Differences in root distribution, nutrient acquisition and nutrient utilization by tropical forage species grown in degraded hillside soil conditions[1]

Diferencias en la distribución de raíces, absorción y utilización de nutrientes por especies forrajeras tropicales en condiciones de suelos degradados de ladera

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Abstract

Low nutrient availability, especially phosphorus (P) and nitrogen (N) supply is the major limitation to forage production in acid infertile soils of the tropics. A field study was conducted at the farm 'La Esperanza' located in Mondomo, Department of Cauca, in the coffee growing zone of Colombia. The main objective was to determine differences in root distribution, nutrient (N, P, K, Ca, Mg and S) acquisition and nutrient utilization of one C_4 forage grass (*Brachiaria dictyoneura*) and two C_3 forage legumes (*Arachis pintoi* and *Centrosema macrocarpum*) grown under two fertilization levels, cultivated either in monoculture or in association and harvested at four different ages.There were no significant differences in root biomass among the grass and legumes and their combinations. The native vegetation had the lowest root biomass; while the introduced grass (*B. dictyoneura*) had the highest root length density among all materials at all depths and ages and the native vegetation had the highest specific root length. As expected, nutrient uptake increased with age and with high fertilization in all species. *Centrosema macrocarpun* had the highest N and Ca uptake among all plant materials tested. Uptake of P, K and Mg was greater in the grass *B. dictyoneura* than in the other plant species and combination planting at all ages. On the other hand, the grass had the lowest Ca uptake. The grass and its mixture with the legumes *A. pintoi* and *C. macrocarpun* had the highest S uptake. A highly significant ($p<0.001$)correlation was found between root length density (depths 0-10 and 10-20 cm) and N and P uptake. Nutrient use efficiency (g of forage produced for g of nutrient uptake) increased with age until 38 weeks. At 55 weeks a sharp decline was observed in nutrient use efficiency. N, Ca and P use efficiency values were higher with the grass than with the two legumes tested. K use efficiency was similar among the three species. For Mg and S the grass had the highest values and the legume, *A. pintoi* the lowest.

Key words: Plant nutrition, nutrient uptake, *Brachiaria dictyoneura*, *Centrosema macrocarpum, Arachis pintoi*, hillside, Colombia.

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Resumen

La baja disponibilidad de nutrientes, especialmente fósforo (P) y nitrógeno (N) es el mayor limitante para la producción de forrajes en los suelos ácidos de baja fertilidad del trópico. En la finca La Esperanza. localizada en Mondomo, departamento del Cauca, zona cafetera de Colombia, se llevo a cabo un estudio con el objeto de determinar las diferencias en la distribución de raíces, absorción y utilización de nutrientes (N, P, K, Ca, Mg, y S) de una gramínea forrajera C4 (*Brachiaria dictyoneura*) y dos leguminosas C3 (*Arachis pintoi* y *Centrosema macrocarpum*) creciendo bajo dos niveles de fertilización y cultivadas en monocultivo y en asociación y cosechadas a cuatro diferentes edades. No se encontraron diferencias significativas en biomasa de raíces entre la gramínea y las leguminosas y sus asociaciones. La vegetación nativa presentó la menor cantidad de biomasa de raíces; mientras que la gramínea introducida (*B. dictyoneura)* presentó la menor cantidad entre todos los materiales en todas las profundidades y edades, y la vegetación nativa presentó la más alta longitud especifica de raíces. Como era de esperar, la absorción de nutrientes se incremento con la edad y con el mayor nivel de fertilización en todas las especies. *Centrosema macrocarpun* tuvo la más alta absorción de N y Ca entre todos los materiales evaluados. La absorción de P, K y Mg fue mayor en la gramínea que en las otras especies solas o asociadas. Por otro lado, la gramínea presentó la más baja absorción de Ca. La gramínea sola y las asociaciones con las leguminosas *A. pintoi* y *C. macrocarpun* presentaron la mayor alta absorción de S. Se encontró una alta correlación ($P < 0.001$) entre la densidad de longitud de raíces (profundidades 0 - 10 y 10 - 20cm) y la absorción de N y P. La eficiencia de uso de nutrientes (forraje producido/nutriente absorbido -g/g)) incrementó con la edad hasta las 38 semanas. A 55 semanas se observó una fuerte caída en la eficiencia de uso de nutrientes. Los valores de la eficiencia de uso de N, Ca y P fueron más altos con las gramíneas que con las leguminosas evaluadas. La eficiencia de uso K fue similar entre las tres especies. La gramínea mostró los mas altos valores de Mg y S, y la leguminosa *A. pintoi* el menor.

Palabras clave: Nutrición de plantas absorción de nutrientes,*Brachiaria dictyoneura*, *Centrosema macrocarpum, Arachis pintoi*, suelos degradados.

Introduction

Plants obtain nutrients and water from the soil by uptake through their roots (Rao and Cramer, 2003). The ability of forage plants to remove nutrients from soil is important both for use of 'natural' nutrients and for the efficiency with which fertilizers are used (Rao et al., 1992; Rao, 2001). Nutrient uptake by plants is related to soil parameters such as nutrient availability, buffering capacity and mobility (Nye, 1966). Inputs of nutrients like phosphorus (P) and nitrogen (N) are essential to increase and sustain forage production but are often unaffordable for poor farmers (Friesen et al.,1997; Rao, 2001). In tropical Oxisols, Ultisols and Andisols much of the P applied is fixed in the soil and become unavailable to the plant (Friesen et al., 1997; Rao et al., 1999). Therefore, it is important to select forage species that more efficiently take up and use nutrients (Friesen et al., 1997; Malagon et al.,1992 ; Reining et al,1992; Rao et al., 1999; Rao, 2001).

Root morphology which comprises, root density, root depth, root length, the number of root hairs, and the root tips, has been considered important for uptake of water and nutrients (Mengel and Kirby, 1987). In many soil conditions rooting density, that is the total length of roots per unit volume of soil and depth penetration is the most important trait influencing nutrient uptake (Barber, 1984), particularly for the uptake of relatively immobile nutrients like P (Rao et al., 1989). Nye and Tinker (1977) and Molz (1981) pointed out that root acquisition of water and nutrients is based more upon root length or root surface area than that of root mass. Eissenstat (1992) considered that plants that invest less root biomass to produce root length (high specific root length) should be able to increase the length of their total root system more readily than those of low specific root length (SRL). Thus, plants with high SRL such as tropical grasses gain an advantage in nutrient and water acquisition over those of low SRL such as tropical legumes

The objective of the present study was to determine differences in root growth and distribution and their influence on nutrient acquisition and utilization as mechanisms of plant adaptation to infertile soils of the Andean hillsides agro ecosystem. This research highlighted the importance of differences in nutrient acquisition and utilization among forage grass and legume species under field conditions. Knowledge on these interspecific differences could contribute to developing better adapted forage systems for recuperating the degraded soils of the Andean hillsides of Latin America.

