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Nitrogen uptake from ^{15}N-enriched fertilizer by four tree crops in an Amazonian agroforest

Harald Dinkelmeyer[1,2], Johannes Lehmann[1,3,6,*], Andreas Renck[1], Lucerina Trujillo[4], Jose Pereira da Silva Jr.[4], Gerhard Gebauer[5] and Klaus Kaiser[1]
[1]*Institute of Soil Science and Soil Geography, University of Bayreuth, 95440 Bayreuth, Germany;* [2]*Institute of Geography, University of Erlangen, 91054 Erlangen, Germany;* [3]*Federal Research Institution for Forestry, 21027 Hamburg, Germany;* [4]*Embrapa Amazonia Ocidental, 69011-970 Manaus, Brazil;* [5]*Institute of Plant Ecology, University of Bayreuth, 95440 Bayreuth, Germany;* [6]*Department of Crop and Soil Sciences, Cornell University, NY 14853 Ithaca, USA; *Author for correspondence (e-mail: CL273@cornell.edu; fax: (607) 255-3207)*

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Abstract

Mixed tree cropping systems have been proposed for sustainable nutrient management in the humid tropics. Yet, the nutrient interactions between intercropped trees have not been addressed sufficiently. In the present study we compare the temporal and spatial patterns of the uptake of applied ^{15}N by four different tree crops in a mixed tree cropping system on a Xanthic Ferralsol in central Amazônia, Brazil, during one year. Most of the N uptake occurred during the first two weeks. Very little N was recovered by peach palm (*Bactris gasipaes*), more by cupuassu (*Theobroma grandiflorum*) and annatto (*Bixa orellana*) and most by Brazil nut (*Bertholletia excelsa*). Due to tree pruning the total accumulation of applied ^{15}N in the above-ground biomass of annatto decreased throughout the year. It remained constant in cupuassu and peach palm and increased in Brazil nut. Brazil nut showed an extensive root activity and took up more fertilizer N applied to neighboring trees than from the one applied under its own canopy in contrast to the other three tree crops. Therefore, trees with wide-spread root systems may not need to receive N fertilizer directly but can take up N applied to other trees in the mixed cropping system. This means that such trees may effectively decrease N leaching when intercropped with trees that have dormant periods or places with low N uptake, but also exert considerable resource competition.

Introduction

High precipitation leads to rapid water percolation in central Amazonian upland soils (Rozanski et al. 1991). Additionally, these Ferralsols are strongly aggregated (Lehmann et al. 2001a) and are therefore highly permeable. Due to high weathering they have low exchange capacities, and nutrient retention in the topsoil is consequently limited (Van Wambeke 1992). As a result, high leaching losses of applied fertilizer were observed, e.g. under maize in the central Amazon (Cahn et al. 1993; Melgar et al. 1992). Trees were reported to reduce nutrient leaching in comparison to annual crops (Buresh and Tian 1998). But even under tree crops with perennial root systems, large losses of fertilizer N from the topsoil were observed which accumulated as adsorbed nitrate in the subsoil (Schroth et al. 1999).

A combination of different trees may reduce these losses because growth cycles and root activity distribution of different tree crops may complement each other (Schroth et al. 2001). This would lead to a higher use efficiency of applied fertilizer and reduce leaching losses. On the other hand, competition for nutrients may decrease the production of one crop or the whole system.

Nutrient interactions between trees in mixed cropping systems are difficult to determine due to their complex geometries. Assessment of the root distribution can give valuable information about the architecture of the belowground biomass, but often fails to quantify short-term dynamics of nutrient uptake. Additionally, trees in tropical lowlands may have very deep root systems (Canadell et al. 1996; Nepstad et al. 1994). Because of the low root abundance in the subsoil, determination of their contribution to total nutrient uptake is difficult. Tracer studies can help to quantify these spatial and temporal patterns of nutrient uptake (Lehmann and Muraoka 2001). Therefore we used ^{15}N-enriched fertilizer to compare the dynamics of N uptake by four intercropped trees on a Xanthic Ferralsol in the central Amazon during one year. The purpose of this study was (i) to compare the spatial distribution of N fertilizer use; and (ii) to describe the temporal dynamics of N uptake by different tree crops in an Amazonian agroforest.

Materials and methods

The study was carried out at the Empresa Brasileira de Pesquisa Agropecuaria (Embrapa)-Amazônia Ocidental 29 km North of Manaus, Brazil (3°8′ S, 59°52′ W, 40–50 m above sea level), in 1998 and 1999. The rainfall distribution is unimodal with a maximum between December and May (211–300 mm per month; 75% of annual rainfall) and a mean annual precipitation of about 2100 mm (1931–1960; Rodrigues et al., 1971, unpublished; and Ribeiro and Adis (1987)). The vegetation is a tropical lowland rainforest. The soils are Xanthic Ferralsols (FAO 1990) and derived from Tertiary sediments. They are very deep and clayey, with low pH (in H_2O; 4.0–4.5), medium levels of organic C (18.9 mg g^{-1}) and N (1.6 mg g^{-1}) but low in P content (6.3 mg g^{-1}), cation exchange capacity (21 $mmol_c$ kg^{-1}) and base saturation (33%) (all data from a 7-year-old fallow within the present experiment (n = 3); Schroth et al. (1999)).

Experimental setup

The site was first cleared in 1980 for a rubber plantation (*Hevea brasiliensis* (Adr. Juss.) Muell. Arg.), which was abandoned in 1986. The developing secondary forest was cut and burned in 1992 in order to establish several cropping systems mainly with fruit trees during the first half of 1993. Here, we investigated the uptake of N in a multi-strata agroforestry system with *Theobroma grandiflorum* (Willd. ex Spreng.) K. Schum. (cupuassu), whose fruit is used for juice and ice cream; *Bactris gasipaes* Kunth. (peach palm), for heart of palm production; *Bertholletia excelsa* Humb. & Bonpl., producing Brazil nut; *Bixa orellana* L., an important local dye (annatto), and a legume cover of *Pueraria phaseoloides* (Roxb.) Benth. (pueraria). Cupuassu and Brazil nut were alternately grown in the same row with a distance of 7 m. In the adjacent rows at a distance of 4 m either annatto (4 m distance within the row) or peachpalm (2 m distance within the row) were grown (Figure 1). The rows on both sides of peach palm and annatto were planted with cupuassu and Brazil nut; therefore peach palm and annatto did not neighbor each other. Four plots of 7 × 8 m as shown in Figure 1 were randomly located in blocks with the dimensions of 48 × 62 m and replicated three times (randomized complete blocks; total amount of plots = 12). Plots within a block were separated from each other by at least two rows of trees (12 m) to avoid cross contamination.

