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Abstract

· **Context** Cocoa (*Theobroma cacao* L.) is often cultivated below legume shade trees, but root interactions between the species are not well known. The first step in understanding these interactions is the description of spatial root system distribution of cocoa and shade trees.

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· **Aims** We studied the root distributions of cocoa and *Inga edulis* Mart. (inga) in an agroforestry plantation in the humid tropics of Costa Rica.
· **Methods** Fine roots were sampled by soil coring, and a fractal root architecture model parameterised with data from partial root excavations was used for determining coarse root distribution.
· **Results** Fine root length in the 0–50 cm soil layer was 26,762 and 22,026 km ha^{-1} for cocoa and inga, respectively, with 24 % and 23 % of fine root length of cocoa and inga, respectively, in the 0–2 cm layer. Horizontally, root distributions of the two species with cocoa at 3×3 m and inga at 9×9 m spacing overlapped strongly, while inga did not cover all points at 18×18 m spacing.
· **Conclusion** Both species seem to efficiently capture nutrients released from the litter layer on the soil surface, and nutrient leaching in shaded cocoa plantations is unlikely. The proximity of root systems may facilitate N exchange between the N$_2$-fixing inga and cocoa, but competition for other nutrients is likely.

Keywords Agroforestry · Fractal networks · Organic farming · Resource sharing · Root architecture · Root length

1 Introduction

Agroforestry has been defined as a land management system that intends to optimise the benefits from biophysical interactions created when trees are combined with crops and/or domestic animals (Gold et al. 2000). Many of these interactions occur belowground: trees and crops may either share or compete for water and nutrients. Although facilitative interactions occur, e.g. via soil C increment by tree root turnover or physical improvement of compacted soil by strong tree roots (Schroth 1999), most research has emphasised the potential competition for soil resources (Jose et al. 2000; Lehmann et al. 1998). Root architecture and distribution of fine root length are important determinants of the sharing of soil resources

between a tree and a crop in agroforestry because they define the soil volume available for the component species. This volume will be called the influence area of a plant in this contribution. Extraradical mycelium of arbuscular mycorrhizal fungi may largely increase the soil volume available for nutrient uptake by accessing soil pores too small for penetration by plant roots. However, arbuscular mycorrhizae do not significantly increase the influence area of a root system because the extraradical hyphae concentrate close to the host root (Smith and Read 2008).

It has been hypothesised that tree roots tend to be deeper than crop roots, thus forming a safety net that captures nutrients leaching through the crop-rooting zone (van Noordwijk et al. 1996). Many trees used in agroforestry systems with annual crops in the dry (Jonsson et al. 1988; Lehmann et al. 1998) and sub-humid tropics (Schroth and Zech 1995) appear to be deeper rooted than associated crops. In systems of perennial crops and shade trees, however, all fine roots seem to concentrate in the topsoil in the humid (Muñoz and Beer 2001) and sub-humid tropics (Dossa et al. 2008). Unfortunately, tree and crop fine roots were not distinguished in the latter studies and the conclusion of tree and crop using the same soil horizons was derived indirectly from comparison of different systems or from coarse root distribution.

Coarse roots form the skeleton of the root system of a tree, in which the nutrient-absorbing fine roots are attached. It has been proposed that the soil volume occupied by the coarse roots of a tree would define the influence area of the tree (Kalliokoski et al. 2010; Nygren et al. 2009). This hypothesis is based on the assumption that fine roots do not grow far from the coarse transport roots that supply carbohydrates for their growth, as implied by the short length of distal roots of several tree species (Atger and Edelin 1994a). However, actual spatial distribution of fine roots within the influence area may be quite variable (Atger and Edelin 1994b). Thus, it is important to study both the coarse root architecture and the fine root distribution for understanding the conditions for soil resource sharing in an ecosystem (Tobin et al. 2007).

Soil core sampling is a generally accepted method for determining fine root mass and length in soil (van Noordwijk 1993; van Noordwijk et al. 1996). Coarse roots are spatially much scarcer and, thus, soil coring would require a very high number of samples. Complete excavation of the coarse roots of a tree is very laborious and causes soil perturbation in large areas. Thus, architectural root modelling has been proposed as an alternative for estimating coarse root length and mass. The FracRoot model (Ozier-Lafontaine et al. 1999) is based on the fractal root architecture model by van Noordwijk et al. (1994). It has been applied for tropical legume trees used in agroforestry (Ozier-Lafontaine et al. 1999; Salas et al. 2004). Visualisation quality of the model was improved by introducing an algorithm for estimating the root branching angles from an observed angle distribution (Salas et al. 2004) and the length

estimates were considerably improved by inclusion of a coarse root turnover factor (Nygren et al. 2009).