Materials and methods

Location

The experimental site was located in Mondomo, department of Cauca, Colombia, which lies at 1500 m.a.s.n., at 2°, 54' north latitude and 76° 34' west longitude. The mean annual temperature is 18 °C. Mean annual rainfall is 1800 mm which is distributed bimodally with maximum values in April/May and October/November during the year. T he area was under a 3 year fallow period after cassava cropping before establishment of the field experiment.

Soils

This part of the Andean Cordillera is characterized by an irregular, rough topography with steep slopes, where large-scale land clearing for agriculture and ranching has left behind leached, acid and infertile soils. Soils in the area are Typic Dystrandetps and Oxic Distropets with high Al saturation, high acidity and low available P (Malagon et al., 1992). The soil characteristics of the experimental site are shown in Table 1.

Growth conditions

Two fertilization rates, low and high, were used. The sources of high (kg/ha) (50 P, 50 K, 50 Ca, 40 Mg 2 Zn, 2 Cu, 0.5 B and 0.2 Mo) and low (kg/ha) (20 P, 20 K, 25 Ca, 20 Mg) fertilization were TSP, KCl, Lime, MgO, $ZnSO_4$, $CuSO_4$, $Na_2B_40_7$ and $Na_2Mo\ 0_42H_20$, respectively. The high rate of fertilization is recommended for crop-pasture rotations and the low rate is for establishing pastures in acid soils. Fertilization was done by broadcasting before planting (CIAT, 1981). Six seeding treatment combinations were used: (1) *Brachiaria dictyoneura* CIAT 6133, (2) *Arachis pintoi* CIAT 17434, (3) *Centrosema macrocarpum* CIAT 5713, (4) *B. dictyoneura* + *A. pintoi*, (5) *B. dictyoneura* + *C. macrocarpum*, (6). the native vegetation. For soil preparation, a team of oxen according to the local cultivation practices was used. The experimental unit was a plot of 4 x 4 m which was divided in to five subplots. Each subplot was sampled at 16, 29, 38 and 55 weeks after planting.

Measurements and analysis

To measure root growth and distribution, an auger with a diameter of 4.8 cm was used. Six cores were taken directly above the root crown after the plant was cut to ground level.

Table 1. Soil chemical properties of the study site. Results are mean values with standard deviation in parenthesis from four randomly located profiles.

Depth (cm)	pH H_20	N total (mg/kg)	SOM (%)	P (Bray II) (mg/kg)	S (mg/kg)	Exchangeable cations ($cmol_c$/kg)				CEC	Al sat (%)
						Ca	Mg	K	Al		
0-20	4.33	1568	5.53	2.63	41	0.62	0.37	0.17	2.95	4.10	72
	(0.17)	(366)	(0.54)	(0.71)	(12)	(0.30)	(0.16)	(0.013)	(0.07)	(0.29)	(14)
20-40	4.63	644	2.80	3.60	46	0.34	0.09	0.06	2.08	2.56	73
	(0.13)	(212)	(0.92)	(3.55)	(13)	(0.17)	(0.03)	(0.02)	(0.78)	(0.59)	(13)
40-60	4.83	476	2.58	1.68	51	0.28	0.05	0.03	1.60	1.97	81
	(0.13)	(392)	(1.38)	(0.21)	(26)	(0.07)	(0.02)	(0.01)	(0.15)	(0.13)	(4)
60-80	4.85	448	2.30	3.20	56	0.30	0.05	0.02	1.29	1.66	77
	(0.10)	(317)	(1.24)	(1.75)	(25)	(0.06)	(0.03)	(0.005)	(0.30)	(0.33)	(6)
80-100	4.88	364	1.88	3.85	57	0.34	0.07	0.02	1.14	1.57	70
	(0.13)	(280)	(0.83)	(2.09)	(26)	(0.12)	(0.03)	(0.005)	(0.48)	(0.45)	(13)

Each core was separated into 10 cm segments to a depth of 40 cm while the deepest segment was 40 to 60 cm soil depth. Soil cores were refrigerated and later washed using a hydroneumatic elutriation system (Gilson's Inc., Benzonia, Michigan, USA). Root length (m/soil volume) was measured with a 'Comair' root length scanner (Commonwealth Aircraft Corp., Melbourne, Australia). Root biomass was determined by drying the roots in at oven at 70 °C and weighing. Root length density (RLD) in terms of length of roots per unit soil volume (cm/cm^3) was calculated. Specific root length (SRL), was expressed as the length of roots per unit of root weight. Nutrient composition of shoot biomass was determined according to the methods suggested by Salinas and García (1985). Nutrient acquisition (uptake) was determined using the values of biomass production (shoot) and nutrient concentration in the biomass. Nutrient utilization (nutrient use efficiency) was expressed in terms of shoot biomass (g) produced/unit of absorbed nutrient (g). The root study data were analyzed as a split-split-split block design with the species as the main plots, fertilization rates as subplots, age at harvest as sub-subplots and soil depth as sub-sub-subplots. The analysis of variance was carried out with the SAS computer program (SAS/STAT, 1990). A probability level of 0.05 was considered statistically significant.

Results

Root parameters

A significant species x depth x age triple interaction was observed in root biomass production. Fertilization level did not influence root biomass production. In general, throughout the experimental period (up to 55 weeks after planting), the forage grass *B. dictyoneura* had similar root biomass to the legumes and to the associations. The native vegetation had the lowest root biomass production (Table 2).

Root biomass of all species decreased with soil depth and was higher in the 0 - 10 cm depth than at the other depths. As expected, root biomass, increased with age. At the end of the experiment, distribution of roots (dry weight basis) indicated that for all plant materials about over 40 percent of root biomass is in the 0 - 10 cm depth soil layer (Table 3).

Root length density (RLD) which is the length of roots (cm) per unit of soil volume (cm^3) showed significant interactions among the species x age x depth and also species x fertility x depth. Throughout the experiment, *B. dictyoneura* had significant higher RLD than the other species at all depths and ages (Table 4). The second highest RLD was found in the two grass + legume associations and the native vegetation and the lowest in the two legumes growing in monoculture. RLD was lower at successive lower depths for all species. As expected, RLD consistently increases with age (Table 3). *Brachiaria dictyoneura* had the highest increments in RLD throughout the experimental period followed by the two associations and the native vegetation (Table 2).

Specific root length (SRL) –length of roots per unit weight–, which is a measure of the fineness of the root system of the grass and the legumes (Rao et al., 1996) presented significant interactions of species x depth and age x depth. There were no significant dif-

Table 2. Differences among tropical forage species in mean values of root biomass, root length density, and specific root length for 16 - 55 weeks after planting and at 0 - 60 cm soil depth.