Peach palm was managed for palmito production (heart of palm) and cut every four to five months. At planting pueraria was sown between the trees and manually cut under the tree canopy every three to four months. At the time of this study, pueraria cover was strongly reduced due to shading and very little ground vegetation was present. Nitrogen uptake by pueraria and ground vegetation was presumed to be low and was therefore not quantified. Fertilizer applications were split equally between the beginning of the rainy season in December and towards the end of the rainy season in May using 95, 42, 85, 42 g N (as ammonium sulfate) per plant and year for cupuassu, peach palm, annatto and Brazil nut, respectively. Dolomitic lime and Atifos (North Carolina Phosphate, 13% P) was broadcast on the soil surface at a rate of 1.9 Mg ha^{-1} and 19 kg P ha^{-1}, respectively, in 1996. By the start of the presented experiment, the trees were six years old and in full production apart from Brazil nut.

During the experimental year, the regular fertilizer application was delayed by a few weeks due to a late start of the rains. On 12/13 January 1999, ^{15}N-enriched ammonium sulfate (10 atom% ^{15}N excess) was added to only one of the four tree species in each plot using 1 g ^{15}N excess per individual tree resulting in a total ^{15}N application of 1, 1, 3, 4 g ^{15}N per plot to Brazil nut, cupuassu, annatto and peach palm, respectively (Figure 1). In any of the four plots only the fertilizer applied to one tree species was labeled, whereas the other trees only received unlabelled N

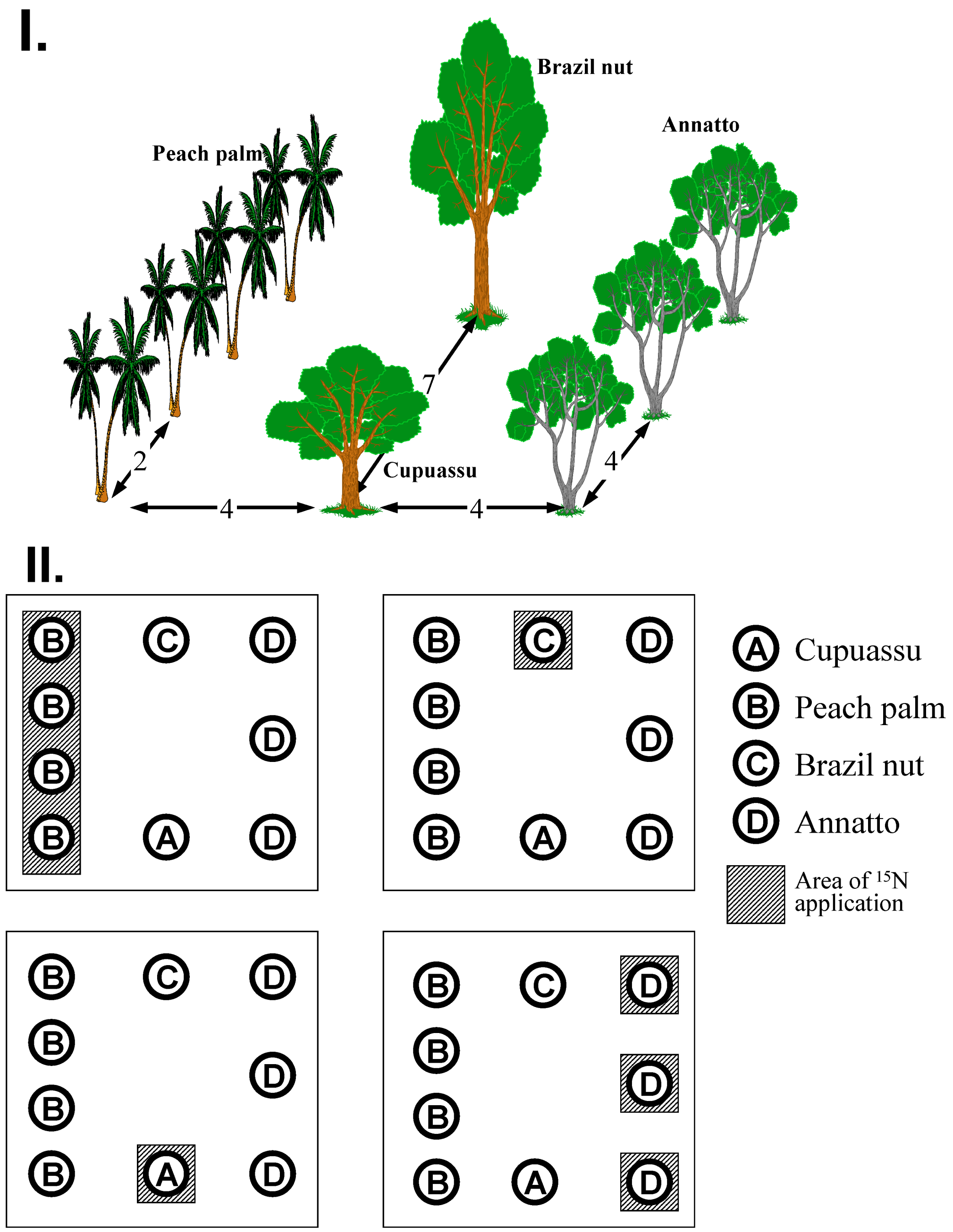

Figure 1. Spatial layout of the experimental unit (I., values denote distances between trees in [m]) and application of ^{15}N (II., distances between plots not to scale) to four different tree crops in the central Amazon; signatures for trees (A–D) correspond to sets of data shown in Figure 2 to Figure 4.

