Root dynamics of native savanna and introduced pastures in the Eastern Plains of Colombia

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Abstract

Understanding of the process of soil C accumulation under introduced pastures on the savannas of South America is limited by lack of information on production, turnover and decomposition of roots. We estimated below-ground net primary productivity (BNPP), assessed the rate of root decomposition, and calculated the annual input of soil organic carbon (SOC) under native savanna vegetation (NS), a degraded pasture of the introduced grass *Brachiaria humidicola* (Bh), and well-managed pastures of the introduced grass *B. dictyoneura* alone (Bd) and in mixture with the legume *Arachis pintoi* (Bd + Ap). Responses were estimated using an in-growth mesh tube method and a flow model for C accumulation. The BNPP of the well-managed pastures was twice that of either NS or Bh. Turnover losses of the well-managed pastures were 1–2 times greater than NS and Bh. Decomposition constant of roots of Bd was lower than that of either NS or Bd + Ap, which resulted in higher residence time for Bd roots. The amount of BNPP remaining in the soil after 1 year of decomposition was about 2.3 times higher under well-managed pastures compared to that under NS. Higher C accumulation under well managed introduced pastures resulted, to some extent, from the high BNPP of the introduced species, possibly stimulated by fertilizer applied at establishment and regularly for maintenance and coupled with lower litter quality as indicated by high C:N and C:P ratios and decomposition dynamics of the below-ground residues.
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1. Introduction

Introduced pastures on the Eastern Plains (*llanos*) of Colombia have been shown to accumulate substantial amounts of organic matter compared with the native savanna species they replace (Fisher et al., 1994, 1997), but the processes through which the accumulation occurs are not known. Soil organic carbon (SOC) accumulation under any vegetation community is a function of above- and below-ground net primary productivity (NPP). In most pasture systems, the major mechanism of depositing C at depth beyond the top few centimeters is through root production, mortality, and decomposition (Fig. 1). Therefore, the assessment of

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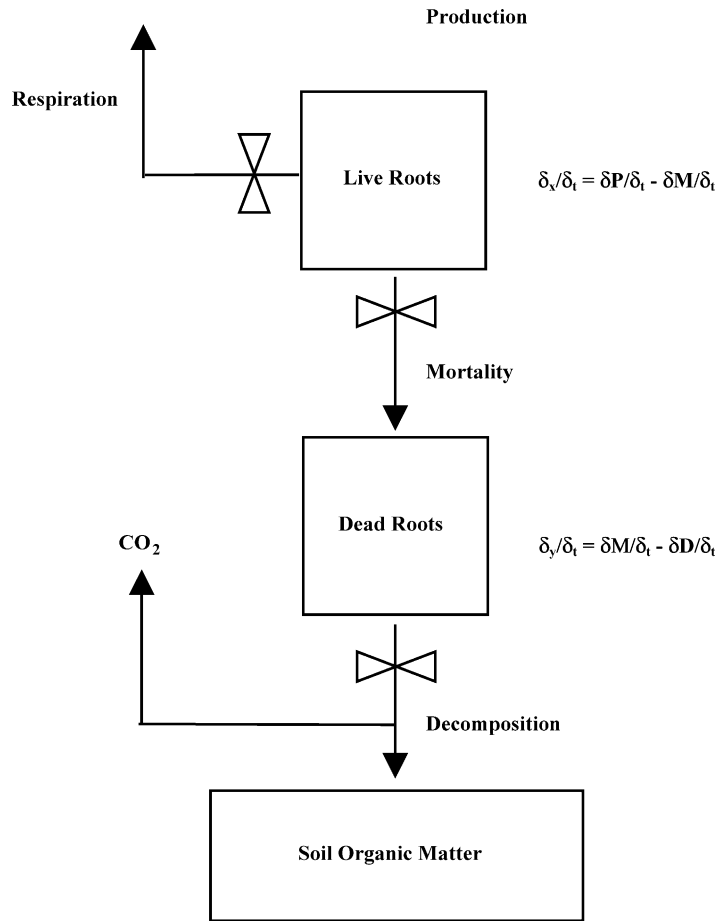*E-mail address:* lal.1@osu.edu (R. Lal).

Fig. 1. Flow model of carbon accumulation in soils. The flow model is represented schematically as three compartments, live roots, dead roots, and soil organic matter linked together by three flows, production (P), mortality (M), and decomposition (D). Valves represent factors that control the flows.

root production and turnover is a key component in understanding the C dynamics in soil. However, there are few data of root dynamics under pastures in the tropics, and none for root dynamics either of introduced pastures or the native grassland species in the treeless savannas of tropical South America.