Species	**Root biomass (g/1085 cm^3 soil)**	**Root length density (cm/cm^3)**	**Specific root length (cm/g)**
B. dictyoneura (Bd)	1.03 a*	2.11 a	25.86 b
A. pintoi (Ap)	1.09 a	0.77 c	18.92 b
C. macrocarpum (Cm)	1.17 a	1.06 c	24.99 b
Bd + Ap	1.07 a	1.61 b	22.51 b
Bd + Cm	1.15 a	1.62 b	21.36 b
Native	0.50 b	1.53 b	33.97 a

* Means in columns followed by different letters are significantly different (P<0.05), LSD test.

Table 3. Differences among tropical forage species in mean values of root biomass (g/1085 cm^3 soil) and specific root length (cm/g) for 16 - 55 weeks after planting and at 0 - 60 cm soil depth.

Species[a]	**Root biomass (g/1085 cm^3 soil)**					**Specific root length (cm/g)**			
	Time (weeks)					**Time (weeks)**			
	16	**29**	**38**	**55**	**Soil depth (cm)**	**16**	**29**	**38**	**55**
					0-10				
Bd alone	1.10	3.17	3.31	3.89		13.34	9.75	16.67	22.39
Ap alone	1.51	5.18	4.68	2.68		5.79	2.68	4.36	15.15
Cm alone	0.80	4.93	4.55	5.93		15.14	2.05	6.07	5.78
Bd + Ap	1.44	4.66	2.92	3.76		8.87	4.47	12.76	16.50
Bd + Cm	1.21	4.41	3.90	6.20		11.20	5.25	11.23	15.69
Native	0.87	0.57	1.16	1.80		29.47	34.4	37.57	45.43
					10-20				
Bd alone	0.33	0.92	1.19	2.11		25.74	30.14	31.64	39.24
Ap alone	0.39	1.77	1.50	1.17		19.12	5.85	11.31	18.39
Cm alone	0.21	1.14	1.11	1.17		34.06	10.62	23.00	31.94
Bd + Ap	0.29	1.50	1.19	1.49		26.31	14.20	21.76	33.33
Bd + Cm	0.53	0.82	0.91	1.63		22.20	21.30	29.14	33.20
Native	0.29	0.30	0.78	1.03		28.79	38.45	34.76	46.73
					20-30				
Bd alone	0	0.46	0.69	0.83		.–	32.49	38.18	48.75
Ap alone	0	0.40	0.69	0.97		.–	26.43	27.27	36.43
Cm alone	0	1.10	0.65	0.63		.–	23.53	32.75	40.98
Bd + Ap	0	0.54	0.67	0.72		.–	31.76	32.58	43.70
Bd + Cm	0	0.49	0.75	0.67		.–	23.07	26.87	37.94
Native	0	0.21	0.64	0.66		.–	49.28	33.99	47.47
					30-40				
Bd alone	0	0.34	0.49	0.53		.–	47.39	38.52	42.77
Ap alone	0	0.18	0.26	0.41		.–	55.99	25.82	29.96
Cm alone	0	0.16	0.23	0.34		.–	56.33	53.29	60.55
Bd + Ap	0	0.31	0.37	0.47		.–	44.87	41.38	37.88
Bd + Cm	0	0.27	0.44	0.39		.–	37.50	34.63	35.43
Native	0	0.10	0.69	0.49		.–	66.04	34.88	47.51
					40-60				
Bd alone	0	0	0.50	0.66		.–	.–	39.88	40.42
Ap alone	0	0	0.20	0.25		.–	.–	40.37	52.74
Cm alone	0	0	0.19	0.21		.–	.–	55.09	50.66
Bd + Ap	0	0	0.45	0.55		.–	.–	34.30	40.21
Bd + Cm	0	0	0.55	0.41		.–	.–	37.12	43.65
Native	0	0	0.48	0.43		.–	.–	48.04	57.84

a. Bd = *Brachiaria dictyoneura*, AP = *Arachis pintoi*, Cm = *Centrosema macrocarpum*

ferences among species in SRL between the two levels of fertilizer application. In general, native vegetation had the highest values of SRL at all ages and soil depths followed by *B. dictyoneura* (Tables 2 and 3). SRL consistently increased with increasing soil depth (from 0 to 60 cm). SRL varied significantly with the age of the plant species. The highest SRL increase throughout the experiment was observed with the native vegetation (Tables 2 and 3).

Nitrogen uptake and nitrogen-use-efficiency

A significant fertilizer level x age interaction throughout the experiment was observed. The legume *C. macrocarpum* had the highest N

Table 4. Differences among tropical forage species in mean values of root length density (cm/1085 cm^3 of soil) at 16, 29, 38 and 55 weeks after planting and at 0 - 60 cm soil depth.

Species	**16**		**29**		**38**		**55**	
	LF	**HF**	**LF**	**HF**	**LF**	**HF**	**LF**	**HF**
				0-10 cm**				
Bd alone	1.14	1.14	1.65	2.83	4.49	5.51	6.75	8.41
Ap alone	0.87	0.50	1.10	1.38	1.30	2.17	1.90	2.11
Cm alone	0.90	0.76	0.87	1.08	1.98	1.99	2.40	2.99
Bd + Ap	1.06	0.92	1.76	1.79	2.49	2.76	4.64	6.92
Bd + Cm	1.56	0.96	1.89	1.61	3.44	3.20	8.53	4.87
Native	0.81	1.07	0.85	2.20	2.83	3.56	5.96	6.35
				10-20 cm				
Bd alone	0.72	0.72	1.72	1.60	3.17	3.51	6.91	6.28
Ap alone	0.65	0.30	0.86	0.75	1.04	1.49	1.58	1.33
Cm alone	0.56	0.61	0.07	0.88	1.54	1.82	2.62	2.85
Bd + Ap	0.69	0.55	1.22	1.25	2.42	2.33	3.68	5.56
Bd + Cm	0.81	0.61	1.24	0.99	1.80	3.04	5.07	4.84
Native	0.72	0.77	0.75	1.15	2.12	2.29	3.01	4.39
				20-30 cm				
Bd alone	0	0	1.32	1.22	2.45	2.5	3.93	3.27
Ap alone	0	0	0.61	1.76	0.84	1.16	1.18	1.22
Cm alone	0	0	0.71	1.55	0.86	1.89	1.89	1.66
Bd + Ap	0	0	1.02	1.82	1.79	2.05	2.17	3.72
Bd + Cm	0.00	0.00	0.87	1.07	1.00	2.07	2.01	2.67
Native	0.00	0.00	0.73	1.12	1.66	2.15	2.25	2.67
				30-40 cm				
Bd alone	0.00	0.00	1.44	1.18	1.32	1.80	2.17	1.53
Ap alone	0.00	0.00	0.73	0.38	0.55	0.68	0.99	0.61
Cm alone	0.00	0.00	0.48	1.13	1.08	1.12	1.60	1.64
Bd + Ap	0.00	0.00	0.79	1.28	1.35	1.54	1.10	2.12
Bd + Cm	0.00	0.00	1.04	1.05	1.27	1.60	1.18	1.16
Native	0.00	0.00	0.65	0.89	1.43	1.50	1.54	1.78
				40-60 cm				
Bd alone	0.00	0.00	0.00	0.00	0.58	0.93	0.95	1.01
Ap alone	0.00	0.00	0.00	0.00	0.30	0.35	0.66	0.52
Cm alone	0.00	0.00	0.00	0.00	0.48	0.36	1.60	0.68
Bd + Ap	0.00	0.00	0.00	0.00	0.71	0.71	0.91	0.88
Bd + Cm	0.00	0.00	0.00	0.00	0.99	0.90	0.80	0.84
Native	0.00	0.00	0.00	0.00	1.04	1.10	1.54	1.25

