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Root activity patterns in an Amazonian agroforest with fruit trees determined by ^{32}P, ^{33}P and ^{15}N applications

J. Lehmann[1, 2, *], T. Muraoka[3] & W. Zech[1]
[1] *Institute of Soil Science and Soil Geography, University of Bayreuth, 95440 Bayreuth, Germany;*
[2] *Federal Research Institute for Forestry and Forest Products, 21027 Hamburg, Germany;* [3] *Centro Energia Nuclear na Agricultura (CENA), 13400-970 Piracicaba, Brazil (*Author for correspondence: E-mail: johannes.lehmann@uni-bayreuth.de)*

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Abstract

In a multi-strata agroforestry system in the central Amazon near Manaus, we studied the root activity distribution of different fruit trees and a legume cover crop in comparison to monocultures and a secondary forest site. Uptake of applied ^{32}P, ^{33}P and ^{15}N from 0.1, 0.6 and 1.5 m depth was compared in both the dry and wet season. The results obtained with ^{32}P were similar to those with ^{15}N but showed a higher variability, probably due to the lower mobility of P than N in soil and thus the labeling of a smaller soil volume with ^{32}P. During the dry season, topsoil root activity measured with ^{15}N was around 80% for all species with the exception of the palm tree *Bactris gasipaes* Kunth., which had a higher uptake from 0.6 m (50%) than from 0.1 m (30%). The subsoil (1.5 m) root activity was higher, when *Bactris* was not regularly cut for heart of palm harvest but grown for fruit production. Additionally, relative subsoil root activity of *Theobroma* increased and topsoil root activity of both *Bactris* and *Theobroma* decreased when intercropped in comparison to the monoculture. During the rainy season, the topsoil tree root activity slightly increased attributable to increasing water availability near the soil surface. The lowest isotope enrichment was noted for the secondary forest trees despite their low above ground biomass. The magnitude of the isotope enrichment was related to the foliar P and less pronounced to the foliar N contents, indicating higher nutrient cycling for nutrient-rich plant species. Despite the significant subsoil root activity (1.5 m) there was little evidence that large amounts of nutrients below 1 m depth can be recycled by the investigated tree species. More important may be a rapid recycling of nutrients from 0–1 m depth.

Introduction

The highly weathered, acid soils in the humid tropics are usually very poor in available nutrients (Van Wambeke, 1992). However, recent studies in agricultural land found large amounts of nitrate in acid subsoils of Ferralsols in East Africa (Mekonnen et al., 1997) and in central Amazonia (Schroth et al., 1999). It was shown that trees are able to retrieve these nutrients in the subsoil (Mekonnen et al., 1997). Mixed cropping of tree crops may enhance the nutrient use efficiency and decrease competition in comparison with monocultures through a complementary nutrient uptake from different soil layers, thus reducing nutrient losses by leaching (Seyfried and Rao, 1991) and utilizing subsoil nutrients (Schroth et al., 2001). This recycling of subsoil nutrients is an impor-

tant process for a sustainable nutrient cycling which has been postulated as a central benefit of agroforestry systems (Buresh and Tian, 1998).

To test for complementary soil nutrient uptake of different tree species, the root activity distribution can be determined by applying tracers at various depths or distances to the trees and measuring their uptake (Hall et al., 1953; IAEA, 1975). A quantitative value of total uptake from a certain depth cannot be given with this method, but the uptake from different depths or distances can be compared. Most studies used the radioisotope ^{32}P (IAEA, 1975), with a few experiments applying stable ^{15}N (Atkinson and White, 1980; Broeshart and Nethsinghe, 1972; IAEA, 1975), non-radioactive Sr (Fox and Lipps, 1964) or a double labeling approach with the radioisotopes ^{33}P and ^{32}P (IAEA, 1975). The double labeling approach especially deserves more attention, because it may considerably reduce random variability and increase the precision of the results (IAEA, 1975). The thorough experimentation initiated by IAEA (1975), however, was not followed by further extensive methodological research.

Some information exists about the root activity distribution of the major tropical cash crops like coconut, cocoa, oil palm, coffee, or banana (e.g. IAEA, 1975), but indigenous fruit crops of the Amazon have not been investigated up to now. No studies exist which compare different tree crops and natural woody vegetation. The existing studies mainly dealt with increasing fertilizer use efficiency (Ahenkorah, 1975), and not with studying the effects of cropping systems. Only very few results have been reported from agroforestry systems (Thomas et al., 1998; Rowe et al., 1999).

The objectives of this study were to (i) compare different tracer applications for root activity distribution measurements in central Amazonian Ferralsols, (ii) compare the root activity distribution of different tree crops and a cover crop which are important for agroforestry systems in the Amazon and a typical secondary forest species, and (iii) assess the effects of season and mixed cropping on root activity distribution.

Material and methods

Study site and experimental design

The study was carried out on the terra firme at the experimental station of the Empresa Brasileira de Pesquisa Agropecuaria (Embrapa)-Amazônia Ocidental near Manaus in 1998 and 1999. The rainfall distribution is unimodal with a maximum between December and May and a mean annual precipitation of 2503 mm (1971–1993). The natural vegetation is lowland tropical rainforest. The soils are classified as Xanthic Ferralsols (FAO, 1997). They are deep and clayey, strongly aggregated, with low pH, medium organic C and N contents, and low P and K contents (Table 1).

The study site was cleared from secondary forest in 1992 in order to plant an experiment with several monoculture and polyculture systems mainly using fruit trees. In this study, four tree species of high regional importance, *Bactris gasipaes* Kunth. (peachpalm, Arecaceae), *Theobroma grandiflorum* (Willd. ex Spreng.) K. Schum. (cupuaçu, Sterculiaceae), *Bertholletia excelsa* Humb. & Bonpl. (Brazil nut, Lecythidaceae) and *Bixa orellana* L. (annatto, Bixaceae) were investigated in a mixed cropping system. One row of *Bactris* (with 2 m distance

Table 1. Physical and chemical characteristics of a Xanthic Ferralsol in an Amazonian agroforest with fruit trees at maximum distance from the trees near Manaus, Brazil.