Long et al. (1989) measured NPP in five tropical grasslands of Mexico, Kenya, Thailand, China, and Brazil. They reported that NPP (including roots to 15 cm depth) of these five grasslands ranged from 14 to 100 Mg ha^{-1}, and concluded that these natural grasslands were potential sites of net C accumulation. There is also an indirect evidence that below-ground NPP (BNPP) under introduced pastures is more than that under native savanna vegetation in the isohy-

perthermic savannas of Colombia. Rao (1998) reported that total root biomass (average biomass of live roots) under pastures of the introduced grass *Brachiaria dictyoneura* alone and associated with the legume *Centrosema acutifolium* was 5.7 Mg ha^{-1} compared to only 1.4 Mg ha^{-1} under native savanna to a depth of 80 cm. Although Rao (1998) did not estimate turnover losses through root death, it was suggested that BNPP of the introduced pastures could be twice as much as that of the native vegetation. The difference was attributed to fertilizer applied to the introduced pastures as compared to no fertilizer applied to the native savanna. Rao (1998) estimated that root turnover was twice as much in grass alone pastures and three times as much in grass–legume pastures compared to native savanna

vegetation. Based on these data and assuming that the BNPP was equal to the above ground net primary productivity (ANPP) reported by Abaunza (1982) for *A. gayanus var. gayanus* (43 Mg ha^{-1}), Fisher et al. (1997) estimated that inputs of organic matter (OM) to the soil under introduced pastures may range from 33.5 to 40.5 Mg ha^{-1} yr^{-1}.

The high BNPP or high input of OM may not necessarily lead to higher SOC accumulation if the rate of decomposition is proportionately higher than that of the native savanna vegetation. Accumulation of SOC under an introduced pasture can occur only if the rate of decomposition of the newly accumulated OM is the same or lower than that of the native savanna. There are some field data on decomposition of roots of introduced pastures in the savannas of Colombia. Celis (1993) and Gijsman et al. (1997) compared decomposition rates of roots of the tropical grasses *B. humidicola* and *B. dictyoneura* and the legumes *A. pintoi* and *C. acutifolium* grown in a clay and a sandy soil during the wet and dry seasons. They observed that roots of the grasses and legumes decomposed faster during the dry than wet season and that soil texture did not affect the decomposition patterns. Decomposition rates of legumes were significantly higher than those of the grasses in both textures and seasons.

Measurement of BNPP is laborious, and can be assessed with a wide range of methods. Ingrowth mesh tubes (Steen, 1983, 1984, 1985; Hansson and Steen, 1984) and the compartment-flow model of Santantonio and Grace (1987) have been used to estimate root production and losses through root death and decomposition. Gijsman et al. (1997) used ceramic pots with a mixture of soil and roots buried in an inverted position (to avoid root ingrowth) to predict in situ losses through decomposition. Data on BNPP are needed to understand C dynamics in different land use systems. The objectives of this study were to estimate the BNPP and root decomposition of contrasting pasture systems, and assess the annual input of OM and the rate of SOC sequestration in acid savanna soils of the llanos of Colombia.

2. Materials and methods

Measurements on root production, turnover, and decomposition were made on long-term grass alone and grass–legume experimental plots and an adjacent native savanna at Matazul, a commercial farm (4°19′N, 72°39′W) near Puerto Lopez, Department of Meta, Colombia. Matazul is in the well-drained isohyperthermic savannas (Cochrane et al., 1985). It has a seasonally dry climate with an annual rainfall of 2700 mm received between late March and mid-December. Mean annual temperature is 27 °C with little variation throughout the year. The soil is a sandy loam (Isohyperthermic Tropeptic Haplustox), with low pH (4.5, 1:1 water), extremely low in N, available P, and exchangeable base contents, especially Ca^{2+} and K$^+$, and high Al^{3+} (saturation >80%).

The experimental plots, *B. dictyoneur*a alone (Bd) and *B. dictyoneura* associated with *Arachis pintoi* (Bd + Ap), were initially converted from native savanna vegetation to a rice (*Oryza sativa*)–pasture system in 1989. Recommended fertilizers (80 kg ha^{-1} N, 50 kg ha^{-1} P, 100 kg ha^{-1} K, and 300 kg ha^{-1} dolomite, were applied (Sanz et al., 1999). After the rice was harvested, Bd alone and Bd + Ap were established by a no-till system following a spray with a no-till system and managed with a stocking rate of 3 cattle ha^{-1}. Maintenance fertilizer was applied (20 kg ha^{-1} P, 20 kg ha^{-1} K, 50 kg ha^{-1} Ca, 12 kg ha^{-1} Mg, and 10 kg ha^{-1} S) in 1993, 1995 and 1997. A *B. humidicola* (Bh) pasture was established in April 1982. Fertilizers (20 kg ha^{-1} P, 100 kg ha^{-1} K, and 300 kg ha^{-1} dolomite lime) were applied at the time of pasture establishment, which was frequently overgrazed (4.5 animals ha^{-1}). Native savanna (NS), being the traditional low-input/low productivity system, received no fertilizer. Management of the NS included burning at least twice a year and continuous grazing at low stocking rate (0.1–0.2 animal ha^{-1}).