* LF = low fertility; HF = high fertility; ** Soil depth
Bd = *Brachiaria dictyoneura*, AP = *Arachis pintoi*, Cm = *Centrosema macrocarpum*

uptake (N_2 fixation + uptake from soil) among the test species at both fertilization rates and at all ages. N uptake increased with age and with high fertilizer application in all species (Table 5). Nitrogen use efficiency (as measured by dry matter production of shoot per unit of N in the shoot) in the grass was 3 times higher than that of the two legumes, which had similar lower values. The two associations Bd + Ap and Bd + Cm had intermediate values (Figure 1). With respect to the age at harvest, N-use efficiency increased successively from 16 weeks to 38 weeks of age. But at the age of 55 weeks, it had decreased sharply.

Phosphorus uptake and phosphorus-use efficiency

The significant interaction between fertilizer level x age shown in (Table 5) demonstrated that P uptake varied differently throughout

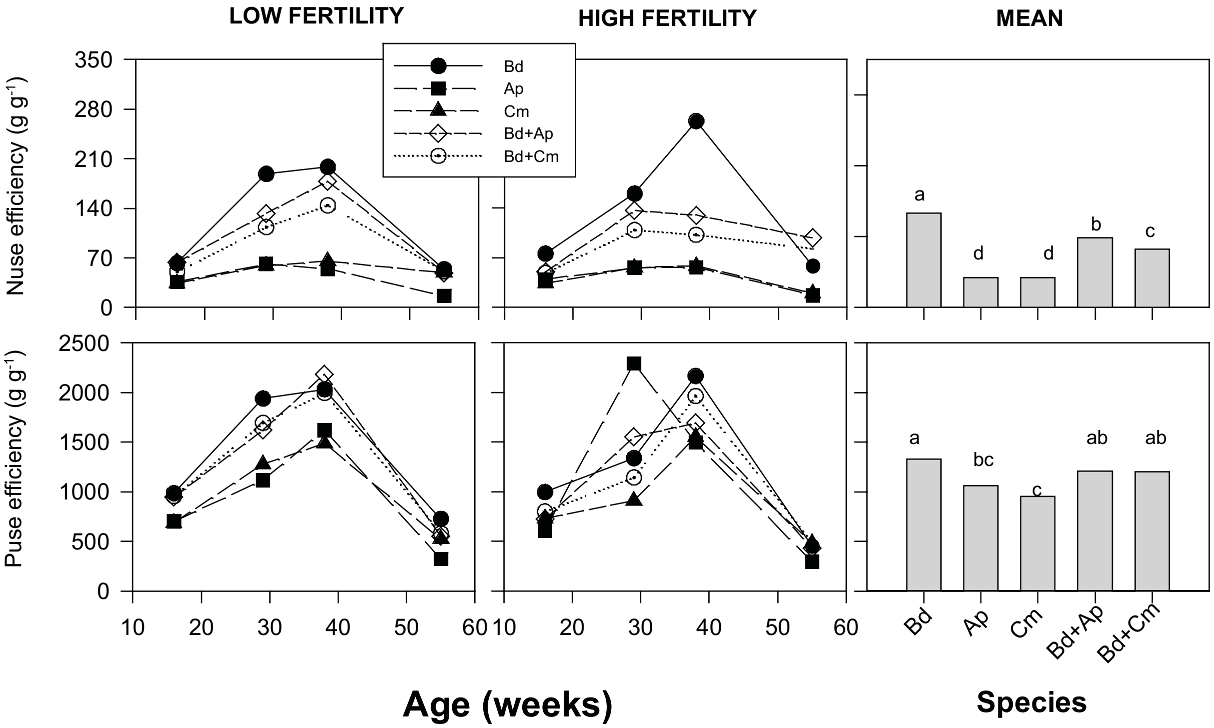

Figure 1. Differences among tropical forage species in values of N and P use efficiency (g/g) for 16-55 weeks after planting. Bars with different letters are significantly different (P<0.05), LSD test.

Table 5. Differences among tropical forage species in mean values of shoot N and P uptake (kg/ha) for 16, 29, 38 and 55 weeks after planting.

Species	16		29		38		55		Mean
	LF	HF	LF	HF	LF	HF	LF	HF	
				Shoot N uptake (kg/ha)					
Bd alone	6	29	11	41	20	53	80	133	43 b
Ap alone	7	17	11	19	19	38	73	137	40 b
Cm alone	6	10	15	39	65	71	149	293	81 a
Bd + Ap	10	13	17	16	22	40	110	146	47 b
Bd + Cm	12	18	21	27	40	57	84	127	48 b
Mean	13 d*		22 c		43 b		133 a		
				Shoot P uptake (kg/ha)					
Bd alone	0.35	2.46	0.86	5.22	1.90	7.10	7.00	21.40	5.74 a
Ap alone	0.37	1.08	0.61	0.54	0.62	1.50	4.00	8.00	2.05 b
Cm alone	0.31	0.45	0.64	2.48	2.42	2.80	6.00	13.30	3.55 ab
Bd + Ap	0.67	0.92	1.41	1.44	1.76	2.80	9.70	15.30	4.26 ab
Bd + Cm	0.59	1.09	1.34	2.44	2.91	3.00	7.40	11.10	3.72 ab
Mean	0.80 b		1.70 b		2.67 b		10.27 a		
				Shoot K uptake (kg/ha)					
Bd alone	6	56	17	91	39	159	147	312	102 a
Ap alone	5	14	6	11	9	24	41	96	26 c
Cm alone	3	6	8	22	40	38	67	135	40 bc
Bd + Ap	16	15	22	23	50	73	202	278	85 ab
Bd + Cm	13	20	27	30	60	52	145	194	68 abc
Mean	15 c		26 bc		54 b		161 a		