Depth [cm]	Horizon	Bulk density [Mg m^{-3}]	Clay content [g g^{-1}]	pH H_2O	C[a] [g kg^{-1}]	N[a] [g kg^{-1}]	P[b] [mg kg^{-1}]	K[b] [mg kg^{-1}]
0–10	Ah	0.82	0.59	4.1	29.1	2.74	14.6	22.0
10–50	B1	0.93	0.65	4.1	15.6	1.18	6.5	14.0
50–150	B2	0.97	0.72	4.3	4.5	0.55	4.1	10.3

[a] Measured with an automatic CN analyzer.
[b] Extracted after Mehlich (1984).

within the row) alternated with a mixed row of *Theobroma* and *Bertholletia* (with 7 m distance within the row) and a row of *Bixa* (with 4 m distance within the row). The rows were planted with a distance of 4 m. *Bactris* and *Theobroma* were also studied in monoculture at 2 by 2 m and 7 by 6.4 m planting density, respectively. Three replicate plots with a size of 48 × 32 m were randomly distributed with a distance of at least 100 m to each other. Additionally, root activity patterns of *Pueraria phaseoloides* (Roxb.) Benth. (Leguminosae) were determined, which was grown as a cover crop in the fruit tree systems. *Bactris* was managed for either fruit or heart of palm production, for which it was cut two months before each application. Secondary forest under *Vismia* spp. served as a control. Tree sizes and foliar nutrient contents are shown in Table 2. Fertilizer was applied to the tree crops according to local recommendation at the beginning of the rainy season in December and at the end of the rainy season in May using 95, 42, 85 and 42 g N (as ammonium sulfate), 77, 11, 40 and 22 g P (as triple-super-phosphate) per plant and year for *Theobroma*, *Bactris*, *Bixa* and *Bertholletia*, respectively. Lime was broadcast on the soil surface at a rate of 2.1 Mg ha^{-1} in 1996. The secondary forest sites were not fertilized.

Isotope placement

The root activity patterns were determined towards the end of the dry season on 11 November 1998 and towards the end of the rainy season on 25 May 1999. It was assumed that these were the times with the most contrasting root activity distribution throughout the year as confirmed by earlier results of lateral root activity patterns (Lehmann et al., 2000a). The uptake of tracer placements at 0.1, 0.6 and 1.5 m depth was measured following the theoretical approach outlined by IAEA (1975). For each depth, four tubes with an inner diameter of 5 mm were installed in a ring around each tree with a distance of 0.5 m. They were closed before and after isotope application. Through these tubes, 1 ml of a solution containing the N or P tracer (together with 1000 mg P l^{-1}) was applied using a dispenser (accuracy ± 1%) and flushed down with a jet of 10 ml of tap water.

The experiments conducted during the two seasons were done in different ways. In the dry season, all tree species described above as well as *Pueraria* were investigated in the mixed cropping system, *Theobroma* and *Bactris* additionally in the monoculture. From the two *Bactris* treatments only those for heart of palm were used. ^{32}P was applied for determining root activity patterns only of the trees in the mixed cropping system and the fallow, while ^{15}N was used at all sites. ^{32}P with an activity of 37 MBq (1 mCi) and 0.1 g ^{15}N as $(NH_4)_2SO_4$ with 10 atom%^{15}N excess

Table 2. Size and foliar P and N concentrations (December 1998) of fruit trees and a legume cover crop (*Pueraria phaseoloides*) in an agroforest and of fallow vegetation (*Vismia* spp.) on upland soils of the central Amazon near Manaus, Brazil.

Species	Height	Stem diameter[a]	P contents		N contents	
			Young leaves	Old leaves	Young leaves	Old leaves
	[m]	[mm]	[mg g^{-1}]			
Theobroma	4.1 ± 0.2	103 ± 5	1.01 ± 0.04	0.63 ± 0.06	15.6 ± 1.1	14.9 ± 1.3
Bactris (heart)	2.4 ± 0.2	nd	1.59 ± 0.12	1.29 ± 0.18	24.8 ± 2.2	20.6 ± 4.8
Bactris (fruit)	16.0 ± 0.6	165 ± 9	1.58 ± 0.10	nd	nd	nd
Bertholletia	12.4 ± 0.6	197 ± 10	1.27 ± 0.21	0.67 ± 0.07	17.7 ± 1.7	17.3 ± 1.5
Bixa	4.1 ± 0.2	114 ± 4	2.88 ± 0.21	1.19 ± 0.26	28.1 ± 2.3	18.5 ± 0.9
Vismia	9.6 ± 0.4	92 ± 5	0.86 ± 0.16	0.54 ± 0.04	14.4 ± 1.7	13.8 ± 1.6
Pueraria	nd	nd	nd	nd	31.5 ± 2.7	nd

[a] At breast height (1.5 m).
nd = not determined.
N = 12.

were applied at every depth under different individual trees of each species using a completely randomized design with three replicates (Little and Hills, 1978). Trees were chosen with a sufficient distance between each other to avoid the danger of cross contamination (> 10 m with one row of trees in between). The youngest fully developed leaves or leaflets exposed to direct sunlight from the upper (*Theobroma*, *Bixa*, *Bactris*, *Pueraria*) or lower crown (*Bertholletia*; due to better accessibility) were collected 7, 13, 21, 36 and 89 days after application. Twenty-one days after application, old leaves were also collected which were not exposed to direct sunlight.