2.1. Root production and turnover

Ingrowth mesh tubes (10 cm long × 10 cm diameter) for root growth and turnover measurements were made from plastic netting with 2.75 mm mesh, opened at the top and closed at the bottom. Tubes were filled with soil free of roots and identifiable OM, having the same texture and packed at bulk densities similar to those in the undisturbed soil for 0–10, 10–20, 20–30, 30–40 and 40–50 cm depths. Packed tubes were carefully inserted into drilled holes of 10 cm

diameter and 12, 20, 30, 40 or 50 cm long. Holes were refilled with excavated soil.

Tubes were retrieved by slicing the soil with a long knife at a distance of 5 cm from the tube, removing the tube plus attached soil from the ground and carefully cutting away excess soil and roots that had penetrated the tube. Retrieved tubes were placed in plastic bags and stored at 4 °C for about 48 h. The roots that entered the tubes were washed free of soil using a hydropneumatic elutriation system (Gillison's Variety Fabrication Inc.). Roots were sorted into live and dead roots based on color and consistency, dried to a constant weight at 60 °C, and weighed, followed by determination of ash-free dry mass in a furnace at 1000 °C for 3 h to correct for any soil that might have been included.

Long- and short-term tubes were deployed with overlapping time periods to allow calculations of biomass losses between sampling intervals. Turnover losses were calculated as the difference in root biomass between the sum of the short-term tubes and the corresponding long-term tubes at each interval, when the sum of the root biomass in the short-term tubes was greater than the corresponding long-term tube:

$$(s_1 + s_2 + S_3 + \cdots + s_n) - l_n$$

where s_n is the root biomass in the short-term tube at the nth sampling date and l_n the root biomass in the long-term tube at the nth sampling date.

The BNPP to 50 cm depth was calculated as follows (Steen, 1985):

  (i) sum of the biomass increments in the short-term tubes,
 (ii) total biomass accumulation in the set of long-term tubes kept in the field for 23 months,
(iii) sum of the peak root biomass in the long-term tubes, and
(iv) total biomass accumulation in the 23-month long-term tubes plus turnover losses.

In May 1997, 540 tubes were set out in each of the four pasture treatments. Six replicated tubes from each depth were then collected at 4-week intervals during the wet seasons (from late June to mid-December 1997 and from early April 1998 to late December 1998) or at 8-week intervals during the dry season (mid-December 1997–early April 1998). In addition, six short-term tubes per depth were set out at each sampling date and collected at the next sampling date (4 or 8 weeks later depending on the season).

Although the experiment layout was not blocked in space, production, turnover and the BNPP of pastures treatments were analyzed for variance using a randomized complete block design (SAS, 1994), followed by pair-wise comparisons using the least significant difference (LSD) at the 5% probability level (Montgomery, 1991).

2.2. Root decomposition

Roots were collected from pure stands of Bd, and Ap, and from an adjacent NS area, washed free of soil, kept in plastic bags at about 4 °C for approximately 24 h, dried between filter paper and cut into pieces about 2 cm long. The amount of roots (dry weight basis) used was calculated based on root mass in a soil volume of 870 cm^3 for each treatment. The proportion of Ap roots in the grass–legume mixture was 10% of the total root mass.

Roots of NS, Bd, Ap, and Bd + Ap were mixed with 750–800 g of sieved (<2 mm) root-free soil, and soil packed to a bulk density corresponding to that observed at 0–10 cm depth in each treatment in 500 cm^3 ceramic pots. The top of the pot was covered with 4 mm mesh plastic netting allowing access to soil macro-fauna. Pots were buried upside down at about 2 cm below the soil surface in the NS and Bd + Ap pasture. The method of filling ceramic pots with mixtures of roots and soil and burying them upside down ensured that the decomposition environment closely resembled that in which roots decompose naturally. Water and gas exchange between the potted soil and bulk soil was facilitated by packing the soil at the bulk density of the surrounding soil and ensuring good contact of the pots with the bulk soil. Water flow in the pots might differ from that in the surrounding soil. Upside down pots also prevented ingrowth of new roots.

Pots were recovered at 1-week intervals during the first 4 weeks. Thereafter, pots were retrieved at 4- or 8-week intervals (depending on the season) for the next 70 weeks. Remaining roots were washed free of soil using a hydropneumatic elutriation system, dried to a constant weight at 60 °C, and weighed, followed by determination of the ash-free dry mass in a furnace at

1000 °C for 3 h to correct for any soil that might have been included.

Root decomposition was determined as the proportion of original mass (ash-free mass) remaining at various times. Values were analyzed for variance among treatments followed by a pair-wise comparison, using LSD at 5% probability level. Values for time $t = 0$ were excluded since all treatments were the same at $t = 0$ (Kelman and Lang, 1982).