fertilizer. The effective amount of applied N (10 g N tree^{-1}) by ^{15}N-enriched ammonium sulfate was deducted from the routinely applied N fertilizer. The nutrients were added uniformly on the surface of the mineral soil in a square of 4 m^2 around each stem. The tracer was applied to 1 m^2 areas at a time using a dilute solution and a sprayer system, which allowed to spray each quadrant several times and thus ensure a homogeneous application. The litter layer was carefully removed before the application and distributed evenly afterwards.

uPlant and soil sampling

The N isotope composition was measured in the four tree species before the tracer application in October 1998, two weeks after the tracer application on 25–27 January, and on 18/19 February, 23 March, 15–23 April, 1 July and 8/9 November 1999. In February, March and July, only leaf samples were collected, whereas at the other dates also stem and branches were sampled. At least 10 leaves from random locations on each tree were collected including old and young leaves exposed to sun or in the shade. Stem samples were obtained with a drill (8 mm diameter) along the trunk to its center, branches were cut and pieces were randomly collected from young and old parts (at least 10 samples per tree).

In December 1998 and January 1999, soil samples were obtained from 0–0.1, 0.1–0.3, 0.3–0.5, 0.5–0.8, 0.8–1.2, 1.2–2 m, in April and November 1999 additionally at 2–3, 3–4, 4–5 m depths. Four subsamples were taken from each depth at 0.5–0.8 m distance from the trunk under those trees which received ^{15}N, and combined to one sample per replicate.

Determination of biomass and calculation of ^{15}N uptake

In September 1998, April and December 1999, total above-ground biomass was determined using allometric relationships in order to calculate total N uptake and ^{15}N recovery: cupuassu (woody biomass = 18.59 × $\text{dia}_{\text{stem at 0.2m}}^{\ 2.82}$, N = 7; leaves = 4.07 × $\text{dia}_{\text{stem at 0.2m}}^{\ 3.42}$, N = 36; all $P < 0.05$ for independent samples; Wolf (1997)); Brazil nut (stem = 0.926 × f, N = 7; branches = 2.50 × $f^{1.51}$, N = 7; leaves = 10.36 × $f^{1.28}$, N = 79; where f = Σ(cross section area$_{\text{(at 10, 20, 30\% of total height)}}$) × height/10; all $P < 0.05$ for independent samples; Wolf (1997)); annatto (stem + old branches = 140.6 × $\text{dia}_{\text{stem at 0.2m}}^{\ 1.657}$, N = 4, $P < 0.05$, Wolf (1997); young branches = 11.97 × $\text{dia}_{\text{branch}}$ + 7.02; leaves = 24.87 × $\text{dia}_{\text{branch}}$ + 17.48, N = 23; $R^2 = 0.71$; own measurements); peach palm (total biomass = 0.587 × height – 0.287, N = 12; $R^2 = 0.93$; own measurements). For production estimates of peach palm, the trees that were cut during harvesting of the heart of palm were quantified separately and the N amounts were added to the difference between values at the beginning and the end of the experiment. Uptake of applied ^{15}N was calculated from the product of above-ground biomass and ^{15}N contents of leaves, branches and stem, respectively:

$$^{15}\text{N}_{\,biomass}[mg\ tree^{-1}] = \Sigma(biomass_{leaf,branch,stem}\,[kg\ tree^{-1}] \times {}^{15}\text{N}_{\,leaf,\,branch,\,stem}[mg\ kg^{-1}])$$

Recovery of ^{15}N in tree and soil was determined in two different ways, as the ratio of uptake to application for the entire cropping system as shown in Figure 1 (Nitrogen System Recovery NSR) and for single tree species (Nitrogen Tree Recovery NTR):

$$NSR[\%] = \frac{^{15}\text{N}_{\,biomass}[mg\ tree^{-1}]}{^{15}\text{N}_{\,fertilized}[mg\ system^{-1}]} \times 100$$

$$NTR[\%] = \frac{^{15}\text{N}_{\,biomass}[mg\ tree^{-1}]}{^{15}\text{N}_{\,fertilized}[mg\ tree^{-1}]} \times 100$$

Total application (100%) was 9 mg ^{15}N excess to the system as shown in Figure 1, and 1, 1, 3, and 4 mg ^{15}Nexcess to single tree species of cupuassu, Brazil nut, annatto and peach palm. Recovery of ^{15}N in below-ground biomass was not determined. It may constitute a large part of total plant recovery, more for peach palm (root-to-shoot ratio 1.0 for heart of palm production) than for Brazil nut, cupuassu and annatto (root-to-shoot ratio 0.3–0.4; Haag (1997)).

Nitrogen isotope analyses

The leaf samples were dried at 70 °C for 48 hours. The soil samples were air-dried at room temperature and all samples were finely ground with a ball mill. The ^{15}N-enriched samples were analyzed using an Elemental Analyzer (Carlo Erba NA 1500; for Dumas combustion) connected to an isotope ratio mass spectrometer (Finnigan MAT delta E) via a split interface. The natural abundance of ^{15}N in plant and soil before application of the ^{15}N-labeled fertilizer was determined with an elemental analyzer (Fisons 1108) coupled via a ConFlo II Interface to a delta S isotope ratio mass spectrometer (Finnigan MAT). Natural abundance of ^{15}N was deducted from calculations of enriched samples to estimate the recovery and uptake distribution of the added ^{15}N.

Statistical analyses

Statistical analyses were computed by analysis of variance (Statistica 5.0) using a randomized complete block design for comparisons between trees in different plots and using a split plot design for comparisons between trees in the same plot (Little and Hills

Table 1. Above-ground biomass of four different tree crops at the end of the experiment in December 1999, biomass production during one year as a proportion of the biomass at the end of the experiment and N concentrations and total above-ground N in a mixed cropping system in the central Amazon.