In the rainy season, only the tree species in the mixed cropping system and the fallow were investigated. *Bactris* was managed for heart of palm as well as for fruit production. A double labeling approach with ^{32}P and ^{33}P was used (IAEA, 1975). Residual ^{15}N enrichment from the experimentation during the preceding dry season did not permit a repeated use of ^{15}N in the rainy season. Both ^{32}P and ^{33}P with activities of 0.74 and 3.33 MBq (0.02 and 0.09 mCi), respectively, were applied to each tree using a completely randomized design with three replicates and two trees per replicate. Originally, 111 and 37 MBq (3 and 1 mCi) were planned for ^{32}P and ^{33}P, but due to problems with the importation of ^{33}P the start of the experiment was delayed. The ^{32}P radioisotope was always applied at 0.1 m, the ^{33}P at either 0.6 or 1.5 m depth of the same tree. The youngest fully developed leaves equal to the dry season sampling were collected after 32 days. All samples were dried at 70 °C for 48 hours and ground.

Isotope analyses

For the P isotope analyses, 0.5 to 1 g of the ground samples were digested in concentrated nitric and perchloric acid until the complete disappearance of the nitric acid and the digest became clear, then diluted to 25 ml with distilled water. Twenty milliliters of the solution were used for direct counting of ^{32}P by the Cerenkov effect during 10 to 30 min, ^{33}P was analyzed in 4 ml digest mixed with 16 ml of scintillation solution at 30 min counting time (Nascimento and Lobão, 1977) using a Wallac 1409 Scintillation Counting System. In the same digest, the total foliar P contents were determined photometrically by the vanadate-yellow color method (Sarruge and Haag, 1974).

For obtaining the ^{15}N values, the leaf samples were analyzed using an Elemental Analyzer (Carlo Erba NA 1500) for Dumas combustion connected to an isotope mass spectrometer (FINNIGAN MAT delta E) via a split interface. The $\delta^{15}N$ values were calculated with the atmospheric N isotope ratio as the standard:

$$\delta^{15}N = \left(\frac{\frac{^{15}N}{^{14}N_{(sample)}}}{\frac{^{15}N}{^{14}N_{(standard)}}} - 1 \right) \times 10^3$$

Calculation of results and statistical analyses

The scintillation and mass spectrometrical results were calculated as the percentage uptake from one depth in relation to the total uptake from all three depths. The data were calculated for the isotope enrichment relative to P (cpm $^{32,33}P\ g^{-1}$ P) or N ($\delta^{15}N$), and relative to foliar dry weight (cpm $^{32,33}P\ g^{-1}$ and µg ^{15}Nexcess g^{-1}, respectively). An analysis of variance was computed using a completely randomized design with three replicates (ANOVA of STATISTICA Version 5). The analysis of the ^{32}P counts and $\delta^{15}N$ values was done after logarithmic transformation due to inhomogeneity of variances. In case of significant effects, means were compared using LSD at $P < 0.05$ (Little and Hills, 1978).

Results

Foliar ^{32}P and ^{15}N dynamics after isotope application

The radioactivity of the leaf material increased rapidly up to 36 days after application of ^{32}P at 0.1 m depth at the end of the dry season and decreased thereafter (Figure 1). The ^{32}P enrichment taking into account the radioactive decay rates of ^{32}P, however, increased steadily in all plants and reached a plateau for *Bixa* after 36 days. The ^{15}N increase in the leaves was initially more rapid than the ^{32}P increase. However, after day 36

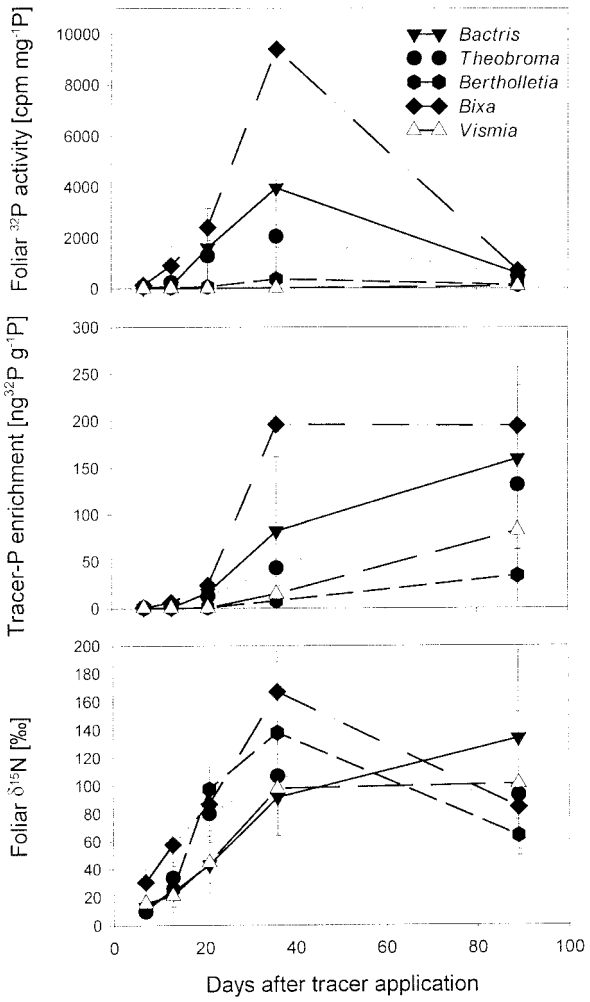

Figure 1. Dynamics of foliar ^{32}P activity, foliar P-tracer enrichment in relation to foliar P contents and foliar $\delta^{15}N$ values of four different fruit tree species and a secondary forest tree species (*Vismia* spp.) in the central Amazon region near Manaus, Brazil, after applying ^{32}P and ^{15}N at 0.1 m depth ($N = 3$).

the $\delta^{15}N$ values decreased, whereas the ^{32}P values continued to increase in all species except *Bactris* (Figure 1). For both ^{32}P and ^{15}N, the trees with the lowest foliar P or N concentrations (Table 2), respectively, also had the lowest tracer enrichment (Figure 2). This relationship was more pronounced for P than for N.