For the purpose of this study, decomposition data were also analyzed by fitting a single exponential decay function (Kelman and Lang, 1982) to describe the loss of mass over time:

$$R = R_0 \exp(-kt)$$

where R is the fraction of the initial mass remaining, R_0 the initial root mass, k the decomposition constant, and t the time. The time required to transform one-half of the initial root mass ($t_{1/2}$) was computed by $0.693/k$. Mean residence time, also called turnover time, was computed by $1/k$. The analysis of variance was computed to compare k, $t_{1/2}$, and $1/k$ among treatments. Means were compared using the $LSD_{0.05}$.

Annual inputs of SOM and SOC were calculated by combining the data provided by the ingrowth and decomposition methods using a two compartment model, standing live and dead roots, and three flows, production (P), mortality (M) and decomposition (D) as indicated in Fig. 1. Thus, it was assumed that roots were produced and senesced in such a way as to maintain the observed standing live and dead roots corrected by the losses through decomposition measured for each sampling date.

Information on standing live and dead roots and the monthly rates of root decomposition enabled estimation of the remaining two processes, production and mortality as described by Santantonio and Grace (1987):

(i) Change in standing live roots: $\delta x/\delta t = \delta P/\delta t - \delta M/\delta t$, where P is the production and M the mortality.
(ii) Change in standing dead roots: $\delta y/\delta t = \delta M/\delta t - \delta D/\delta t$, where D is the decomposition.
(iii) Remaining dead roots after decomposition: $y_i = y_0 \exp(-kt)$, where y_0 is the amount of dead roots in the previous interval $(i - 1)$, k the decomposition constant, and t the time.

(iv) Amount of decomposition during a given interval: $D_t = y_0[1 - \exp(-kt)]$.
(v) Rate of decomposition: $\delta D/\delta t = -y_0[\exp(-kt)](-k) = ky$.

Since daily temperature and soil water content were considered almost constant during the wet season in the isohyperthermic savannas of Colombia, it was assumed that $\delta M/\delta t$ was constant and small during an interval, but it could vary between intervals $\delta y/\delta t = M_j - kt$ (j refers to a definite interval i to $i + 1$). Then:

(vi) Production: $P_j = x_{i+1} - x_i + M_j$.
(vii) Decomposition: $D_j = y_i - y_{i+1} + M_j$.

Since roots that die during an interval are assumed not to begin to decompose until the next interval decomposition, production and turnover were calculated as:

(viii) Decomposition: $D_j = y_i[1 - \exp(-kjtj)]$.
(ix) Production: $P_j = x_{i+1} - x_i + M_j$.
(x) Turnover: $M_j = y_{i+1} - y_i + D_j$.

3. Results and discussion

3.1. Root production and turnover

3.1.1. Live roots

Accumulation of live roots in the long-term tubes is presented in Fig. 2. The Bd + Ap pasture had significantly higher live root mass compared with either Bh or NS. Compared to NS, Bd also had significantly higher live root mass. The degraded Bh also had significantly more live roots than the NS.

The amount of ingrowth roots showed a cyclic pattern in the long-term tubes. Roots appeared to undergo multiple cycles of growth, death, and replacement during the study duration. As expected, all pastures had no accumulation of live root mass during the dry season. Maximum production occurred during the wet season, although the pattern of accumulation during the wet season differed among pastures. The NS attained a maximum yield of 5.3 Mg ha^{-1} in September 1998, while Bh attained its maximum yield of 6.4 Mg ha^{-1} at the end of the wet season in December 1997. Maximum yield for Bd (15.9 Mg ha^{-1}) was measured in August 1998 and for Bd + Ap (16.5 Mg ha^{-1}) in June 1998. The well-managed pastures were managed in a rotational system in
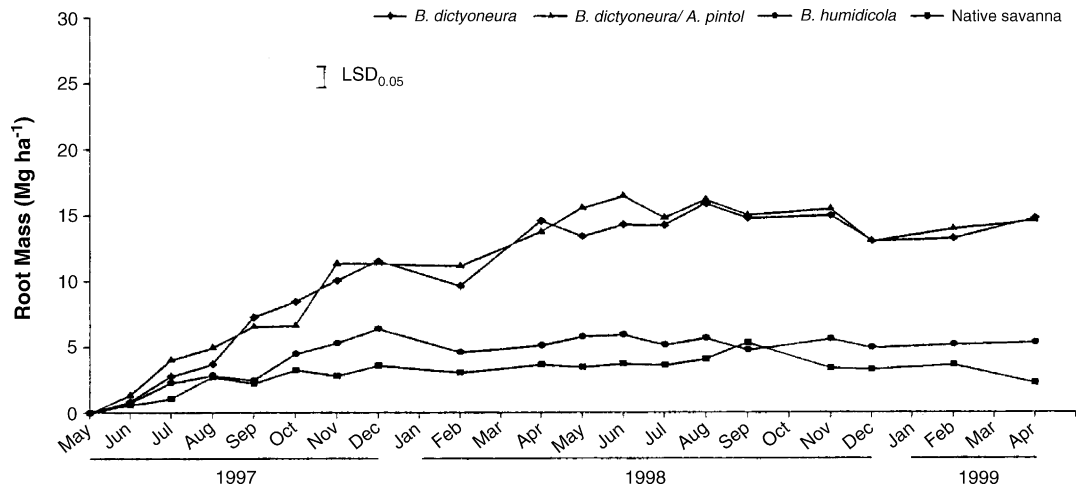
Fig. 2. Accumulation of live root mass of introduced pastures compared to NS.

contrast to NS and Bh, which were continuously grazed. It is likely that the fluctuations in root accumulation of well-managed pastures were related to cycles of grazing and sampling time, which were not synchronized.