The aim of this study was to describe the distribution of both coarse and fine roots of cocoa (*Theobroma cacao* L.) and the legume shade tree *Inga edulis* Mart. (hereafter inga) in an organically grown cocoa plantation under humid tropical conditions. The specific objectives were to test the FracRoot model in an agroforestry system with two woody components and determine the vertical distribution of the fine roots of the component species. The results are discussed in the context of soil resource sharing.

2 Materials and methods

2.1 Fine root sampling

The fieldwork was conducted in the Academic Farm of EARTH University in Guácimo in the Caribbean coastal plain of Costa Rica (10°10′ N, 83°37′ W, 64 ma.s.l.). Average annual rainfall in 1996–2009 was 3,694 mm, distributed fairly evenly throughout a year, and mean annual temperature was 25.0 °C. The cocoa plantation of the farm is situated on uniform soils (an andic humitropept with pH in water of approximately 4.7) and it is divided into four plots of approximately 1 ha each. Two organically managed plots with inga shade were used in this study. Average total N concentration in the plantation was 5.49, 2.61, and 1.92 mg $[N]g^{-1}$ [soil] in the layers 0–10, 11–25, and 26–50 cm, respectively. The respective Olsen-extractable P concentrations were 12.4, 1.79, and 2.02 μg $[P]g^{-1}$ [soil] and bulk densities were 0.68, 0.84, and 0.85 kg dm^{-3} (Mogollón Frasca 2007). Variation between plots with respect of pH, bulk density, and N and P concentrations was negligible. Cocoa was periodically pruned and the trees had the same size in all plots of the plantation irrespective of age and slight management differences.

Fine roots were sampled in a plot established in 1992 and managed organically since 1997. The shade trees were thinned from 9×9 to 18×18 m spacing in December 2005. Cocoa was planted at 3×3 m spacing and naturally thinned to 680 trees ha^{-1} by mortality. At the time of fine root sampling, the mean basal diameter (0.5 m height) of ingas was 36.8 cm (standard deviation [SD]=8.5 cm). Fine roots were sampled in March and August 2008, which corresponded to the least and most rainy month of a year. Rain accumulation in 30 days prior to the sampling was 121 mm in March and 527 mm in August. The sampling area was limited with an inga in each corner, with sides of 18 m. In both samplings, a 50-cm-deep soil core with a 10-cm-diameter auger was taken in 15 randomly selected points. The soil core was divided into 0–2, 2–6, and 6–10 cm layers and thereafter to 10-cm layers down to 50 cm. Each sample was dry-sieved over a successive series of 5, 2, and 0.5 mm

sieves. All roots with diameter ≤2 mm recovered over the sieves and soil over the smallest sieve were washed on the 0.5-mm sieve for recovering all fine roots.

The fine roots were divided into living and dead roots of inga and cocoa according to their colour and stiffness. Length of living fine roots in a sample was determined using the line intersection method (van Noordwijk 1993). The roots were placed in a water-filled 145×110-mm tray with a 5×5-mm grid in the bottom. Because some samples, especially from deep soil, had very few roots, samples were combined for achieving enough intersections between the roots and the grid. The tray with roots was photographed using a Canon Powershot S3 IS digital camera mounted in a repro support. The tray filled the whole image area; at this distance, a 100-μm-thick root equalled 1 pixel width in the photo, making this the lowest limit for fine root detection. The root length in each photo was calculated as a function of the number of intersections of the roots with the grid and the grid size (van Noordwijk 1993).

After photographing, the fine root samples were dried for 72 h at 60 °C and weighed. Carbon and N contents in both fine root biomass and necromass were determined from samples of 0–2, 10–20, and 40–50 cm depth by an element analyzer (Series II CHNS/O Analyzer 2400, Perkin-Elmer, Norwalk, CT, USA).

2.2 Coarse root measurements

In the description of coarse root architecture, the concept link refers to a piece of a root between two branching points. An axis is formed by subsequent links; the main axis of a root is formed by the thickest link attached to a proximal root and is always continued by the thickest link in a branching point. Proximal root is a link directly attached to the root collar. The concept root refers to the main axis starting from a proximal root and all laterals attached to it, and the root system refers to all roots of a tree.