Species	Plant part	Above-ground biomass [kg tree^{-1}]		Above-ground biomass [Mg ha^{-1}]		Biomass production [% yr^{-1}]		N concentration [g kg^{-1}]		N amount [kg ha^{-1}]	
Peach palm	total plant	2.7 d	±0.5	0.8 d	±0.1	56.7 b	±17.5	8.9	±0.9	6.3 d	±0.9
Brazil nut	wood	169.7	±15.2	15.8	±1.4	60.6	±6.7	6.4	±0.4	101.3	±11.8
	leaves	63.1	±5.2	5.9	±0.5	64.4	±7.3	23.1	±0.7	137.8	±13.0
	total plant	223.8 a	±19.1	21.7 a	±1.6	61.6 ab	±6.9	nd		238.1 a	±15.3
Annatto	stem	9.3	±0.2	1.4	±0.0	8.6	±1.4	6.3	±0.5	9.3	±0.8
	branches	2.7	±0.2	0.4	±0.0	94.5	±15.7	7.8	±0.6	3.1	±0.3
	leaves	3.0	±0.2	0.5	±0.0	79.8	±14.4	28.4	±0.9	13.6	±1.3
	total plant	15.3 c	±0.4	2.4 c	±0.1	86.4 a	±15.0	nd		26.4 c	±1.7
Cupuassu	wood	19.4	±1.4	1.8	±0.1	52.2	±6.7	5.3	±0.4	10.6	±1.6
	leaves	18.6	±1.6	1.7	±0.2	66.7	±9.0	20.0	±0.5	35.9	±3.7
	total plant	38.0 b	±1.9	3.6 b	±0.2	59.0 b	±7.8	nd		46.5 b	±3.8
Effect[1]		***		***		**		nd		***	

[1] $P < 0.01$ (**), $P < 0.001$ (***). Values in one column followed by the same letter are not significantly different at $P < 0.05$; means and standard errors ($n = 12$). nd not determined.

1978). For the analysis of the foliar $\delta^{15}N$ values, the logarithmic values were used due to inhomogeneity of variances. In case of significant effects, individual cell means for the respective level were compared using least significant differences (LSD at $P < 0.05$ if not indicated otherwise) (Little and Hills 1978).

Results

Biomass and N accumulation

The highest above-ground biomass was found in both wood and leaves of individual Brazil nut trees, the lowest in peach palm (Table 1). On an area basis peach palm still showed the lowest biomass, although four peach palm trees were planted for every Brazil nut or cupuassu. Annatto branch biomass had the highest relative production during the experimental period with an increase of more than 90% in one year (Table 1). Foliar N contents were highest in annatto (28.4 g kg^{-1}), whereas total above-ground N accumulation was largest for Brazil nut (238 kg ha^{-1}), followed by cupuassu (47 kg ha^{-1}), annatto (26 kg ha^{-1}) and peach palm (6 kg ha^{-1}) (Table 1).

Enrichment of ^{15}N in plant and soil

The uptake of applied ^{15}N was rapid and all tree species had the highest foliar ^{15}N enrichment during the period 14 to 96 days after fertilization (Figure 2). The enrichment in both peach palm and annatto decreased rapidly afterwards but remained relatively constant in cupuassu. The highest relative enrichment was noted in peach palm. Cupuassu, peach palm, and annatto had a higher ^{15}N enrichment when the fertilizer was applied underneath their own canopy, whereas the enrichment did not differ according to the place of application for Brazil nut. Only 18–43% of its foliar N derived from the fertilizer N which Brazil nut received directly by a placement around its stem, while 8–12% came from the fertilizer N applied to cupuassu, 12–28% and 23–54% from that applied to annatto and peach palm, respectively (range indicates variability over time; Figure 3). In contrast, the other tree species took up more than 85% of the fertilizer N from the fertilized area underneath their own canopies. Whereas the proportion of uptake from the N directly applied around the stem of the trees decreased with time for peach palm, annatto and cupuassu, it increased for Brazil nut (Figure 3). Consequently, the total uptake of ^{15}N by Brazil nut from the area underneath its own canopy increased during the study period (Figure 4). By the end of the experiment the ^{15}N uptake by Brazil nut from the N applied