3.1.2. Standing roots

Standing roots combine both live and dead roots and so reflect the three components of root dynamics: production, turnover, and decomposition. Accumulation of standing roots in the long-term tubes was

lower in the two low-input systems (NS and Bh) than in either Bd or the Bd + Ap (Fig. 3). Standing root mass of Bd and Bd + Ap was 3–5 times higher than that of NS, and 2.4 times more than that of Bh. In turn Bh had about 2.5 times greater standing root mass than NS.

As with live roots, all pastures had no accumulation in standing root mass during the dry season. Root mass in NS reached a maximum (8.38 Mg ha^{-1}) in September 1998. Standing root mass of Bh reached
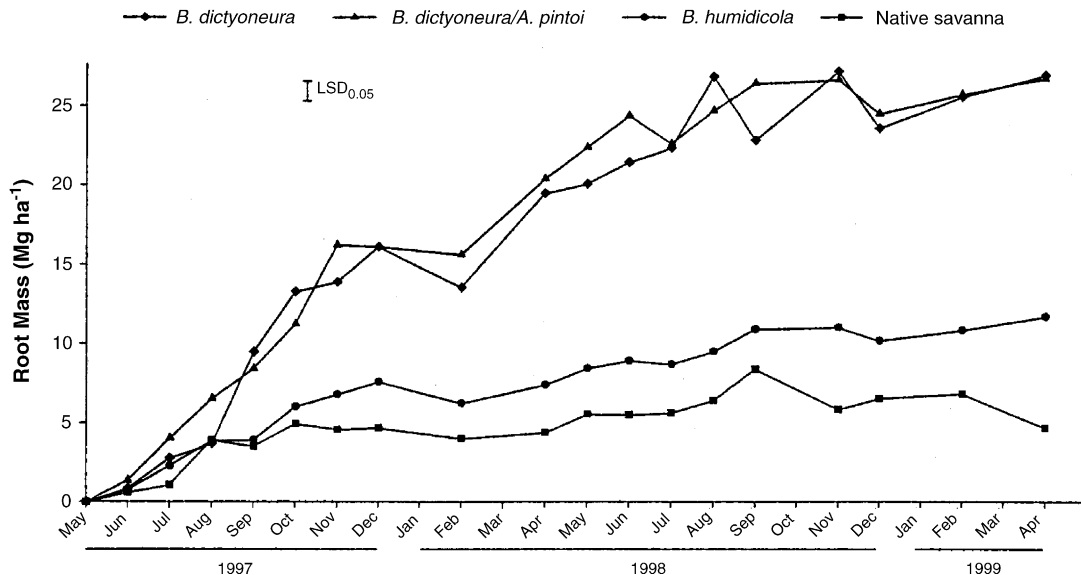

Fig. 3. Accumulation of standing roots of introduced pastures compared to NS.
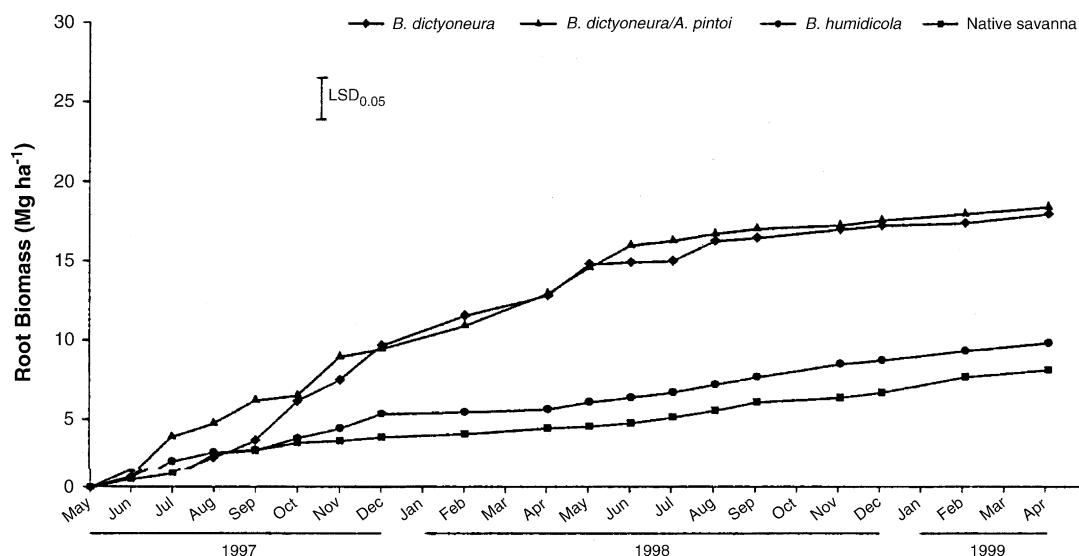
Fig. 4. Cumulative root biomass of introduced pastures compared to NS.