Because coarse root excavation caused extensive soil perturbation, which would have seriously disturbed fine root sampling and another study conducted in the fine root sampling plot (Nygren and Leblanc 2009), coarse roots were measured in an adjacent cocoa plot. In this plot, cocoa was planted at 3×3 m spacing and shade trees at 9×9 m so that an inga replaced a cocoa. Natural mortality of cocoa trees had thinned the population from the initial 988 to 885 trees ha^{-1}. The plot was established in 1995, it was converted to organic management in 1998, and coarse roots were excavated from June through August 2005. The basal diameter of ingas was 31.6±5.1 cm (mean±SD).

Root systems of six inga and nine cocoa trees were excavated as described by Nygren et al. (2009). All proximal roots of a tree were exposed to the first branching point. The link diameter at root collar and before the first branching point, azimuth and inclination of the proximal root were recorded.

One to three roots were selected from each tree for complete excavation. The roots were selected so that, when completely excavated roots of all trees of a species were pooled, they covered the observed diameter range of proximal roots of the sample trees. The roots were carefully dug using small hand tools for avoiding changes in their position. The excavation was started following the main axis. All lateral, sub-lateral, etc. axes were exposed to the minimum diameter of 2 mm that was assumed to be the limit between coarse and fine roots. All axes were followed as far and deep as they had grown. The data measured on these roots included:

1. branching generation according to West et al. (1997);
2. link diameter before each bifurcation and diameters of the bifurcating links;
3. link length;
4. vertical and horizontal angles between the bifurcating links (bifurcation angle); and
5. wood basic density from root pieces of different diameters.

2.3 Simulation of coarse root distribution

Coarse root length and mass were estimated applying the FracRoot model version described by Nygren et al. (2009). The programme also provided a visualisation of the root system of a tree or a group of trees. A tree root was described as a continuously branching hierarchical network of connected links. Scaling factors between subsequent links were assumed invariant in the whole tree (Ozier-Lafontaine et al. 1999; van Noordwijk et al. 1994), which has been shown to give an adequate correspondence with field data (Nygren et al. 2009). The branching generation of a link (West et al. 1997) was assigned following a developmental sequence, i.e. starting from the root collar with proximal roots having branching generation 1.

Root architecture was reiterated using a recursive algorithm (Ozier-Lafontaine et al. 1999), which was applied until the final branches of the network links of minimum diameter D_m were reached (here D_m=2 mm). The scaling factor p was defined as the ratio of the square of link diameter before bifurcation (D_b^2) to the sum of squared diameters of bifurcating daughter links ($\sum D_a^2$):

$$p = D_b^2 \Big/ \sum D_a^2 \tag{1}$$

The allocation factor of link cross-sectional area, q, was estimated:

$$q = \max\left(D_a^2\right) \Big/ \sum D_a^2 \tag{2}$$

Except for the biggest link, all other daughter links were assumed to have the same diameter. Diameter for the biggest

daughter link (D_{amax}) was estimated:

$$D_{a\,max}^2 = \frac{q \times D_b^2}{p} \qquad (3)$$

and diameters for all other daughter links were estimated:

$$D_a^2 = \frac{D_{a\,max}^2 \times (1-q)}{q \times (n-1)} \qquad (4)$$

where n is the total number of daughter links formed in the branching event. Each new link had a random bifurcation angle generated from the cumulative bifurcation angle frequency (Salas et al. 2004). Link length was estimated as a logarithmic function of its own branching generation. New links with diameter bigger than D_m had further bifurcations generated as described above.

Number of new links was estimated from the observed percentages of two, three, and four daughter links in the field data. Root turnover factor was introduced as a case of "zero links"; this referred to abnormal termination of a root before reaching the D_m (Nygren et al. 2009). The sum of the percentages of zero, two, three, or four links formed in a branching event totalled 100 %. The number of daughter links was randomly selected from the cumulative frequency range of the number of links formed in a branching event. Because the FracRoot model includes several stochastic factors, the mean of 75 model runs was used as the simulated value for a tree in this contribution, unless otherwise stated.