The isotope enrichment of different plant parts was compared in order to test whether the sampling strategy affected the results and to identify the best method for leaf sampling. The ^{32}P and ^{15}N values of old leaves were only weakly related to those of young leaves (^{15}N $r^2 = 0.454$; ^{32}P $r^2 = 0.375$; $P < 0.001$). However, the correlation of the root activity distribution determined from young against old leaves was better, more so with ^{15}N than ^{32}P (^{15}N $r^2 = 0.682$; ^{32}P $r^2 = 0.432$; $P < 0.001$). In all relationships, the slopes were lower than unity (^{15}N 0.5; ^{32}P 0.8). In comparison, the foliar P contents of young leaves were 1.2–1.9 times higher than those of old leaves, the foliar N contents just 1–1.5.

Depth distribution of root activity determined with ^{32}P and ^{15}N during the dry season

The foliar ^{32}P and ^{15}N contents decreased when the tracer was applied at larger depths for all plants apart from *Bactris* (Figure 3). Low isotope enrichments were noted for the *Vismia* fallow trees. Mixed cropping of *Bactris* and *Theobroma* significantly increased the ^{15}N enrichment from applications at 0.6 and 1.5 m depths compared to the monoculture ($P < 0.05$ and 0.01 for depths, respectively), but not at the topsoil ($P > 0.05$).

From the foliar ^{32}P counts per unit weight and the ^{15}N contents in excess of natural abundance, the root activity distribution was calculated as the relative uptake from one depth in comparison to all three depths using analyses of young leaves. A calculation of the root activity distribution either per leaf weight or N or P contents yielded the same results ($P > 0.05$; data not shown). Also the methods using ^{32}P or ^{15}N applications had no significant effect on the root activity distribution ($P > 0.05$; Table 3), but the variation was much higher with P than with N as seen from the standard errors (Figure 4) and from the significance of the species effect for ^{15}N in contrast to ^{32}P (Table 3). Looking at the individual trees, good matches between the two methods were achieved for *Bixa*, *Theobroma* and *Bactris*, less satisfying were the differences for *Vismia* and especially *Bertholletia*.

All trees and the cover crop took up around 80% of their N from the topsoil at 0.1 m depth, apart from *Bactris* with 35% as determined by ^{15}N applications (Figure 4). The ^{32}P measurements indicated lower values for *Bertholletia* and *Vismia* with 42 and 48%, respectively. The root activity decreased rapidly with depth and amounted to less

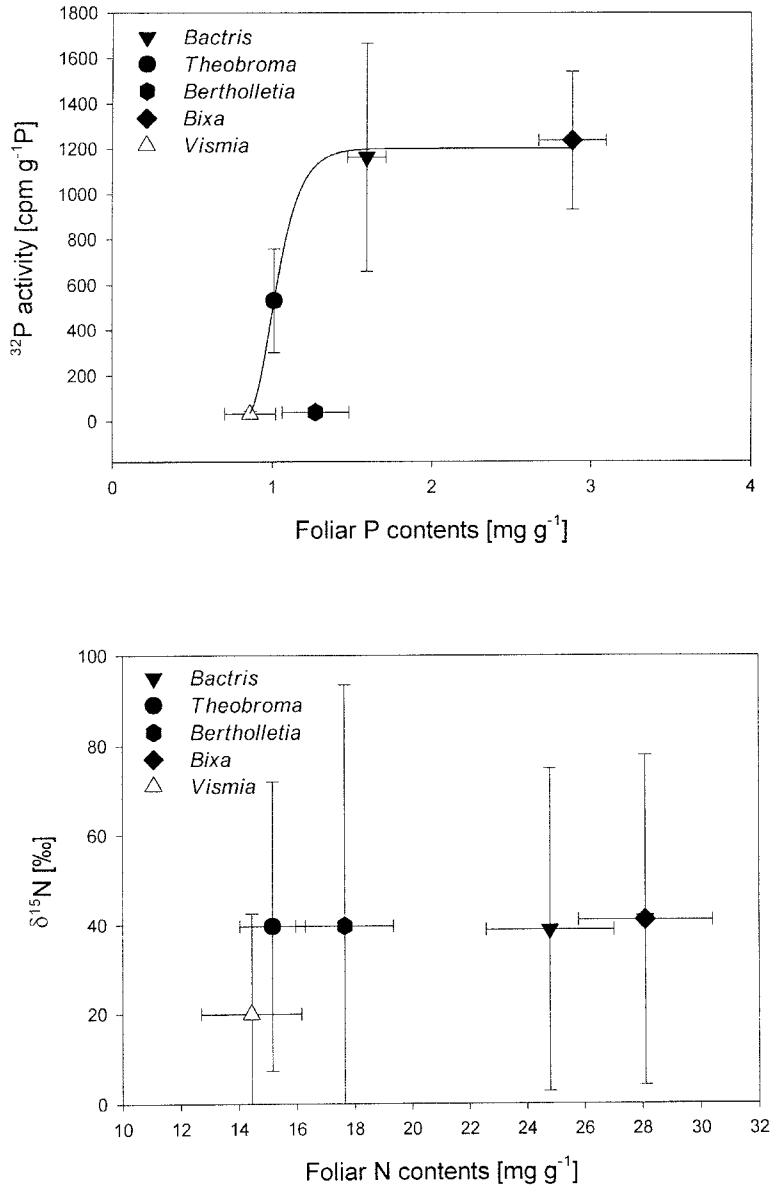

Figure 2. Relationship between the foliar P and N concentrations and the foliar ^{32}P activity or δ^{15}N values of four different fruit tree species and a secondary forest tree species (*Vismia* spp.) in the central Amazon region near Manaus, Brazil, after application of ^{32}P and ^{15}N at different depths at the end of the dry season; means and standard errors of all depths and replications (N = 9).

than 20% at 0.6 m and not higher than 10% at 1.5 m depth for all tree species apart from *Bactris*. For *Pueraria*, no uptake was noted from 1.5 m depth. In contrast to all other species, *Bactris* had a higher root activity at 0.6 than 0.1 m depth (Figure 4). The differences between the trees were generally more pronounced at the topsoil (0.1 and 0.6 m) than the subsoil (Table 3).