* Means in columns followed by different letters are significantly different (P<0.05), LSD test.
Bd = *Brachiaria dictyoneura*, AP = *Arachis pintoi*, Cm = *Centrosema macrocarpum*

the experiment with respect to the fertilization rate and age. In general P uptake was higher in *B. dictyoneura* than in the other plant species and the two grass + legume associations at all ages. The two grass + legume associations had higher P uptake than the two legumes in monoculture. *A. pintoi* had the lowest P uptake. Uptake of P was higher at the high rate of fertilization and at all ages. Whit the high fertilization rate, at 29 weeks of age P uptake was higher than that at 16 weeks. In turn, P uptake at 55 weeks of age was higher than that at 38 weeks. Phosphorus use efficiency of the grass was also higher than that of legumes (Figure 1). There were no significant differences in P-use efficiency related to fertilization level. A sharp decline in P-use efficiency from 38 weeks to 55 weeks of age was observed.

Potassium uptake and potassium-use efficiency

Because of the significant fertilizer level x age interaction, species responses varied differently throughout the experimental period. K uptake increased with increase in K supply and with the high fertilization rate at all ages (Table 5). *Brachiaria dictyoneura* had the highest K uptake and the monocultures of *A. pintoi* and *C. macrocarpum* the lowest (Table 5). Neither among species nor between fertilization rates were differences in K use efficiency detected. Only differences in age at harvest related to K-use efficiency were observed (K-use efficiency increased with age) (Tables 6 and 7).

Calcium uptake and calcium-use efficiency

The tendency toward nutrient uptake increase with age and with fertilization as observed

Table 6. Differences among tropical forage species in mean values of shoot K, Ca and Mg uptake (kg/ha) for 16, 29, 38 and-55 weeks after planting.

Species	16		29		38		55		Mean
	LF	HF	LF	HF	LF	HF	LF	HF	
Potassium									
Bd alone	6	56	17	91	39	159	147	312	102 a
Ap alone	5	14	6	11	9	24	41	96	26 c
Cm alone	3	6	8	22	40	38	67	135	40 bc
Bd + Ap	16	15	22	23	50	73	202	278	85 ab
Bd + Cm	13	20	27	30	60	52	145	194	68 abc
Mean	15 c*		26 bc		54 b		161 a		
Calcium									
Bd alone	0.5	2.8	2.0	7.1	5.0	19.1	17.1	27.5	10.1 b
Ap alone	1.5	5.7	4.0	9.1	7.0	18.0	20.7	46.0	14.0 b
Cm alone	1.4	3.0	3.8	10.1	20.4	27.7	38.7	79.9	23.2 a
Bd + Ap	1.4	4.0	4.8	5.4	7.1	19.0	23.5	40.8	13.3 b
Bd + Cm	1.6	3.1	5.1	8.9	14.4	29.0	21.8	35.3	14.9 b
Mean	2.5 c		6.1 c		16.7 b		35.1 a		
Magnesium									
Bd alone	0.8	4.9	3.3	12.7	7.7	30.0	29.2	41.3	16.2 a
Ap alone	0.8	2.1	2.1	3.8	4.6	9.7	10.5	21.3	6.9 c
Cm alone	0.5	0.7	1.5	3.8	7.3	9.0	15.7	30.9	8.6 bc
Bd + Ap	1.2	1.8	4.1	4.0	8.6	13.6	28.4	36.0	12.2 abc
Bd + Cm	1.2	1.8	4.9	5.3	16.7	13.0	32.4	34.6	13.7 ab
Mean	1.6 c		4.5 bc		11.9 b		28.0 a		
Sulfur									
Bd alone	0.6	3.4	1.8	5.9	3.4	12.2	14.0	24.4	8.2 a
Ap alone	0.6	1.4	1.1	1.4	1.8	3.5	6.6	11.8	3.5 b
Cm alone	0.7	1.1	1.3	2.9	5.2	4.2	16.6	34.4	6.7 ab
Bd + Ap	1.2	1.4	2.6	2.1	3.2	5.0	18.6	35.3	8.7 a
Bd + Cm	1.1	1.7	2.5	2.9	6.0	5.0	15.6	18.5	6.7 ab
Mean	1.3 b		2.4 b		4.9 b		18.5 a		

* Means in columns followed by different letters are significantly different ($P < 0.05$), LSD test.
Bd = *Brachiaria dictyoneura*, AP = *Arachis pintoi*, Cm = *Centrosema macrocarpum.*

in N, P, and K, was also observed for Ca uptake. The legume *C. macrocarpum* had 2-fold higher Ca uptake than the grass followed by its association with *B. dictyoneura*, the association Bd + Ap and the legume *A. pintoi* in monoculture (Tables 6 and 7). The highest Ca uptake rate of all materials was observed with the high fertilization rate. On the other hand, Ca-use efficiency of the grass was about five times greater than that of the legumes and two times greater than the associations Bd + Ap and Bd + Cm (Table 8).

Magnesium uptake and magnesium-use efficiency

The grass had the highest Mg uptake rate of all evaluated plant materials. The legumes in monoculture *A. pintoi* and *C. macrocarpum* had the lowest Mg uptake rate, respectively, (Table 6). The highest Mg uptake was observed with the high fertilization rate. Magnesium use efficiency varied differentially among species and ages. Mg-use efficiency was slightly higher at 29 weeks of age than that at the other ages (Table 7). No differences related to the level of fertilizer application were observed. Similar to the behavior of N, P, K and Ca, the Mg-use efficiency declined at 55 weeks.

Sulfur uptake and sulfur-use efficiency

Sulfur uptake varied among species with the age at harvest and with the level of fertilizer application. *Centrosema macrocarpum* had

Table 7. Differences among tropical forage species in mean values of K, Mg and S use efficiency (g/g) for 16, 29, 38 and 55 weeks after planting.

Nutrient and species	Weeks				
	16	29	38	55	Mean
Potassium					
Bd alone	46.6	83.6	103.0	30.1	65.8
Ap alone	52.0	104.5	102.0	28.7	71.8
Cm alone	65.5	100.8	100.0	43.3	77.4
Bd + Ap	44.1	94.2	75.1	25.1	59.6
Bd + Cm	40.2	89.2	105.2	28.25	65.7
Mean	49.6b	94.4a	97.1a	31.1c	
Magnesium					
Bd alone	503	716	507	190	479 a
Ap alone	308	314	227	111	240b
Cm alone	445	629	490	210	443a
Bd + Ap	441	592	451	183	417a
Bd + Cm	450	543	435	150	393a
Mean	429a	559a	422a	168b	
Sulfur					
Bd alone	583	966	1179	314	761a
Ap alone	436	699	647	188	492b
Cm alone	291	708	818	226	511b
Bd + Ap	497	912	1065	249	681a
Bd + Cm	475	913	540	278	683a
Mean	457b	840a	850.0a	251.0c	

* Means in columns or in rows followed by different letters are significantly different ($P < 0.05$), LSD test.

