops. For our partners in national programs, determination of total nitrogen in the top 10 cm of soil profile at 2-cm

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Table 6. Potential N mineralization rates of soil under *B. decumbens* or *B. decumbens* + kudzu pasture measured by two methods.

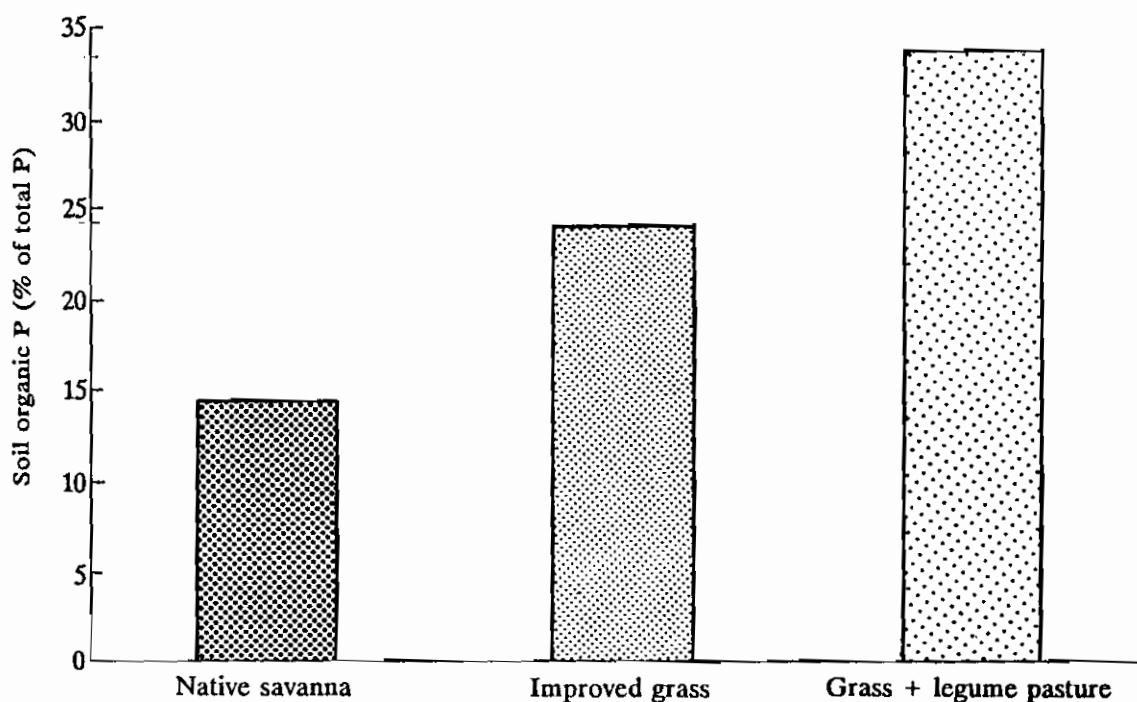| Method	*B. decumbens*	*B. decumbens* + kudzu
	(μg N g^{-1} soil day^{-1})	
Incubation in pots in glasshouse for 4 weeks	0.519 ± 0.085	0.913 ± 0.116
Anaerobic incubation at 40 °C for 7 days	3.86 ± 1.33	6.84 ± 1.69

Mean ± S.E. of 15 samples.