3 Results

3.1 Coarse root characteristics

The means of scaling parameter p and allocation parameter q of the FracRoot model were determined with narrow confidence intervals because of the high number of branching points measured (Table 1). The equation for estimating the link length was satisfactory for inga but had a low R^2 value for cocoa. However, both regressions were significant. The mean vertical bifurcation angle of inga was 0.48° down (SD=10.63°, N=843) and 90 % of the angles were between 15° up or down from the mother link; 36.2 % of daughter links continued the same vertical direction as the mother link. The mean vertical bifurcation angle of cocoa was 1.71° down (SD=12.29°, N=532) and 90 % of the angles were between 10° up and 20° down from the mother link; 43.2 % of daughter links had a vertical bifurcation angle of 0°. Horizontal bifurcation angles were normally distributed with the mean±SD 1.96°±38.28° for inga and 1.02°± 53.80° for cocoa.

Table 1 Mean and 95 % confidence interval of FracRoot model parameter values and equations for estimating coarse root link length for *I. edulis* and *T. cacao*

| Parameter	*Inga edulis*	*Theobroma cacao*
Scaling parameter p	1.06 (1,009) 1.039–1.075	1.00 (645) 0.980–1.022
Allocation parameter q	0.68 (1,009) 0.673–0.693	0.71 (645) 0.697–0.720
Basic density ($g\,cm^{-3}$)	0.36 (74) 0.349–0.375	0.37 (58) 0.355–0.376
Link length equation	$L=60.2-15.422\times\ln(B)$ $R^2=0.78$, $P<0.0001$	$L=41.976-6.7937\times\ln(B)$ $R^2=0.48$, $P=0.0080$

Numbers in parentheses indicate the number of observations used for determining the parameter value

L average link length (in centimetres), B branching generation of the link

The proportion of missing links, i.e. termination of a root axis at diameter >2 mm, was 31 % in inga and 24 % in cocoa. These numbers included both the cases of real missing links and loss of links during digging due to root breakage or forceful stop of digging (e.g. a root entered an ant nest). The proportions of missing links excluding digging loss were 13 and 16 % for inga and cocoa, respectively, which were assumed to reflect the coarse root turnover for natural reasons. The turnover factor thus defined refers to the loss of coarse roots during the whole life span of a tree (Nygren et al. 2009). The FracRoot model could be tested only using the total proportion of missing links, i.e. including digging loss. Further, because scars left by dead and decomposed links may easily go unnoticed during digging, we optimised the turnover factor by searching for a factor that resulted in a significant regression slope close to unity between the measured and simulated length of a root. The search was performed by Monte Carlo type iteration (Nygren et al. 2009).

The best fit between observations and simulations was achieved with turnover factors 34 and 31 % for inga and cocoa, respectively. Regression slopes for both species were significant, very close to unity with a good R^2 value for cocoa and satisfactory R^2 value for inga (Fig. 1). Because the link loss due to digging was accurately reported, we assumed that, the increases in the apparent turnover factors were caused by turnover unnoticed during digging. Thus, we estimated the length and mass of coarse root systems using both the field-observed natural turnover factors (inga, 13 %; cocoa, 16 %) and adding the increase in the turnover factor that resulted the best fit for Fig. 1 (inga, 13 %+3 % units=16 %; cocoa, 16 %+9 % units=25 %). The latter turnover factor is called optimised. The mean values for individual trees were determined with a good accuracy (Fig. 2). Thereafter, we calculated the mean values for the
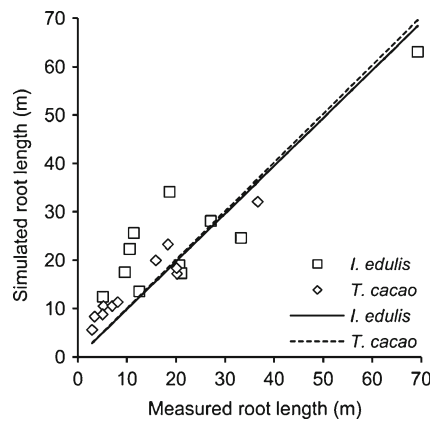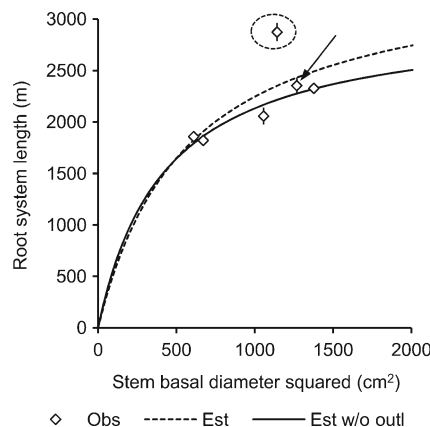
Fig. 1 Relationship between measured (L_o) and simulated (L_s) coarse root length of *I. edulis* and *T. cacao*. The simulated value is the mean of 75 runs of the FracRoot model. The regression between L_s and L_o was $L_s = 0.98752 \times L_o$ ($R^2 = 0.74$, $P<0.0001$) for *I. edulis* and $L_s = 1.00499 \times L_o$ ($R^2 = 0.84$, $P<0.0001$) for *T. cacao*