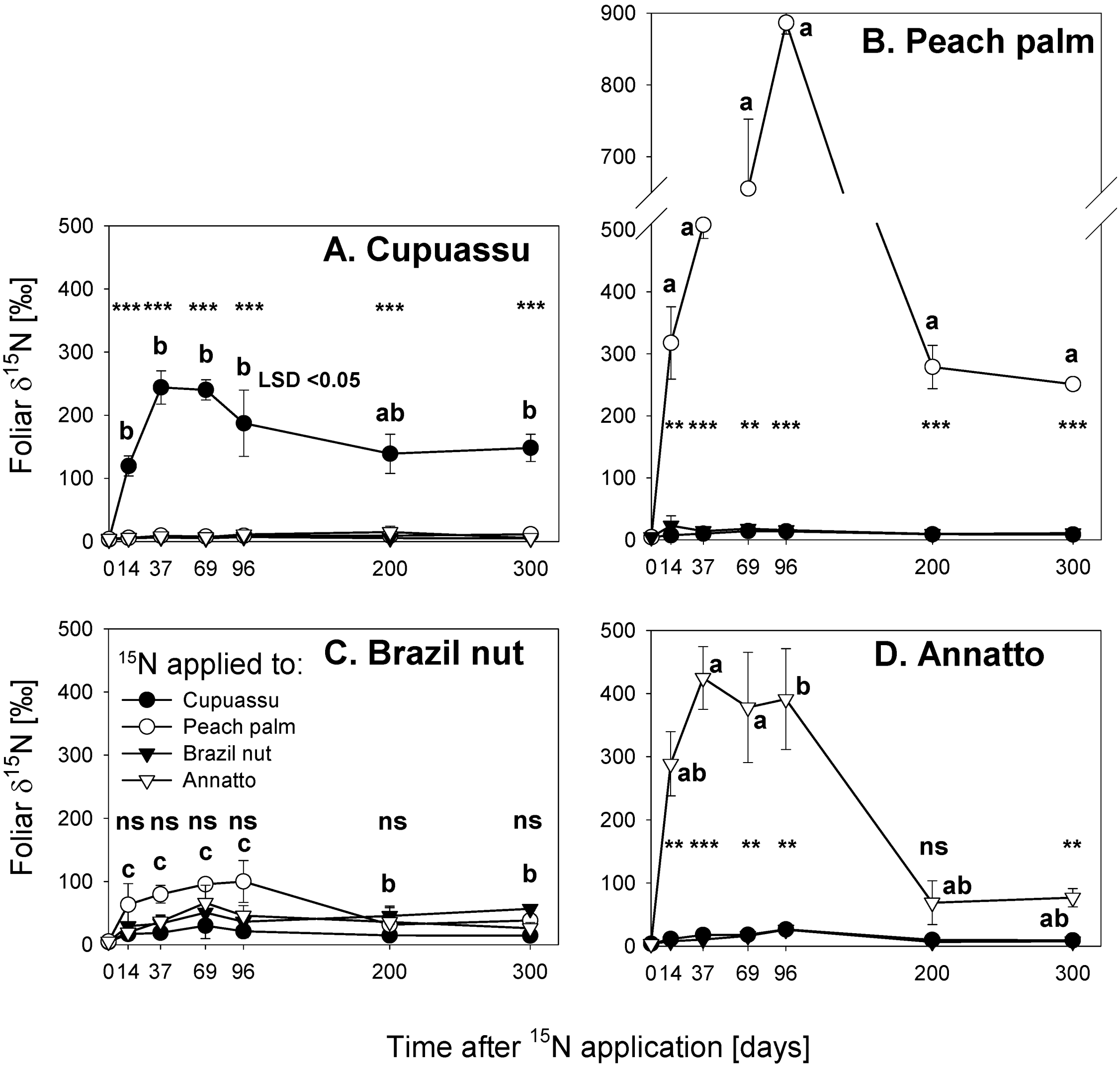

Figure 2. Foliar ^{15}N dynamics of four different tree crops (A. to D. compare with Figure 1) as affected by ^{15}N application under their own canopy or to the adjacent three tree crops (within each graph) from December 1998 (before the application of ^{15}N enriched ammonium sulfate) to November 1999 in a mixed cropping system in the central Amazon. Differences and main effects computed by analysis of variance; ns not significant, *, **, *** significant at $P < 0.05$, 0.01, 0.001, respectively; values with the same letter across all species at the same date are not significantly different at $P < 0.05$ (means $n = 3$).

around its stem (601 mg ^{15}N tree^{-1}) was in the order of magnitude of the uptake from all other locations and by all other trees in the system (869 mg ^{15}N tree^{-1}) (Figure 4). However, also the total ^{15}N uptake by Brazil nut from fertilizer applied to the other trees was significant: Brazil nut took up more N from the fertilizer applied to annatto (only by the end of the experimental period) or peach palm than these tree species themselves (Figure 4).

Recovery of applied ^{15}N

At the end of the rainy season 54% of the applied ^{15}N were recovered in plant and soil (Table 2). Less ^{15}N was taken up by plants (25%) than was found in the soil to a depth of 5 m (29%). The recovery in the soil decreased from 73 to 29 to 7% throughout the year whereas it increased in the plants from 14% in January to 25% in April but decreased to 17% in December. During the same time the total recovery in plant