Figure 21. Proportion of soil organic P as % of total P in different pastures.
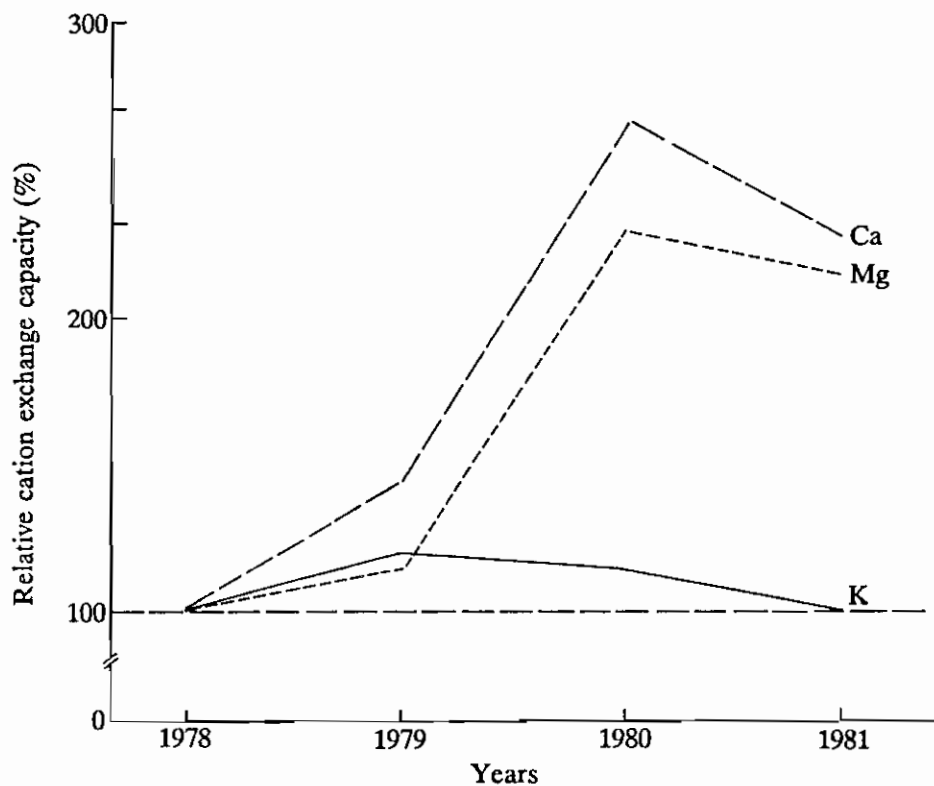
169

Figure 22.   Relative increases of Ca, Mg, and K in a grass + legume (*A. gayanus* + *P. phaseoloides*) pasture.

Table 7. Soil physical properties in different pastures in a medium-texture Oxisol of Carimagua, Colombia.

Pastures	% of soil aggregates > 0.5 mm	Water sorptivity (cm/sec$^{1/2}$)
Native savanna	9.6 a	0.20 a
Improved grass	25.5 b	0.40 b
Grass-legume pasture	31.9 b	0.39 b

Means in a column not followed by the same letter differ.

(T test, P = 0.05).

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Table 8. Comparison of soil biological activity in different pastures.

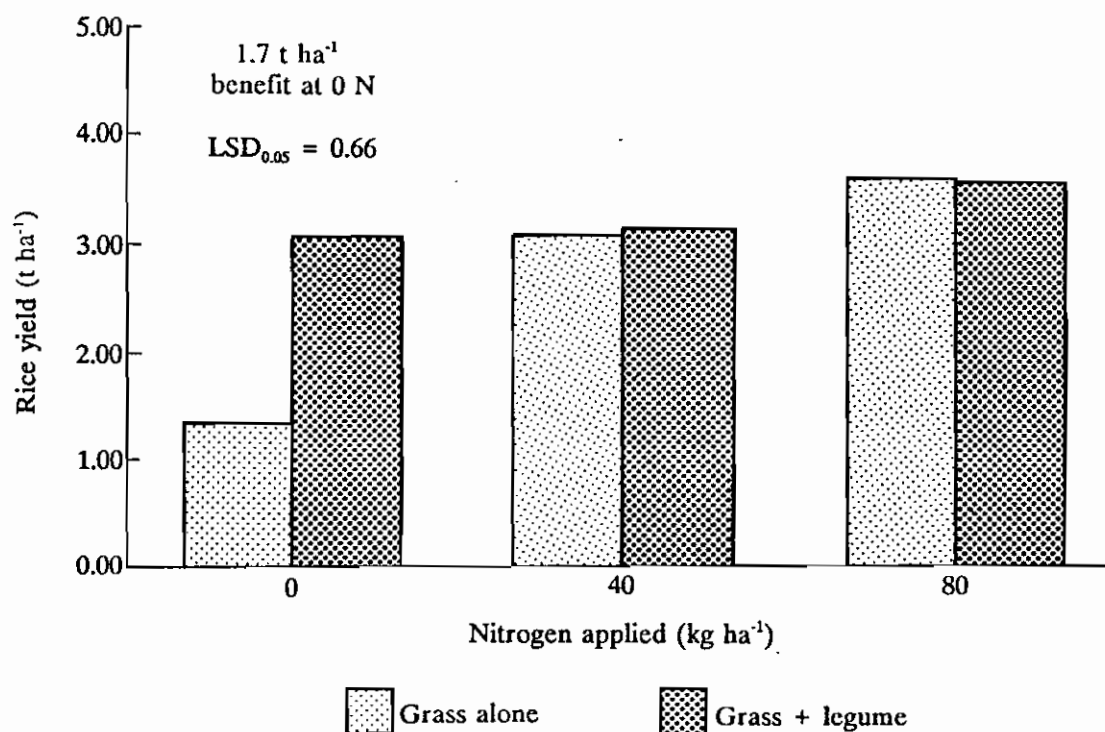| Soil biological characteristic	Savanna	Improved grass	Grass + legume
Nitrifying bacteria (number/g soil)	3.9×10^6	2.7×10^8	—
VA mycorrhizal fungi spore population (spores/100 g soil)	50	190	275
Root infection with VA mycorrhizae (%)	31	54	58
Earthworm activity (casts/m^2)	0.9	2.1	3.1