Bd = *Brachiaria dictyoneura*, AP = *Arachis pintoi*, Cm = *Centrosema macrocarpum.*

Table 8. Differences among tropical forage species in mean values of Ca use efficiency (g/g) for 16, 29, 38 and-55 weeks after planting.

Species	**16**		**29**		**38**		**55**		**Mean**
	LF*	HF*	LF	HF	LF	HF	LF	HF	
Bd alone	711.9	776	1430.1	943.5	891.6	732	266.5	281	7540a
Ap alone	164.8	117	174.8	127.9	144.3	125	58.3	50.5	1203c
Cm alone	135.4	109	227.0	198.1	193.5	142	80.1	70.7	1445c
Bd + Ap	461.4	170	514.2	427.4	604.7	355	238	157	3659b
Bd + Cm	387.1	291	461.3	408.2	427	212	197.2	148	3153b
Mean	332.4ab**		491.2a		382.6a		154.6b		

* LF and HF are low and high fertility, respectively.

** Means in columns or in rows followed by different letters are significantly different ($P<0.05$), LSD test.

Bd = *Brachiaria dictyoneura*, AP = *Arachis pintoi*, Cm = *Centrosema macrocarpum.*

Table 9 Pearson correlation coefficients between root length density (0 - 10 and 10 - 20 cm depth) and N and P uptake by a grass and two legumes growing whether in monoculture or in an association (r and p values are reported).

Nutrient	**Bd alone**		**Ap alone**		**Cm alone**		**Bd + Ap**		**Bd + Cm**	
	0-10	**10-20**	**0-10**	**10-20**	**0-10**	**10-20**	**0-10**	**10-20**	**0-10**	**10-20**
N										
	0.68	0.73	0.53	0.51	0.64	0.70	0.80	0.74	0.56	0.52
r	0.0003	0.0001	0.01	0.01	0.0007	0.0001	0.0001	0.0001	0.004	0.09
P										
	0.51	0.46	0.50	0.46	0.60	0.67	0.85	0.79	0.60	0.55
r	0.01	0.02	0.01	0.02	0.001	0.0004	0.0001	0.0001	0.001	0.005

Bd = *Brachiaria dictyoneura*, AP = *Arachis pintoi*, Cm = *Centrosema macrocarpum*

slightly higher S uptake than *A. pintoi* which had the lower S uptake. The two mixtures Bd + Ap and Bd + Cm had similar S uptake of the grass alone. The highest S absorption rates throughout the experiment were observed at the high fertilization rate and increased with the age at harvest (Table 6). For sulfur use-efficiency, the significant interaction of species x age demonstrated that the species varied differentially throughout the experimental period. No differences related to the fertilizer level were observed. *B. dictyoneura* had the highest values of S use-efficiency followed by the two associations. The two legumes in monoculture had the lowest values (Table 7).

Relationships between root length density and N and P uptake

Correlation analysis (Table 9) showed high positive correlation coefficients between root length density (depths 0-10 and 0-20 cm) and N and P uptake.

Discussion

Plants obtain nutrients and water from the soil by their roots. Roots account for between 40 and 85% of net primary production (standing crop) in a wide range of ecosystems from grasslands to forest (Fogel, 1985). The cost of constructing and maintaining roots systems are important in the resource budget of plants (Cadwell, 1979). Typically, plant growth in non agricultural conditions is limited more by soil derived resources than by CO_2 or solar radiation (Fitter,1986). Therefore, an understanding of the functioning of plants within natural communities must be accompanied with a reasonable understanding of the behavior of roots and roots systems. From the present work distinct differences were found between the grass and the two legumes in nutrient acquisition and utilization when grown in a degraded hillside Andisol. These differences could be explained partially by differences in root system morphology. Caldwell (1994) and Hutchings and de Kroom (1994) pointed out that root proliferation in patches of fertile soils promotes extensive exploration of the soil and increases root surface area for greater water and nutrient uptake. Blue and Dantzman (1977) argued that in P deficient soils, P supply increases root elongation and proliferation.

It is well known that the highest distribution of roots is located in the topsoil layer 0 - 20 cm (Ricaute, 2006). Thus, in grass-legume mixtures, greater competition between the roots of the components take place in the upper layer (NCSU, 1980; Cuesta, 1982). Root diameter influences the volume of soil explored by roots and the surface area for nutrient absorption (Fitter et al., 1991) Thinner roots are characteristic of rapid root extension (Jackson and Caldwell,1989). Thus, it could be expected that the grass *B. dictyoneura* which had a thinner (higher SRL) and longer root (RLD) system than the legumes *A. pintoi* and *C. macrocarpum* (Rao et al., 1994) could have the greater ability for nutrient uptake. Root acquisition of nutrients and water is based more upon root length density or surface than on root biomass (Nye and Thinker, 1997; Moltz, 1981; Barber, 1984). Plants that invest less biomass to produce greater root length (high SRL) should be able to increase the length of their total root system more readily than those with low SRL. The native vegetation and *B. dictyoneura* because of their higher SRL values produced roots with smaller diameters and with less weight per unit of length. Total root weight and root length decreased with increase in soil depth. These results are consistent with the results obtained on tropical forages when grown in infertile acid soils of the Llanos of Colombia (Rao, 1998).

Differences among species in nutrient uptake and nutrient use efficiency were evident. It is well known that the physiological nutrient uptake capacity is determined by the genetic constitution of a plant, the soil nutrient status, and the demand for a particular nutrient by the plant. Therefore , the markedly higher N uptake of all species tested, specially *C. macrocarpum* under the high rate of fertilization, could be due to the synergistic effect caused by the P and K fertilization which enhanced N uptake (Howeler, 1983; Cadisch et al., 1989; Rao et al., 1997). Also P fertilization could have helped in N fixation by the legume species (Moore, 1962; Cadisch et al., 1989). These findings agree with those of Rao et al (1992; 1995). The greater N use efficiency of the C_4 species may give them an adaptive advantage over the C_3 legumes, particularly on sites of low N. It is posible that this advantage in N use efficiency was a major factor in evolution of C_4 photosynthesis (Brown, 1978). In the case of legumes, it is possible that the symbiotic relationship with rhizobium bacteria obviated their need for more efficient utilization of N and reduced the evolutionary pressure for acquiring C_4 characteristics (Brown, 1978).