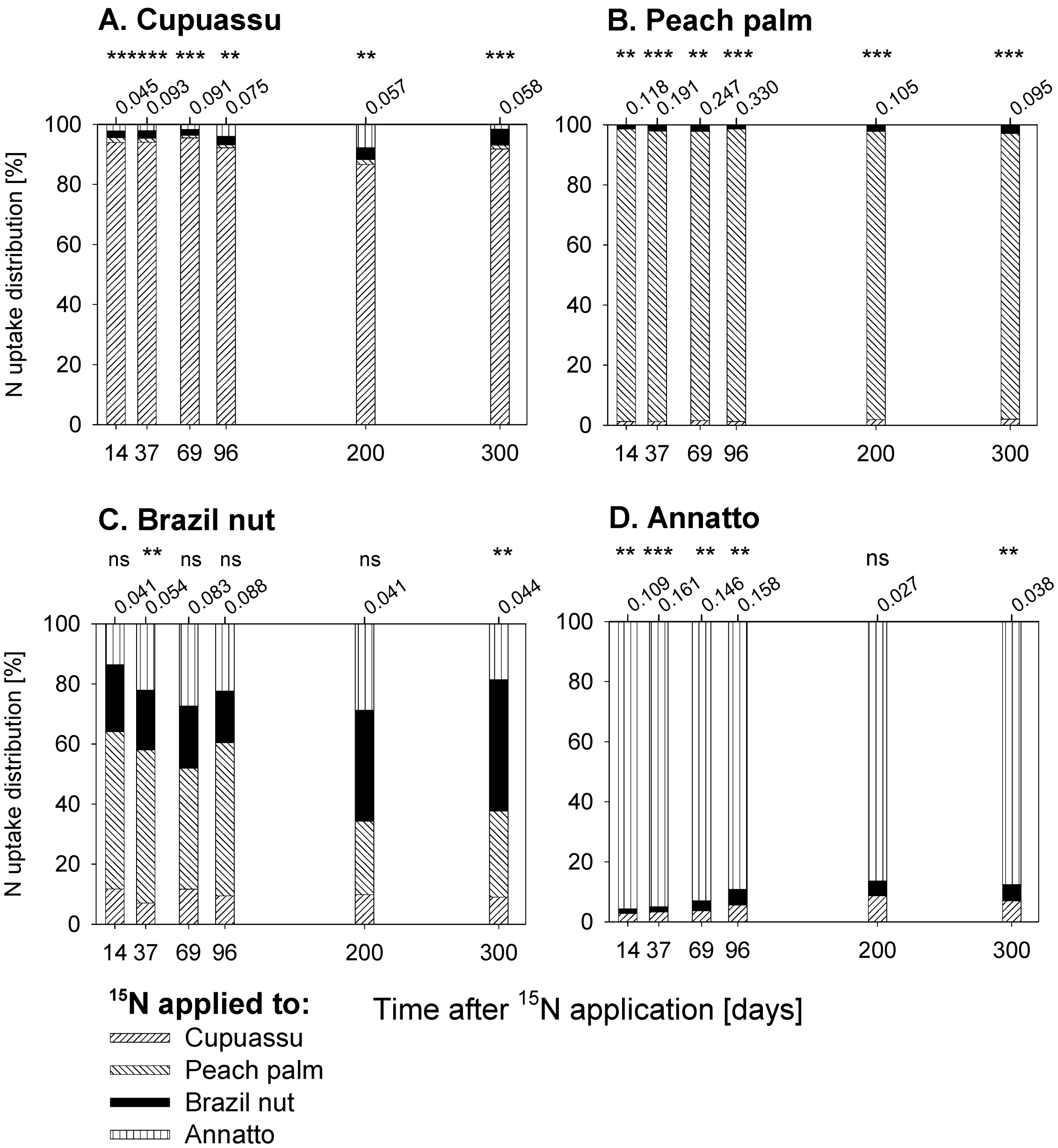

Figure 3. Spatial distribution of relative fertilizer N uptake by four different tree crops (A. to D. compare with Figure 1) from N applied under their own canopy or to the adjacent three tree crops (within each graph) in a mixed cropping system in the central Amazon. Values above columns show the sum of the atom% ^{15}N excess; main effects computed by analysis of variance; ns not significant, *, **, *** significant at $P < 0.05$, 0.01, 0.001, respectively (means $n = 3$).

and soil decreased from 87 to 54 to only 24% (data not shown).

In relation to the amount applied to each tree (nitrogen tree recovery NTR, equation 3), soils under cupuassu tended to have slightly lower ^{15}N recovery than soils under Brazil nut two weeks after application (P = 0.08; Figure 5). At other times, soil recovery was not significantly different between any of the trees. In the above-ground biomass, the largest amount of ^{15}N applied directly to the tree was initially recovered in Brazil nut and cupuassu, the lowest in peach palm ($P < 0.05$). After 10 months, Brazil nut had taken more than half of the ^{15}N applied to it (61%), followed by cupuassu (34%), whereas the

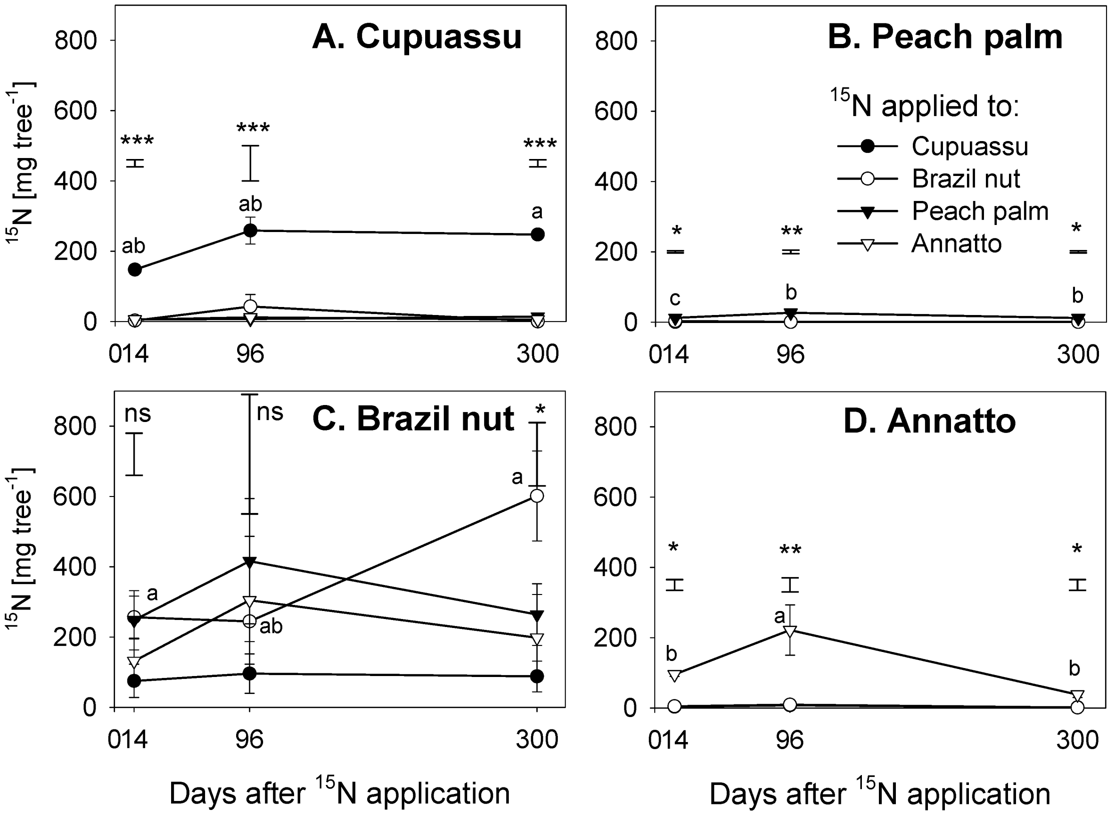

Figure 4. Dynamics of ^{15}N uptake by four different tree crops (A. to D. compare with Figure 1) from N applied under their own canopy or to the adjacent three tree crops (within each graph) in a mixed cropping system (Figure 1) in the central Amazon during one year. Differences and main effects computed by analysis of variance; asterics (main effects) and bars (LSD) indicate significant differences between locations of application for each sampling date (differences between lines within one graph): ns not significant, *, **, *** significant at $P < 0.05$, 0.01, 0.001, respectively; letters indicate significant differences across all sampled species (differences between graphs A. to D.) for the each sampling date at $P < 0.05$ (means and standard errors; $n = 3$).

lowest proportions of applied fertilizer were found in the above-ground biomass of annatto (11%) and peach palm (8%) (Figure 5).