At the topsoil (0.1 m), intercropped *Theobroma* and *Bactris* had a lower relative root activity than in the monoculture, whereas it was reversed in the subsoil (1.5 m) ($P < 0.05$; not significant for *Bactris* in the subsoil; Figure 4). At 0.6 m depth, the cropping system had no effect on the root activity of *Theobroma*, though *Bactris* had a higher relative N uptake in agroforestry than in

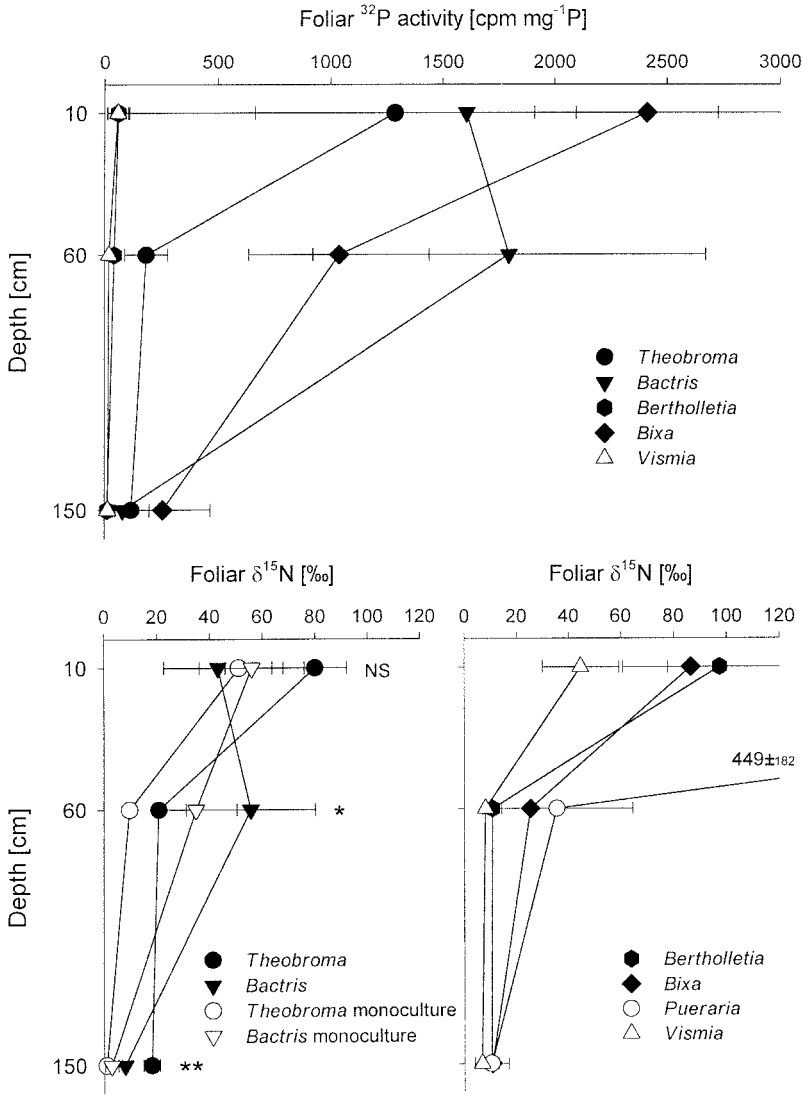

Figure 3. Foliar ^{32}P activity and $\delta^{15}N$ values of four different fruit tree crops and a cover crop (*Pueraria*) planted in agroforest (all species) or monoculture (only *Theobroma* and *Bactris*) in comparison to secondary forest trees (*Vismia* spp.) in the central Amazon region near Manaus, Brazil, after application of ^{32}P or ^{15}N at different depths at the end of the dry season; *, ** and NS denote significant effects at $P < 0.05$, 0.01 and not significant effects, respectively, calculated by analysis of variance for the effect of intercropping only ($N = 3$).

monoculture ($P < 0.05$). The root activity at 1.5 m depth was negligible in both monoculture plantations.

Root activity distribution during the rainy season

Using a double labeling approach (^{32}P and ^{33}P) at the end of the rainy season, the variability of the root activity measurements could be considerably reduced apart from *Bactris* (Figure 5). *Theobroma*, *Bixa* and *Bertholletia* in the mixed cropping system took up only less than 10% of their P from 0.6 and 1.5 m depth. *Bactris*, however, showed a lower root activity at 0.1 m but a higher one at 0.6 m depth than the other fruit tree species ($P < 0.05$), similar to the dry season. When *Bactris* was managed for fruit production and not