maximum yield (11.68 Mg ha^{-1}) before the onset of the wet season in April 1999. Maximum yield of standing root mass of Bd (27.13 Mg ha^{-1}) occurred in November 1998. The Bd + Ap treatment reached a maximum (26.67 Mg ha^{-1}) in April 1999. Any effects of defoliation (grazing) on live roots were more likely compensated for by complementary change in dead.

3.1.3. Cumulative root biomass

Cumulative ingrowth of root biomass into short-term tubes is presented in Fig. 4. The cumulative ingrowth for NS and Bh was significantly lower than either of Bd or Bd + Ap.

3.1.4. Turnover losses (through death and decomposition)

Turnover losses calculated as the difference in root biomass between the sum of the short-term tubes and the corresponding long-term tubes at each interval,

were 2.2 times more for Bd and 1.3 times greater for the Bd + Ap than for NS, which was similar to Bh (Table 1). Losses accounted for 49% of the BNPP for NS, 58% for Bd, and 67% for Bd + Ap.

3.1.5. Below-ground net primary productivity (BNPP)

In general, BNPP was lower for NS and Bh compared to either Bd or Bd + Ap (Table 1). The BNPP was 2.2 times more for Bd, and 1.8 times greater for Bd + Ap compared to NS. The BNPP calculated from the in-growth into long-term tubes was lower than the BNPP calculated by the sum of short-term tubes (Table 1). Peak root biomass was higher than biomass in the last set of long-term tubes. Gains and losses of ingrowth roots in the long-term tubes indicated that older roots were lost, but growth of new roots continued during intervals. Adding estimated losses to total live root mass in the long-term

Table 1
Mean net annual below-ground primary productivity calculated from ingrowth tubes

Parameter	NS (Mg ha^{-1} yr^{-1})	Bh (Mg ha^{-1} yr^{-1})	Bd (Mg ha^{-1} yr^{-1})	Bd + Ap (Mg ha^{-1} yr^{-1})
Sum of short-term tubes	2.42 c[a]	5.33 b	9.74 a	9.99 a
Last long-term tube	1.22 c	2.89 b	8.03 a	7.91 a
Peak in long-term tubes	2.88 b	3.47 b	8.63 a	8.96 a
Turnover	5.88 c	5.11 c	11.06 a	7.66 b

[a] Treatment means followed by the same letter in rows did not significantly differ at the 5% probability level.

tubes gave the highest estimated value of BNPP (Table 1).

Consistently higher biomass in the long-term tubes than the sum of short-term tubes indicated a disturbance effect of about 20% associated with the insertion of the tubes. Frequent disturbance resulted in underestimation of BNPP because losses were only estimated when the sum of the short-term tubes was higher than that in long-term tubes. Also, the estimate of annual BNPP obtained from the peak biomass in the 23-month long-term tubes may be biased, because it did not take into account losses. When monthly losses were included, BNPP increased. Losses were calculated from incremental differences only when they were negative. Therefore, a portion of annual loss was probably due to sampling error.

3.1.6. Root decomposition

Chemical composition of the roots at the start of the experiment is presented in Table 2. Nitrogen and P concentrations were greater in NS and Ap roots than in Bd and Bd + Ap roots, resulting in different C:N, C:P, and lignin:N ratios. The Ap roots had almost four times greater N compared with NS, but P contents were similar. Roots of Bd and Bd + Ap did not differ in N, P and lignin concentrations, which was expected because the legume only comprised 10% of root mass. Roots of Bd had significantly higher C:N and C:P ratios than roots of other pastures.

The proportion of initial root mass remaining at different times had a significant ($P < 0.001$) time - × pasture interaction. A week after burying the ceramic pots, NS and Ap lost approximately 23% of their initial root mass, while Bd and Bd + Ap only lost about 13% of the initial weight (Table 3).

Decomposition of NS and Ap roots were similar, but differed significantly from that of either Bd or Bd + Ap in the first 4 weeks. By week 16, decom- position of root mass of NS and Ap was close to 50%, while that of Bd and Bd + Ap was about 40%. By week 44, loss of root mass of Ap (73% of initial weight) differed significantly from that of Bd (65%). Loss of root mass of NS, Bd and Bd + Ap was not significantly different and ranged between 65 and 69% of the initial weight. From weeks 44 to 52, residual root mass decreased dramatically from 54 to 35% and was associated with the onset of the wet season in April 1998. The greatest proportional loss was in the roots of the savanna species. After this massive loss, subsequent losses were more gradual and similar between roots of different pastures (Table 3). By week 76, root mass loss was 97% for NS, 96% for Ap, 95% for Bd + Ap and 92% for Bd. Decomposition of roots of NS and Ap was similar, but differed ($P < 0.05$) from that of Bd and Bd + Ap during the first 45 weeks. After 60 weeks, decomposition pattern of Bd + Ap was similar to that of NS and Ap alone, but significantly differed from that of Bd.