From the whole cropping system (nitrogen system recovery NSR, equation 2), the highest proportion of the applied ^{15}N after the rainy season was taken up by Brazil nut with 12% and annatto with 8% (Table 2). Whereas most of the ^{15}N taken up by either annatto or peach palm originated from the N applied to the respective trees themselves, Brazil nut took up 4.6 and 3.4% of the total applied N in the system from peach palm and annatto, respectively (Table 2). Therefore, the high efficiency of Brazil nut was not caused by uptake of the N fertilizer it received directly (2.7% recovery), which was lower than the uptake by cupuassu from the N applied to cupuassu (2.9%), but by an uptake of N applied to associated trees. Thus, Brazil nut recovered 12% of the total N applied, but received only 11% directly around its stem. The lowest efficiency was noted for peach palm, which retrieved 1.3% but received 45% of the total applied N to the entire system (system as shown in Figure 1).

The efficiency of investing N fertilizer was lowest when applied to peach palm, as all plants together retrieved only 5.9% of the total N applied to peach palm, although peach palm received 45% of the total N in the system (calculating to 13% efficiency) (Table 2). The highest efficiency was found for N fertilized to cupuassu, from which 4.2% were taken up while 11% were applied to cupuassu (38% efficiency), with only slightly lower efficiencies for N applied to annatto (33% efficiency) and Brazil nut (32% efficiency).

A large proportion of the unused N was found in the soil under peach palm (15% of the total N applied,

Table 2. System recovery (NSR, equation 2) of ^{15}N applied to different tree crops as ammonium sulfate fertilizer in a mixed cropping system in the central Amazon after 3 months in April 1999.

^{15}N recovery by	Recovery [%] of ^{15}N applied to									
	Cupuassu		Brazil nut		Peach palm		Annatto		total area	
Cupuassu	2.9 a A	±0.4	0.5 b B	±0.4	0.1 c B	±0.0	0.1 c B	±0.0	3.6 b	±0.4
Brazil nut	1.0 b C	±0.6	2.7 a B	±0.6	4.6 a A	±2.0	3.4 b A	±2.0	11.7 a	±3.0
Peach palm	0.0 c B	±0.0	0.0 c B	±0.0	1.2 b A	±0.2	na		1.3 b	±0.2
Annatto	0.2 c B	±0.1	0.3 b B	±0.1	na		7.4 a A	±2.4	7.9 a	±2.4
Sum of plants	4.2 B	±0.4	3.5 B	±0.5	5.9 B	±1.7	10.9 A	±4.4	24.5	±4.2
Soil (0–5 m)	3.1 C	±0.4	3.0 C	±0.9	14.9 A	±1.9	8.3 B	±2.0	29.3	±0.7
Total sum	7.3 B	±0.3	6.5 B	±0.3	20.8 A	±2.1	19.2 A	±3.0	53.8	±6.0
Applied ^{15}N [g] and trees per experimental unit ([% of total]) according to Figure 1	1 (11)		1 (11)		4 (45)		3 (33)		9 (100)	

na = not applicable: rows of annatto and peach palm are not adjacent. Values in one column or row followed by the same small or capital letter, respectively, are not significantly different at $P < 0.05$; means and standard errors ($n = 3$).

being 33% of the amount it received directly). Substantially less N remained in the soil under annatto (8.3% of the total N applied, being 25% of the amount it received).

Discussion

Biomass and nitrogen uptake

Above-ground biomass of all trees determined in our study was similar to that determined in an extensive study including destructive sampling of entire trees conducted by Schroth et al. (2002) in the same experiment. Nitrogen contents of leaf and woody biomass were slightly higher than those from 6- to 8-year-old Brazil nut, peach palm and cupuassu (not available for annatto) reported by McGrath et al. (2000) from the southern Amazon basin. This can be explained with the fact that no annual fertilization was practiced in the cited study. Therefore, our values for total N uptake are typical for agroforests with similar species composition.

Biomass and N uptake by roots were not assessed in the present study and total N sequestration in plant biomass was therefore underestimated. Using a maximum estimate for root-shoot ratios (Haag 1997) and root N contents total recovery may only slightly increase from 53 to 62%. This calculation assumes similar N concentrations in roots as in above-ground biomass which is most likely much smaller as demonstrated by McGrath et al. (2000). The conclusions about the distribution of N uptake are not affected by neglecting root N contents, since the annatto, Brazil nut and cupuassu have similar root-shoot ratios (Haag 1997) and peach palm has very low total biomass.

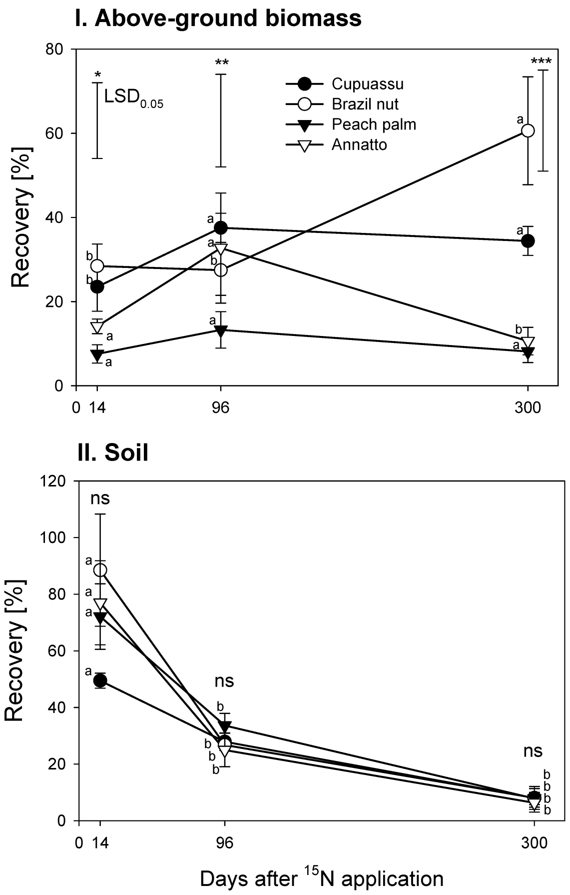

Figure 5. Recovery of the ^{15}N applied to each tree (single-tree observation; NTR from equation 3) in its own above-ground biomass (I.) and in the soil (II.) in a mixed cropping system in the central Amazon during one year. Differences and main effects computed by analysis of variance; asterics (main effects) and bars (LSD) indicate significant differences between trees for each sampling date: ns not significant, *, **, *** significant at $P < 0.05$, 0.01, 0.001, respectively; LSD bars are not shown if main effects were not significant; letters indicate significant differences between sampling dates for the same species at $P < 0.05$ (means and standard errors; $n = 3$).