Table 2 Simulated coarse root characteristics of individual trees of *T. cacao* and *I. edulis* in an organically grown cocoa plantation

Species	Turnover factor (%)	Root system length (m)	Root system mass (kg)
T. cacao	Observed[a], 16	290±142	1.441±0.960
T. cacao	Optimised[b], 25	162±68.4	1.206±0.786
I. edulis	Observed[a], 13	2,872±597	44.62±18.57
I. edulis	Optimised[b], 16	2,216±393	41.96±17.12

The simulations were conducted based on measured proximal root data. The root system length and mass were first determined for each individual tree as the mean of 75 runs of the FracRoot model. The mean±SD applying two different root turnover factors for six and nine *I. edulis* and *T. cacao* trees, respectively, is presented here. See text for simulation details

[a] Observed turnover because of natural factors (excluding estimated digging loss)

[b] Turnover factor optimised for best fit with observed root length using a Monte Carlo-type simulation

six inga and nine cocoa tree root systems excavated, using both turnover factors. The estimates (Table 2) are assumed to limit the probable range of root system length and mass of inga and cocoa trees in the study plantations.

Because the FracRoot model was parameterised in a plot with inga of different size than in the fine root measurement plot, we studied the relationship between measured stem basal diameter and simulated root system length and mass (Salas et al. 2004). The best fit for root system length of a tree (L_s) was obtained using a Michaelis–Menten-type dependence on stem basal diameter squared (D_s^2):

$$L_s = \frac{\alpha \times D_s^2}{\beta + D_s^2} \qquad (5)$$

where α and β are Michaelis–Menten parameters. The data included an apparent outlier tree (Fig. 2). The fit of Eq. 5 was poor when the outlier was included in the analysis, but good without the outlier (Fig. 2). Root system mass (M_s) had a linear relationship with the D_s^2 (outlier excluded):

$$M_s = 0.03562 \times D_s^2; \ R^2 = 0.80 \qquad (6)$$

The coarse root system of an inga was about 10–13 times longer than that of a cocoa (Table 2). The difference in root system mass was almost 40-fold, probably because of thick proximal roots of inga. Equation 5 with the parameters estimated without the outlier (Fig. 2) gave the average root system length±SD of 2,248±330 m in the fine root measurement plot. This is quite close to the estimate based on the trees used for FracRoot parameterisation (Table 2). The difference in the root system mass of an inga was much larger: Eq. 6 applied to the trees in the fine root measurement plot gave the average root system mass±SD of 50.37± 20.26 kg. Because the tree size affected much less the root system length estimates than the turnover factor (Table 2), we used data from the original coarse root measurements in all the subsequent analyses.

The differences between the root systems of inga and cocoa were also apparent in the visualisation (Fig. 3). Both species had superficial root systems, but inga had a few deep brace roots approaching almost 2 m depth, while the coarse roots of cocoa were found in the top 40 cm of soil. It should

Fig. 2 Root system length simulated using the FracRoot model with optimised turnover factor as a function of measured stem basal diameter squared of *I. edulis* in an organically grown cocoa plantation at 9× 9 m spacing. The regression for all observations has Michaelis–Menten parameters (Eq. 5) $\alpha=3518$ and $\beta=567$ ($R^2=0.52$) and the regression without the outlier (*circled observation*) has parameters $\alpha=3035$ and $\beta=423$ ($R^2=0.90$). The markers indicate the mean of 75 FracRoot model runs for the simulated root system length and *error bars* indicate the 95 % confidence interval of the mean; some confidence intervals are so narrow that they are within the marker. The *arrow* points the *I. edulis* individual root system of which is visualised in Fig. 3