The marked increase in grass root length density found in the high rate of P fertilization gave the grass higher competitive advantage over the legumes. This suggests that under the conditions of the study site, in the more fertile patches, greater root length density of the grass should contribute to greater P acquisition in these patches. Low P uptake by the legume *A. pintoi,* could be due to the fact that low growth rate is usually accompanied by low rates of nutrient uptake (Clarkson, 1967). Grime (1977) and Grime and Hunt (1975) pointed out that the inherently low growth rates are characteristic of species found in nutrient deficient soils and are associated with herbaceus species with prostrate growth habit. Therefore, it could be suggested that an adaptation mechanism to nutrient poor soils in *A. pintoi* is the ability to maintain itself in low P soils such as those used in this study and to inherently slow growth which placed a lower demand for P supply. Several researchers have reported higher P use efficiency in grasses than in legumes (Caradus, 1980; Rao, 1992, 1995; Baligar and Duncan, 1990). Results from the present study are in agreement with those reports.

The grass responded more than legumes in K uptake particularly at high level of fertilizer application. Drake et al. (1951) and Hynes (1981) found that roots of legumes have roughly double the cation exchange capacity (CEC) of grasses. This difference in CEC could partially explain why grasses are able to take more K than the legumes. In the case of Ca, the legumes, especially *C. macrocarpum* with it highest uptake, confirmed that legumes have higher Ca uptake capacity and demand than the grasses (Loneragan and Snowall,1969). In turn, the grass confirmed its greater efficiency in the use of Ca than the legumes (Rao et al.,1995). Foy et al., (1967, 1969, 1974a,b) reported that interactions of Ca and Mg with other minerals like K, Mn, Al and Fe could play important roles in the efficiency with which plants can take them up. Also, Ca and Mg use efficiency in plants may be associated with Al tolerance in plants

The higher uptake and use efficiency of S and Mg found in the grass at high level of fertilizer application compared to that of the legumes confirm that Mg and S concentration in forages varies greatly depending on factors such as plant species and their stage of growth and soil nutrients (Minson, 1990). The general sharp decline in nutrient use efficiency at mature stage (38 to 55 weeks of age) could be due to factors such as decline in the rate of photosynthesis per unit leaf area, decrease in leaf nutrient status, increase in rate of respiration, decline in root uptake capacity, and nutrient reabsorption during leaf senescence (Waring and Schlesinger, 1985). It is known that in perennial plants, rate of respiration increases with stand age, consuming more of the gross photosynthesis which causes a reduction in the rate of plant growth (Waring and Schlesinger, 1985).

Differences in nutrient use efficiency among terrestrial ecosystems might be due to species differences among sites with vegetation on poor sites being dominated by species that use nutrients efficiently. Also, differences in nutrient use efficiency might appear within species as a result of responses to differing nutrient availability (Schlesinger,1991). Selection within species, ecotypes, or cultivars with higher nutrient uptake capability is not necessarily a criteriea for higher yield because it can vary in efficiency of nutrient use (Silverbush and Barber, 1985).

Conclusions

In general, results from this study indicate that nutrient uptake and nutrient use efficiency varied considerably among the tropical forage species depending on age of the plants and the level of fertilizer application. The C_4 pathway of photosynthesis in grasses compared to that of C_3 pathway in legumes could give advantage to grasses to use more efficiency N, Ca and P. However, legume roots may have developed efficient mechanisms to extract nutrients, particularly Ca and P from degraded infertile Andisols.

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References

Baligar, V. C and R. R Duncan (eds.). 1990. Crops as Enhancers of Nutrient Use. Academic Press, San Diego, CA.

Barber, S. A .1984- Soil nutrient bioavailability. John Wiley and Sons. Nueva York.

Blue, W. G. and Dantzman, C. L.. 1997. Soil chemistry and root development in acid soils. Soil and *Crop Sc. Soc. Fla. Proc.* 36:9-15.

Brown, R.H. 1978. A difference in N use efficiency in C_3 and C_4 plants and its implications in adaptation and evolution. *Crop Sci.* 18:93-98.

Cadisch, G.; Sylvester-Bradley, R. and Nosberger, J. 1989. ^{15}N-based estimation of nitrogen fixation by eight tropical forage legumes at two levels of P, K supply. *Field Crops Res.* 22:181-194.

Caldwell, M. M 1994. Exploiting nutrients in fertile soils microsites. In: Caldwell, M. M. and Peacy, R. W. (eds.). Explotation of environmental heterogeneity by plants. Academic Press, San Diego

Caldwell, M. M. 1979. Root structure: the considerable cost of below -ground function. In: Solbing, O. T. (ed.). Topics in plant population biology. Columbia University Press, Nueva York. p. 408 - 427.

Caradus,J. R. 1980. Distinguishing between grass and legume species for efficiency of phosphorus use. N.Z.J. *Agric. Res.* 23:75 - 81.

Clarkson, D. T. 1967. Phosphorus. Supply and growth in species of agrostis. L. J. *Ecol.* 55:11 - 118.

Cuesta, P. A. 1982. Above ground production and rooting patterns of six tropical grasses in association with two legumes or with or without nitrogen fertilization. M.S. Thesis, New Mexico State Univ., Las Cruces. 144 p.

Drake, M. C.; Vengris, J.; and Colby, W. G.. 195. Cation exchange capacity of plants roots. *Soil Sci.* 723:139 - 147.

Eissentat, D. M. 1992. Cost and benefits of constructing roots of small diameter. *J. Plant Nutr.*15(6&7)763 - 782.

Fitter, A. H.; Strickland, T. R.; Harvey, M. L.; and Wilson, G. W. 1991. Architectural correlates of explotation efficiency. *New Phytol.* 118:375 - 382.

Fogel, R. 1995. Roots as primary producers in below-ground ecosystems. In: Fitter, A. H.; Atkinson, D.; Read, D. J.; and Usher, M. B. (eds.). Ecology Interactions in Soil. Special publication of the British Ecological Society, No 4 Blackwell Scientific, Oxford, p. 23 - 36.

Foy, C. D. 1974a. Effects of calcium availability on plant growth In: Carson, E. W. (ed.). The plant root and its environment. Univ. Press Va., Box 3608, Univ. Station, Charlottesville, VA. p. 565 - 608

Foy, C. D. 1974b. Effects of aluminum on plant growth. In: Carson, E. W. (ed.). The plant root and its environment. Univ. Press VA., Box 36008, Univ. Station, Charlottesville, VA. p. 601 - 642

Foy, C. D.; Fleming, A. L.; and Armiger, W. H. 1969. Aluminum tolerance of soybean varieties in relation to calcium nutrition. *Agron. J.* 61: 505 - 511.

Foy, C. D.; Fleming, A. L., Burns, C. R.; and Armiger, W. H. 1967. Characterization of differential aluminum tolerance among varieties of wheat and barley. *Soil Sci. Am. Proc.* 31:513 - 521.