Uptake distribution of applied N fertilizer

Brazil nut had the most widespread root activity among the studied tree crops, taking up more applied N from neighboring trees than from the fertilizer applied under its own canopy. Brazil nut was the tallest tree with the largest above-ground biomass and N accumulation in the studied cropping system. This will certainly reflect the amount of below-ground biomass. Peach palm and annatto were periodically pruned which usually decreases root growth and extension as shown for an acacia in Kenya (Peter and Lehmann 2000). The restricted lateral root activity of pruned peach palm was assumed to be responsible for the low utilization of biologically fixed N from an intercropped legume cover (Lehmann et al. 2000). Additionally, pruning the peach palm for heart of palm harvest also decreased root activity in the subsoil at the same site (Lehmann et al. 2001b).

The high proportion of N uptake by Brazil nut from associated trees may not only be a result of an uptake of N at the topsoil, but may also be derived from subsoil N. Already two weeks after N application, significant amounts were found at 0.8 to 2 m depth and up to 5 m depth three months later (Dinkelmeyer 2000). We were not able to identify with our experimental approach whether the trees were taking up fertilizer N from the topsoil or the subsoil. The strong taproot formed by Brazil nut (Haag 1997) may indicate a significant uptake also from the subsoil, although Lehmann et al. (2001b) could not verify a pronounced subsoil root activity. However, since the total uptake by Brazil nut as shown in the present study is very high even a low relative uptake from the subsoil may still result in a relevant amount of subsoil N depletion.

Nitrogen use efficiency and nitrogen losses

Two mechanisms contribute to high fertilizer N uptake by a mixed tree cropping system: (1) high N uptake from the fertilizer directly applied to the tree, and (2) high nutrient uptake by associated tree crops. For example, the efficiency of the N applied to cupuassu and annatto was not only an effect of a high uptake by cupuassu or annatto, respectively, but a co-uptake by Brazil nut. The efficiency of the N applied to Brazil nut was lower than that to cupuassu and annatto due to the fact that no other tree took up N from the fertilizer applied to Brazil nut. The larger uptake of N by Brazil nut as compared to the amount that the tree actually received by fertilizer application demonstrates the importance of introducing tree species with extensive root activities into plantations of trees that have spatially restricted root activities.

The high efficiency of fertilizer N use by Brazil nut may be due to a possible uptake from the subsoil as discussed above. Both an uptake from the topsoil but especially from the subsoil will result in lower leaching losses, which are generally large in the studied soil due to high rainfall (Rozanski et al. 1991). The soils in the central Amazon are strongly weathered and have high anion exchange capacity due to variable charge clays, which can adsorb large amounts of nitrate (Cahn et al. 1992). Several studies showed significant storage of nitrate in the subsoil in annual (Cahn et al. 1993; Melgar et al. 1992) and perennial (Schroth et al. 1999) cropping systems in the central Amazon.

The rapidly decreasing total recovery of 87 to 54 to 24% at one, three and twelve months after N application, respectively, has to be attributed to N losses from the system, either by denitrification or leaching. Even considering N in root biomass, this value will only increase by about 10%. The relative contribution of the two types of N losses to the total losses can only be estimated. After 63 days Alfaia (1997) found an N loss of 36–38% from applied ammonium sulfate in a greenhouse experiment with rye-grass (*Lolium multiflorum* L.) using a Central Amazonian Oxisol. Similar values were reported using a ^{15}N balance after 3-months periods in a mixed tree crop plantation of peach palm and cupuassu at an adjacent site (Lehmann et al. 2000). The significant amounts of applied ^{15}N found in the subsoil (Dinkelmeyer 2000) indicate that N leaching even beyond 5 m depth was possible during three months and may have led to substantial N losses.

Competition for nitrogen between trees

Peach palm, annatto, and cupuassu exerted no competitive effects on associated trees. Their uptake was too low to affect the N uptake of the surrounding trees. In contrast, the significant root activity and total N uptake by Brazil nut from fertilizer N applied to neighboring tree crops may result in competition for N. In the studied system, the competition by Brazil nut was beneficial for the total N use efficiency as demonstrated above. However, fertilization has to take this competition into account. Fertilizer applications in mixed cropping system must compensate for competition for one nutrient (possibly P in our system) where synergistic effects through competition for other nutrients (N) proved to be favorable. The mobility of different nutrients may play an important role in this respect. Competition may lead to a higher use efficiency of mobile nutrients (such as N in the form of nitrate), which are prone to leaching losses, whereas it may primarily decrease tree nutrition for immobile nutrients (such as P in P-fixing soils).

Conclusions

The most efficient way of fertilizing N in the studied agroforest was the application to cupuassu and annatto. This was partly an effect of the efficient uptake of N by these two trees, but mostly due to the N uptake by the neighboring Brazil nut. On the other hand, an application to Brazil nut itself was slightly less efficient. Therefore, these large trees do not need to receive fertilizer directly but can take up nutrients applied to other trees in the mixed cropping system. This means that these trees may effectively decrease nutrient leaching when intercropped with trees, which have periods or areas of low nutrient uptake. Since the roots spread from the Brazil nut to the associated trees, they may form a root system throughout the whole cropping system thereby increasing the use efficiency of soil nutrients between the trees. This may also enhance the use efficiency of biologically fixed N from legume cover crops between the trees.

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