Our results are consistent with decomposition of selected tropical grasses and legumes in Colombia and Brazil. Lower decomposition rates were observed for grasses such as *B. dictyoneura*, *B. humidicola* (Gijsman et al., 1997), *B. decumbens* and *A. gayanus* (Urquiaga et al., 1998), compared to the legumes *A. pintoi*, *C. acutifolium* (Gijsman et al., 1997), *Centrosema* spp. and *Stylosanthes guianensis* (Urquiaga et al., 1998).

In addition, analysis of variance of k, $t_{1/2}$, and $1/k$ showed significant differences among pastures. The Bd had significantly lower k compared to those of NS, Ap, and Bd + Ap (Table 4). The time needed to transform one-half of the initial root mass and the mean residence time were significantly higher for Bd compared with NS. Root half-life and mean residence time did not differ among Ap, Bd + Ap and NS treatments.

It is well known that decomposition is regulated by the chemical quality of the decomposing material,

Table 2
Chemical composition of roots at the start of the decomposition study

Pasture	C (g kg⁻¹)	N (g kg⁻¹)	P (g kg⁻¹)	Lignin (g kg⁻¹)	C:N (g g⁻¹)[a]	C:P (g g⁻¹)	Lignin:N (g g⁻¹)
Native savanna	413 b	6.1 b[b]	0.4 a	152 a	67.7 b	1031.5 b	24.9 ab
B. dictyoneura	353 c	3.5 c	0.3 b	119 b	100.8 a	1764.5 a	33.9 a
Arachis pintoi	501 a	2.4 a	0.4 a	112 b	20.8 c	1251.8 b	4.7 c
B. dictyoneura + A. pintoi	395 b	4.4 c	0.3 ab	116 b	93.6 a	1315.3 b	25.6 b

[a] Means of C:N ratios for different treatments followed by same letters in the columns do not differ significantly at the 5% probability level.

[b] Treatment means followed by same letters in the columns do not differ significantly at the 5% probability rate.

Table 3
Proportion of root mass of native savanna and introduced pastures remaining at different times during an 18-month decomposition experiment

Time (weeks)	Native savanna (%)	A. pintoi (%)	Brachira dictyonerura (%)	B. dictyoneura + A. pintoi (%)
1	76 bA[a]	77 bA	88 aA	85 aA
2	69 bB	69 bB	87 aA	83 baB
3	62 bC	65 bC	78 aB	81 baB
4	61 cC	64 cC	72 bC	80 aB
8	60 cC	57 cD	72 bC	76 aBC
12	53 cD	50 cE	67 bD	70 aD
16	52 bD	50 bE	59 aE	58 aE
20	46 bE	34 cF	52 aF	50 aF
24	41 cE	31 dFG	48 aF	44 bG
32	33 bF	31 bFG	42 aG	41 aG
44	31 bcF	27 cG	35 aH	31 abH
48	16 cG	20 bH	24 aI	24 abI
52	11 cH	14 bI	18 aJ	14 bJ
56	8 cHI	11 bI	18 aJ	12 bJK
60	7 bHI	5 bJ	13 aJ	9 abK
64	7 bHI	6 bj	11 aJK	7 bKL
72	3 bI	4 bj	8 aK	7 abL
76	3 cI	4 bJ	8 aK	5 abL

Lower case letters are used to compare pasture treatments for each week. Upper case letters are used to compare weeks within each pasture treatment.

[a] Treatment means followed by same letters do not differ significantly at the 5% probability level.

especially contents of nutrients and recalcitrant or inhibitory components, such as lignin, tannins, and polyphenols (Melillo et al., 1989). In this study, decomposition of Ap, Bd and Bd + Ap compared to that of NS suggested that decomposition was not only controlled by the initial N content of the roots, but also by the concentration of P.

A conceptual model of the interaction between various nutrients and recalcitrant or inhibitory components in litter was developed by Sinsabaugh et al. (1993). The model assumes that the microbial production of degrading enzymes (i.e. ligno-cellulase) is directly related to the availability of both N and P. Therefore, if either of the nutrients is limited, the decomposers will expend more metabolic energy to produce the degrading enzymes, thus, resulting in a slow decay process. This could explain the similar decomposition pattern of Ap and NS roots. Root decomposition of Ap appeared to be limited by the initial P concentration. In contrast, decomposition of NS roots appeared to be limited by low N concentration. The same argument is relevant to explaining the decomposition patterns of roots of NS, Bd, and Bd + Ap. Roots of Bd and Bd + Ap had lower initial N and P contents as compared to those of NS.