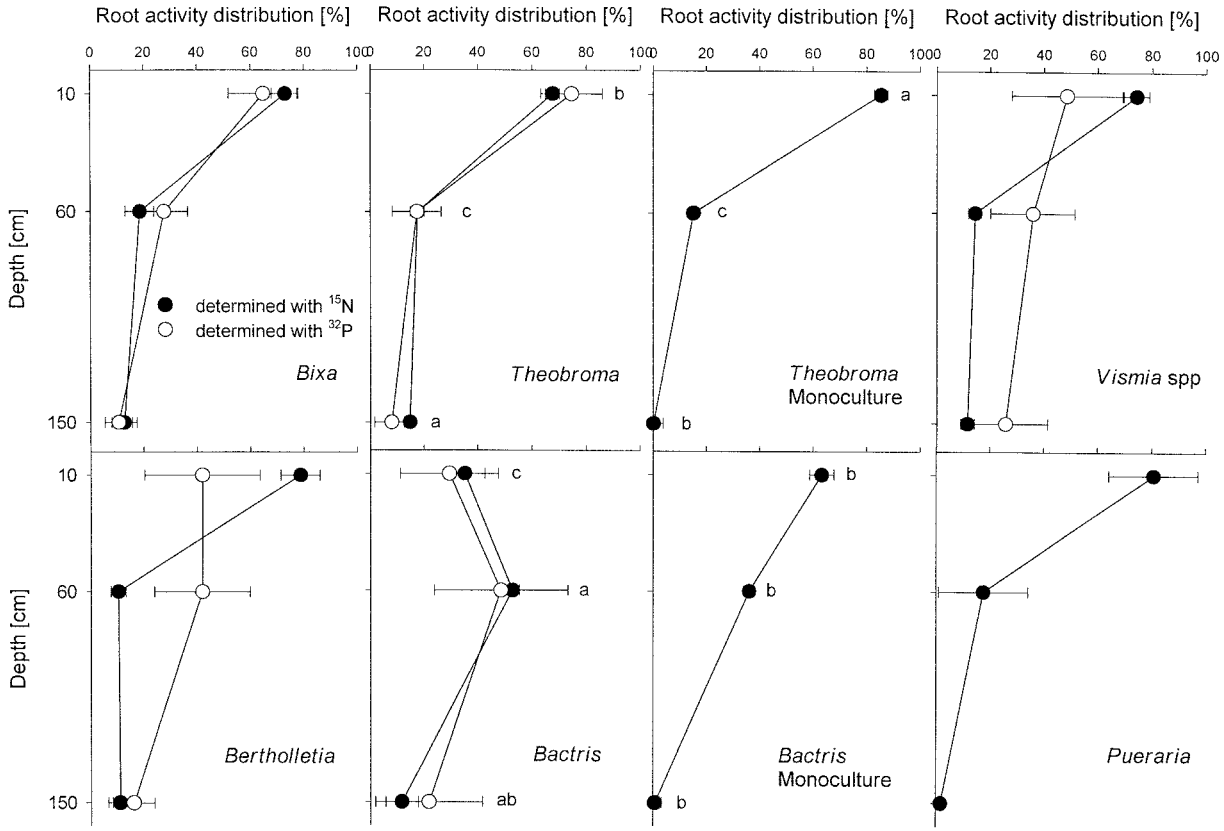

Figure 4. Root activity distribution of four different fruit tree crops and a cover crop (*Pueraria*) planted in agroforest (all species) or monoculture (only *Theobroma* and *Bactris*) in comparison to secondary forest trees (*Vismia* spp.) determined with ^{32}P and ^{15}N in the central Amazon region near Manaus, Brazil, at the end of the dry season. Values with the same letter at the same depth are not significantly different at $P < 0.05$ (only ^{15}N method) ($N = 3$).

Table 3. Significance levels from analysis of variance of the effects of plant species, method (^{32}P or ^{15}N applications) and cropping system (agroforest or monoculture) on root activity distribution of four fruit trees and a cover crop in an agroforest and of secondary vegetation in the central Amazon near Manaus, Brazil, during the dry season.

Effects	Method	Depth [m]		
		0.1	0.6	1.5
Comparison of species:				
Species	^{32}P	0.42 NS	0.70 NS	0.84 NS
Species	^{15}N	0.025 *	0.018 *	0.30 NS
Comparison of method:				
Species	^{32}P, ^{15}N	0.60 NS	0.11 NS	0.94 NS
Method	^{32}P, ^{15}N	0.14 NS	0.19 NS	0.56 NS
Species × method	^{32}P, ^{15}N	0.49 NS	0.55 NS	0.79 NS
Comparison of system:[a]				
Species[a]	^{15}N	0.0028 **	0.0000 ***	0.84 NS
Cropping system[a]	^{15}N	0.0065 **	0.0090 **	0.029 *
Species × system[a]	^{15}N	0.39 NS	0.030 *	0.68 NS

[a] Only *Theobroma* and *Bactris*; NS = not significant; see also Figure 4.

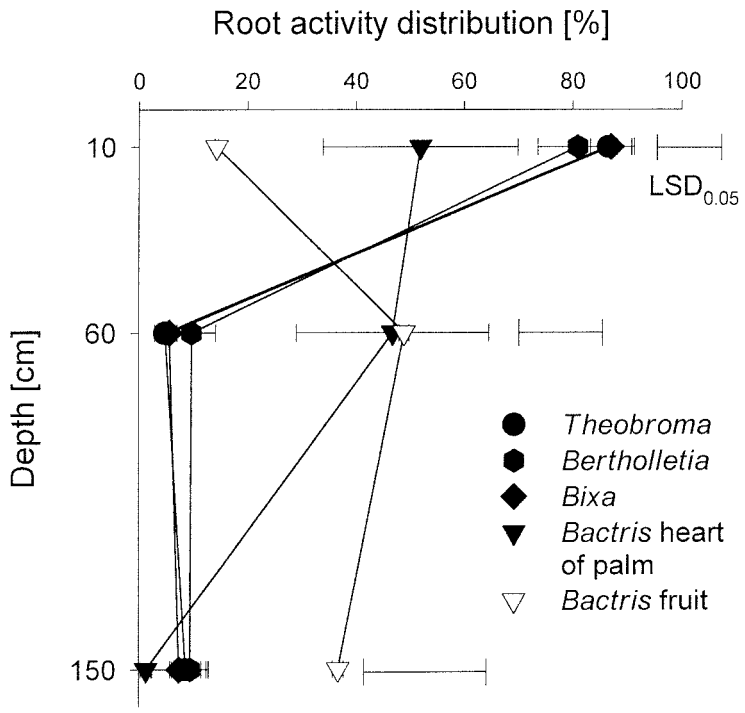

Figure 5. Root activity distribution of four different fruit tree crops planted in an agroforest (*Bactris* managed for both heart of palm and fruit production) in comparison to secondary forest trees (*Vismia* spp.) determined with double labeling ^{32}P (0.1 m) and ^{33}P (0.6 or 1.5 m) in the central Amazon region near Manaus, Brazil, at the end of the rainy season ($N = 3$).

regularly cut as for the heart of palm harvest, the relative nutrient uptake further decreased in the topsoil and increased in the subsoil ($P < 0.05$).