Friesen, D. K.; Rao, I. M., Thomas, R. J.; Oberson, A.; and Sanz, J. I. 1997. Phosphorus acquisition and cycling in crop and pasture systems in low fertility tropical soils. *Plant and Soil* 196:289 - 294.

Grime, J. P and Hunt. R. 1975. Relative growth rate: its range adaptative significance in a local flora. *J. Ecol.* 63:393 - 442.

Grime, J. P. 1977. Evidence for the existence of three primary extrategies in plants and its relevance to ecological and evolutionary theory. *The Amer. Nat.* 111:1169 - 11694.

Haynes, R. J. 1981. Competitive aspects of the grass-legume associations. Associations. Advances in agronomy. 33:227 - 261.

Howeler, R. H. 1983. Analisis del tejido vegetal en el diagnostico de problemas nutricionales en algunos cultivos tropicales, Centro Internacional de Agricultura Tropical (CIAT). Cali, Colombia. 28 p.

Hutchings, M. J. and Kroom, H de. 1994. Foraging in plants: the role of morphological plasticity in resource acquisition. *Adv. Ecol. Res.* 25:165 - 238.

Jackson, R. B and Caldwell, M. M. 1989. The timing and degree of root proliferation in fertile-soil microsites for three cold desert perennials. *Oecologia* 81:149 - 153.

Loneragan, J. F. and Snowall, K. 1969. Calcium requirements of plants. *Aust. J. Agric. Res.* 20:465 - 478.

Malagon, C. D.; Pulido, R. C. and Llinas, R. R. 1992. Génesis y taxonomia de los Andisoles colombianos. In: Suelos Ecuatoriales, Revista de la Sociedad Colombiana de la Ciencia del suelo. 22(1):50 - 68.

Mengel, K. and Kirbi, E. A. 1987. Principles of plant nutrition. Publisher: International Potash Institute. p. 113 - 164.

Minson, D. J.1990. Forages in ruminant nutrition. Nueva York. Academic Press.

Molz, F. J. 1981. Models of water transport in the soil-plant system: a review. water resources Res. 17:1245 - 1260.

Moore, J. E. 1962. The influence of a legume on soil fertility under a grassland tropical pasture. *Empire J. Exp. Agric.* 30(119).

NCSU (North Carolina State University) Raleigh, N.C Soil Science Department 1980. Agronomic Research on soils of the Tropics. 1978-1979 *Report*. p. 127 - 137.

Nye, P. H. 1966. The effect of nutrient intensity and buffering power of a soil, the absorbing power, size and root hairs of a root, on nutrient absorption by diffusion. *Plant soil.* 25:81 - 105.

Nye, P.H. and Tinker, P. B. 1977. Solute movement in the soil-root system. Blackwell Scientific pub., Oxford, Reino Unido.

Rao, I. M. 1998. Root distribution and production in native and introduced pastures in the south American savannas. In: J. E. Box Jr. (Ed.). Root demographics and their efficiencies in sustainable agriculture, grasslands, and forest ecosystems. Kluwer Academic Publishers, Dordrecht, The Netherlands. p. 19-42.

Rao, I. M. 2001. Role of physiology in improving crop adaptation to abiotic stresses in the tropics: The case of common bean and tropical forages. In: M. Pessarakli (ed.). Handbook of Plant and Crop Physiology. Marcel Dekker, Inc., Nueva York, USA p. 583 - 613.

Rao, I. M.; Ayarza, M. A.; and Thomas, R. J. 1994. The use of carbon isotope ratios to evaluate legume contribution to soil enhancement in tropical pastures. Plant soil 162:177 - 182.

Rao, I. M.; Ayarza, M.A.; and García, R. 1985. Adaptative attributes of tropical forage species to acid soils. I. Differences in plant growth, nutrient acquisition and utilization among C_4 grasses and C_3 legumes. *J. Plant Nutr.* 18(10):2135 - 2155.

Rao, I. M. and Cramer, G. 2003. Plant nutrition and crop improvement in adverse soil conditions. In: M. Chrispeels and D. Sadava (eds). Plants, Genes, and Crop Biotechnology. Published in partnership with the American Society of Plant Biologists and ASPB Education Foundation. Jones and Bartlett Publishers, Sudbury, Massachusetts, USA, p. 270-303.

Rao,I. M.; Ayarza, M. A.; Thomas, R. J.; Fisher, M. J.; Sanz, J. I.; Spain, J. M.; and Lascano, C. E. 1992. Soil-plant factors and processes affecting productivity in ley farming.. In: Pastures for the tropical lowlands: CIAT´s contribution, CIAT, Cali, Colombia. p. 145-175

Rao, I. M; Borrero, V.; Ricaurte, J.; Garcia, R.; and Ayarza, M. A. 1996. Adaptative attributes of tropical forage species to acid soils. II. Differences in shoot and root growth responses to varying phosphorus supply and soil type. *J. Plant Nut.* 19(2),323 - 352.

Rao, I. M; Borrero, V.; Ricaurte, J.; Garcia, R.; and Ayarza, M. A. 1997. Adaptive attributes of tropical forage species to acid soils III. Differences in phosphorus acquisition and utilization as influenced by varying phosphorus supply and soil type. *J. Plant Nut.* 20(1):155 - 180.

Rao, I. M.; Friesen, D. K.; and Osaki, M. 1999. Plant adaptation to phosphorus-limited tropical soils. In: M. Pessarakli (ed.). Handbook of Plant and Crop Stress. Marcel Dekker, Inc., Nueva York, USA. p. 61 - 96.

Reining, L. 1992. Erosion in Andean Hillside farming: characterization and reduction of soil erosion by water in small scale cassava cropping systems in the southern central cordillera of Colombia. Center for Agriculture in the Tropics and Subtropics, University of Hohenheim, Germany. 219 p.

Ricaute, J. 2006.Impacto de genotipos de Brachiaria tolerantes a aluminio sobre la calidad de un Oxisol de Altillanura en el Meta, Colombia. Tesis de Maestría, Universidad Nacional de Colombia, Palmira. 122 p.

Salinas, J. G y García, R. 1985 Métodos químicos para el analisis de suelos ácidos y plantas forrajeras. Centro Internacional de Agricultura Tropical (CIAT), Cali Colombia). 83 p.

SAS/ STAT. 1990. SAS/ STAT User guide. Version 6. SAS Istitute Inc., Cary, NC. USA.

Schlesinger, W.H. 1991. Biogeochemistry : an analysis of global change. Academic press, Inc.443.p

Sliverbush, M. and Barber, S. A. 1985. Root growth, nutrient uptake and yield of soybean cultivars ground in the field.

Waring, R. H and chlesinger, W. H. 1985. Forest ecosystems. Academic press. Orlando Florida.