In the humid tropics, where soils are commonly low in available P (Sánchez, 1976), little attention has been given to the role of P in altering decomposition rate.

Table 4
Means of initial substrate, decomposition constant, half-life, and turnover time of roots of introduced grass, legume and grass–legume pastures compared to NS at Matazul

Pasture	Initial substrate, R_0 (%)	k[a] (week^{-1})	$t_{1/2}$ (week)[b]	$1/k^4$ (week)
Native savanna	75	0.030	15	22
A. pintoi	75	0.033	21	31
B. dictyoneura	89	0.027	25	37
B. dictyoneura + A. pintoi	92	0.031	21	30
LSD(0.05)	6	0.003	7	9

[a] Decomposition constant.
[b] Time required to transform one-half of the initial substrate ($0.693k$).

Table 5
Mean net annual ground primary productivity calculated from the compartment-flow model

Parameter	Native savanna (Mg ha^{-1} yr^{-1})	*B. dictyoneura* (Mg ha^{-1} yr^{-1})	*B. dictyoneura + A. pintoi* (Mg ha^{-1} yr^{-1})
Change in live roots	1.9 b	7.3 a	7.9 a
Change in dead roots	1.8 b	6.3 a	5.2 a
Amount of decomposition	7.5 b	16.4 a	18.3 a
Turnover	9.3 b	22.7 a	23.4 a
Below-ground net primary productivity	12.5 b	30.0 a	31.3 a
Input of soil organic carbon	5.0 b	10.3 a	11.6 a

Treatment means followed by the same letter do not significantly differ at the 5% probability level.

Low P availability of these soils was confirmed by low P concentration and high C:P ratios in the root material of all species. The differences in the decomposition patterns of Bd and Bd + Ap, or NS were probably due to some extent to the differences in the initial P concentrations.

Gijsman et al. (1997) reported that the C:P ratios of the microbial decomposer population ranged from 34 to 50 in selected soils in the savanna of Colombia. Therefore, the wide difference in C:P between roots and the microbes suggests that considerable immobilization of inorganic P from the soil may be needed for decomposition of roots.

In two different experiments carried out at the Carimagua Research Station (at about 200 km NE of Matazul), Celis (1993) and Gijsman et al. (1997) emphasized the importance of P in regulating decomposition of roots in these P-deficit soils. Both studies reported a significant correlation between decomposition rate and initial P concentrations of the roots. In contrast, Bloomfield et al. (1993) reported no correlation between decomposition rate and initial P concentration of roots of selected tropical trees grown in a soil with low available P. They suggested that the results obtained were due to formation of complex compounds of litter-P with Al^{3+} in the soil during the decomposition process, making P unavailable to the decomposer population. This explanation does not exclude the possibility that P was rate-limiting in the decay process since available P may have been low in all roots in the present study.

3.1.7. Annual inputs of SOC

Estimates of annual root production, mortality and decomposition, using the compartment-flow model, are presented in Table 5. Introduced pastures had significantly higher changes in standing live and dead roots, amount of decomposition, turnover and consequently greater BNPP than NS. Turnover losses and BNPP for Bd and Bd + Ap were about 2.5 times greater than under NS. Decomposition and death accounted for 75% of the BNPP in all three pastures. Inputs of C under the well-managed introduced pastures were twice that of NS.

Estimates of BNPP by the ingrowth tubes were lower than values obtained by using the compartment-flow model. Differences were probably due to lower turnover estimates as the live root mass in the long-term tubes was consistently higher than the sum of root mass in the short-term tubes.

The amounts SOM and SOC remaining up to 50 cm depth at the end of 1 year of decomposition were significantly higher under introduced pastures than under NS (Table 6). The amount of OM remaining under introduced pastures was 2.4–2.8 times higher compared to that of NS. Similarly, the amount of SOC

Table 6
Soil organic matter and carbon remaining at 50 cm depth after 1 year of decomposition

Pasture	k (week^{-1})	Below-ground net primary productivity (Mg ha^{-1} yr^{-1})	After decomposition (Mg ha^{-1} yr^{-1})	
			Soil organic matter	Soil organic carbon
Native savanna	0.03 a	12.5 b	2.6 b	1.1 b
B. dictyoneura	0.027 b	30.0 a	7.4 a	2.6 a
B. dictyoneura + A. pintoi	0.031 a	31.3 a	6.3 a	2.5 a

remaining under introduced pastures was 2.3–2.4 times higher than that under NS.

4. Conclusions

Type of forage had a significant effect on BNPP. The small amount of fertilizers applied to tropical pastures at the establishment and regular maintenance increased BNPP. Inappropriate management such as overgrazing of tropical grasses and frequent burning of the native vegetation had negative effects on BNPP.

The major difference in C accumulation between the well managed introduced pastures and the native grasses resulted, to some extent, from the high BNPP of the introduced species. Litter quality as indicated by high C:N and C:P ratios apeared to control decomposition.

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