Discussion

Methodology of root activity distribution measurements

The best time for plant sampling was around 40 days after application of both ^{32}P and ^{15}N, when the isotope signals and the differentiation between trees were highest (highest ratios of differences-to-standard errors; data not shown). A longer exposure did not further increase the differentiation between the trees, but the scintillation counts decreased pronouncedly. In root activity measurements of various tree crops done by IAEA (1975), sampling was done from 10 up to 90 days after ^{32}P application and counts were continuously increasing for most trees in contrast to our study.

There were no relevant differences of root activity results whether young or old leaves were analyzed for the investigated tree species. Also IAEA (1975) did not find an effect of sampling different plant parts, with the exception of coconut. Using young leaves, however, was preferable as the isotopes were highly concentrated and therefore easier to analyze.

Both methods using ^{32}P and ^{15}N yielded similar results, which was also observed by Broeshart and Nethsinghe (1972) for apple trees. There are several advantages and disadvantages of choosing one of the investigated tracers over the other for root activity measurements. Reasons for recommending the radioactive P are: (i) inorganic P is relatively immobile in soils especially when oxides are present, as in many highly weathered tropical soils; therefore P stays at the point of application in contrast to N, which is mostly present as nitrate and may easily be leached; (ii) the sensitivity of the scintillation counting is extremely high; (iii) using the radioisotopes, the tracer applications can be done at various times on the same tree for obtaining seasonal variations of

root activity distribution, since the half life of both ^{32}P (14.3 days) and ^{33}P (25.3 days) is very low; this is not possible with ^{15}N and repeated determinations of root activity on the same tree individual are not recommended due to the carry-over effect; (iv) the double labeling approach with ^{32}P and ^{33}P allows measurement of even two depths at the same tree, thus reducing the variation as shown in this study and by IAEA (1975); (v) ^{32}P is less expensive than ^{15}N (this is not true for ^{33}P, which is very expensive), especially when highly enriched ^{15}N has to be applied due to high soil N contents. Reasons for using the stable ^{15}N isotope are: (i) The root activity results obtained with ^{15}N showed less variation than with ^{32}P, which may be caused by the higher mobility of N than P in soil, and led to a higher distribution of N and a larger area of ^{15}N- than ^{32}P-labeled soil; (ii) the stable ^{15}N isotope is not hazardous and can be handled without health precautions in contrast to the P radioisotopes, making the stable isotope also more easily available for experimentation; (iii) the N uptake was shown to be more rapid and more similar among plant parts and tree species than the P uptake, and therefore the measurements have the same sensitivity for the studied species.

In soils with a lower anion exchange capacity than in the studied, highly weathered Ferralsol, however, nitrate movement may be too rapid to refer plant tracer uptake to the exact point of application. This constraint also applies to periods of high rainfall and large water percolation. Simultaneous application of carbon sources for microbial immobilization of N may help to stabilize the isotope (Rowe et al., 1999).

Nutrient uptake dynamics

Uptake of ^{15}N started immediately after application and continued linearly, whereas initial ^{32}P uptake was very low and followed an exponential curve. Therefore, the movement to the root surface and the uptake seemed to be more rapid for N than for P. It was also shown that there was a closer relationship between foliar content and relative uptake of P than of N. These observations may mean that tree species with a higher foliar P content recycle P more rapidly than tree species with a lower foliar P content, even more than their foliar P content would suggest. This conclusion is only valid for our data, if the above ground biomass is not lower for the high P-containing trees resulting in lower dilution with native foliar P, which was not the case here. The relationship was not as clear for N as for P, which may be an effect of the higher availability of N than P in the soils at our site. Schroth et al. (unpublished data) found a very high N mineralization of more than 300 kg N ha^{-1} yr^{-1} at the topsoil (0–0.1 m), whereas native P availability was generally low in the studied Ferralsols (Lehmann et al., 2001).

Seasonal root activity changes

The differences of root activity patterns between dry and wet season were most likely caused by fluctuations of soil water availability. Several published studies showed that the root activity in the topsoil decreased due to a lack of water e.g. during the dry season for coffee in Kenya (Huxley et al., 1974). As shown in our work, most studies found the highest root activity in the topsoil as reported for *Theobroma cacao* on a Ferralsol in Ghana (Ahenkorah, 1975), and negligible activity in the subsoil (1.8 m) for coffee in Kenya (Huxley et al., 1974).

Bactris had a different root activity distribution than the other trees in both seasons. The root system of the monocot palm tree had a higher relative activity deeper in the subsoil than the other trees. In contrast to our results, Ferreira et al. (1980) found 58% of the root biomass of *Bactris* managed for fruit production in the first 0.2 m. However, in a study in Costa Rica Vandermeer (1977) could show that this was only true for the area immediately below the trunk. At 0.6 m distance, he found that *Bactris* root mass did not decrease with depth and even had its highest value at 1.4 m depth, explaining why we found higher or similar root activity in the subsoil than the topsoil. Cutting the shoots for heart of palm harvest increased the relative root activity at the topsoil and reduced subsoil root activity. Similar observations were made for root length densities when pruning *Acacia* spp. (Lehmann et al., 1998).