Figure 23. Grain yield response of rice crop to N application following 10-year-old grass-alone (*B. decumbens*) or grass + legume (*B. decumbens* + *P. phaseoloides*) pasture.

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intervals and rate of potential N mineralization could serve as simple research methods to evaluate the contribution of forage legumes to soil enhancement.

Integration of Processes

Pastures under grazing are more complex than annual cropping systems. As shown before, the limiting processes and regulatory mechanisms are numerous and varied, and they all have to be studied simultaneously and continuously over a long period of time in order for the system to be understood in its totality. However, weaknesses exist in our ability to effect a detailed integration of the various processes and their relations. Therefore, the holistic analysis offered by a "Modeling Approach" can enable us to predict the net results from different interacting processes.

Modeling is only a tool to put things together holistically and aim at a cause-effect assessment of a complex system. A model can provide the functional framework to organize and identify key processes (within the soil-plant-animal factors) and to focus experiments to better understand how pastures respond to strategic inputs and management. A good model will provide a reduced description encapsulating the essence of the processes involved. The modeling approach will make us become increasingly aware of the need to think quantitatively and to view our results within the context of the whole soil-plant-animal system. In collaboration with Prof. John Thornley of the United Kingdom and Prof. W. Parton of the United States, we are in the process of modeling legume-based tropical pastures under grazing. We are also interacting with the Tropical Soil Biology and Fertility (TSBF) program.

* * *

As Aldo Leopold (1949) said, "For every atom lost to the sea, the prairie pulls another out of the decaying rocks. The only certain truth is its creatures must suck hard, live fast, die often, lest its losses exceed its gains."

Conclusions

Adaptation attributes

Improved grasses and legumes adapt to nutrient-poor acid soils by maintaining their photosynthetic activity per unit leaf area and allocating fixed carbon to root growth and production at the expense of shoot growth and production.

The greater root and shoot production in grasses is associated with more efficient use of nitrogen and phosphorus. The higher phosphorus uptake

efficiency in legumes is associated with greater activity of the enzyme acid phosphatase in roots.

Recycling of nutrients

Compared with grass litter, legume litter has more nutrients (N, Ca, K) and they are released faster, thereby contributing to the superior soil organic matter quality of legume-based pastures.

^{13}C natural abundance in soil organic matter, total nitrogen status of topsoil profile, and potential rate of nitrogen mineralization in the soil are useful indicators of soil enhancement in legume-based pastures.

Soil conditions

Soil improvement in legume-based pastures is due to increased soil fertility from nutrient recycling through plant and animal residues, improved soil structure, and greater soil biological activity.

Summary

Integration of improved germplasm with sound management technologies is essential for the development of viable production systems in different agroecosystems in lowland tropics. An interdisciplinary research team was assembled at CIAT for improved understanding of soil-plant-animal factors and processes in order to design better systems of ley farming. In addition to management, productivity in legume-based leys, in nutrient-poor acid soils, is affected by adaptation attributes of forage germplasm, recycling of nutrients, and soil conditions. Tropical forage species adapt to acid soils by maintaining their photosynthetic activity per unit leaf area and allocating a significant proportion of fixed carbon to root growth and production. Soil enhancement in legume-based leys is due to increased soil fertility from biological nitrogen fixation and nutrient recycling through plant and animal residues, improved soil structure, and greater soil biological activity. Carbon-13 natural abundance in soil organic matter, total nitrogen status of the soil surface horizon, and the potential rate of nitrogen mineralization in the soil are useful indicators of soil enhancement in legume-based leys.

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