Bertholletia was reported to have a pronounced tap root (Haag, 1997), but did not show a higher relative subsoil root activity than the other trees in our study. Short-range root activity differences

around the trunk as reported above for *Bactris* may have been the reason that the extent of the tap root was not registered. In 0.5 m distance to the trunk of *Bertholletia*, the root activity distribution decreased very rapidly with depth as demonstrated here, whereas directly underneath the trunk root activity may possibly have been higher at greater depths due to the tap root. This would also mean that the tap root had little capacity for nutrient retrieval, if root activity at 0.5 m distance to the trunk is reduced to the extent shown in the present study.

Mixed cropping effects on root activity distribution

Competition for soil resources was higher at the topsoil than the subsoil in the mixed cropping system compared to the monoculture and therefore the roots of *Theobroma* and *Bactris* were taking up relatively less of the applied isotopes from the topsoil. Lehmann et al. (1998) could show that the more competitive root system of intercropped sorghum induced associated acacias to root deeper. Whereas *Bactris* had the same tracer uptake from the subsoil in both cropping systems, *Theobroma* took up more ^{15}N from the subsoil in the agroforest than in the monoculture. This may be explained by the wide spacing of the Theobroma monocultures.

Root activity patterns and nutrient cycling

Despite the low uptake from 1.5 m depth, the measured 10 to 20% of the total root activity during the dry season was still a relevant contribution for crop nutrition, especially considering the volume of subsoil present. If the root activity distribution was linearly interpolated between the application depths, 40 to 70% of the root activity between 0.1 and 1.5 m was at 0.1 to 0.6 m, and 30 (*Theobroma*) to 60% (*Bactris*) at 0.6 to 1.5 m depth. With an above ground N turnover of 21 and 90 kg N ha^{-1} yr^{-1} for *Theobroma* and *Bactris*, respectively (Lehmann et al., 2000b), 6 and 54 kg ha^{-1} yr^{-1} were taken up from 0.6 to 1.5 m depth, not considering the N uptake from 0–0.1 and below 1.5 m depth. Even though these values are in fact lower due to omission of the upper 0.1 m, this is still a relevant amount for *Bactris* compared to 175 kg mineral N ha^{-1} found in 0–2 m at the end of the dry season, but not for *Theobroma* with 535 kg mineral N ha^{-1} (Schroth et al., 1999).

Nevertheless, the danger of nutrient leaching is high for the described cropping system. There were no indications that the high amounts of nitrate which were found in the subsoil at the same site can be effectively recycled by the trees, considering the large rates of water percolation in the highly permeable soils. Rozanski et al. (1991) measured a seepage of 700 mm to 2 m depth during 139 days at a nearby site.

A higher potential for nutrient recycling and therefore reduction of nutrient losses by leaching at our site was considered not to be in the subsoil (1.5 m) but close to the topsoil (0.1 and 0.6 m). At these depths, root activity can be managed by species selection and relevant amounts of nutrients were taken up. *Bactris* was shown to be more likely to recycle large amounts of nutrients than the other species from 0.1–0.6 m. Apart from the vertical distribution of nutrient uptake, also the total amount of nutrient incorporation, litter fall and nutrient release are important for rapid nutrient recycling. *Bixa* was shown to return a larger amount of P than the other tree species leading to higher amounts of available soil P at the topsoil (Lehmann et al., 2001). The cover crop *Pueraria* recycled even more N than *Theobroma* or *Bactris* in the same experiment, while *Theobroma* was shown to return the lowest amount of P and N (Lehmann et al., 2000b, 2001).

Root activity in natural fallow

The fallow vegetation dominated by *Vismia* had the lowest isotope enrichment of all investigated tree species. Since *Vismia* did not have a higher above ground biomass than the other trees as estimated from their stem diameter and height, the low enrichment also indicates a low total uptake. Additionally, the fallow tree had a low root activity proportion in the subsoil similar to the other tree species. Schroth et al. (1999) found lower amounts of subsoil N in the same fallow than under the fruit trees or even adjacent primary forest sites. An effective recycling of this subsoil N by *Vismia* did not seem to be a plausible explanation according to the results presented

here. More likely, the topsoil and litter N mineralization were lower than at the other sites therefore reducing mobile soil N. In contrast to our results, a significant reduction of subsoil N in *Sesbania sesban* fallows compared to unfertilized maize was reported from Kenya (Mekonnen et al., 1997). These fallows, however, have a much higher nutrient uptake and turnover than the studied natural fallows in central Amazonia.

Conclusions

The assessment of root activity patterns using ^{15}N had some advantages over the other isotopes for the presented study, especially showing lower variability. This may be a result specific to our experimental conditions and needs to be verified for other soils and rainfall regimes. The obtained results may not be transferable to conditions of sandy soils or soils with high pH, low contents of variable charge clay minerals and low anion exchange capacity. The techniques using P and N isotopes complemented each other and led to a higher certainty of the results. The investigated tree species in the agroforestry system and in the secondary forest were taking up significant proportions of their nutrients from as deep as 1.5 m, considering the large volume of subsoil present. The root activity in the subsoil, however, was not high enough to efficiently utilize the subsoil N sources observed at this site. *Bactris*, however, took up significant amounts of nutrients from 0.6 depth throughout the year. If *Bactris* was not cut for heart of palm harvests, subsoil root activity even increased. *Theobroma* was the least suitable for nutrient recycling. According to the presented results, strategies for nutrient conservation should aim at the prevention of nutrient leaching already near the topsoil rather than the retrieval of leached nutrients below 1 m depth. To achieve this, mixed cropping of trees with varying root activity distribution may be a valuable and feasible strategy.

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