Fig. 3 Coarse root system of *T. cacao* simulated using the FracRoot model with optimised turnover factor seen from the top (**a**) and side (**b**) and respective views of *I. edulis* (**c**, **d**). Both root systems are shown in the same horizontal and vertical scale. The total length of the root system of the *I. edulis* individual shown is 2,353 m and the total root system length of the *T. cacao* individual shown is 154 m. The *horizontal line* crossing **b** and **d** indicates the fine root sampling depth, 0.50 m
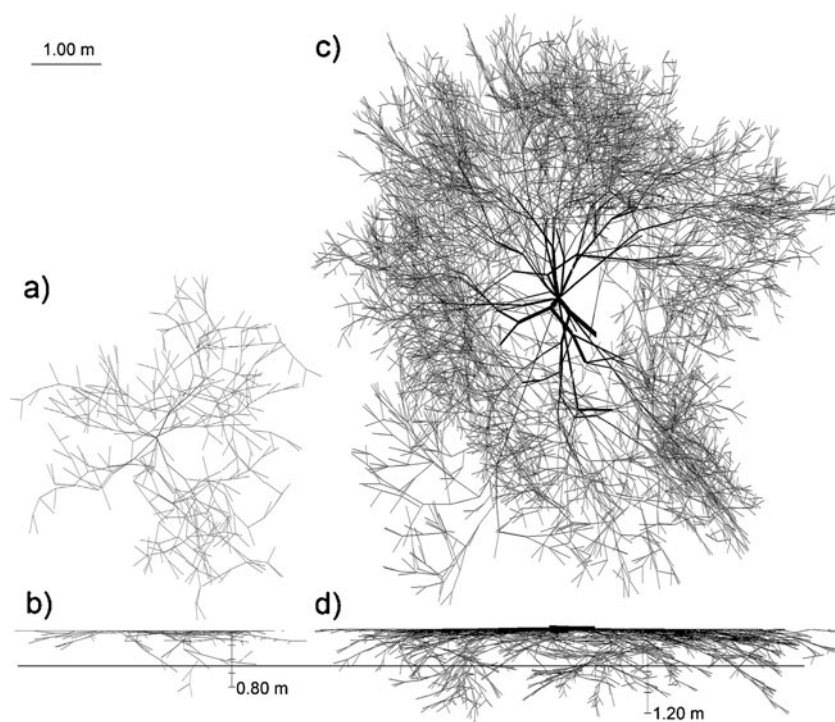
be noted that the visualisation overemphasises the proportion of deep roots because all deep roots appear in the image but many superficial roots overlap (Fig. 3b, d: note the thick black top layer in the vertical view). Root system lengths differ from the average values in Table 2 because the visualisation is based on one run of the FracRoot model for a tree individual (the inga is marked in Fig. 2). Because no tree was exactly the average, we show the tree that had the smallest deviation from the mean.

We also calculated the root shallowness index (van Noordwijk et al. 1996) based on the proximal root data of both species. The shallowness index was determined as the ratio of the sum of squared diameters of shallow proximal roots to the sum of squared diameters of all proximal roots (Salas et al. 2004). We used two threshold values for shallow roots, insertion angle to root collar either ≤45° or ≤10° (Table 3); the first is the criterion originally proposed by van Noordwijk et al. (1996). The root systems of both species of the agroforestry system were superficial with approximately 86 and 94 % of proximal roots with insertion angle ≤10° in inga and cocoa, respectively. Only inga had roots with insertion angle >45°.

We estimated the mean horizontal influence area by applying the bounding box method (Kalliokoski et al. 2010): a box was drawn around a visualised root system so that it touched the extreme ends of the roots. These estimations were performed based on simulations with the optimised turnover factors (Table 2) for both species. The root systems of both species were slightly ellipsoidal. The average long and short axes of a cocoa root system were

4.83 and 4.30 m, respectively, and 8.88 and 7.89 m in inga, respectively. Thus, the average influence areas were 66.5 and 219.2 m² for a cocoa and an inga, respectively.

3.2 Fine root characteristics

Differences in fine root length, biomass and necromass density were small and non-significant between the March and August samplings (Gómez Luciano 2008). Thus, the data of the samplings were pooled (Fig. 4). Fine root length densities of both species were significantly higher in the 0–2 cm layer (least square means with Tukey–Kramer adjustment for multiple comparisons, $P<0.05$) than in the deeper soil horizons. In the case of cocoa, no significant differences were observed between the deeper horizons, while in inga, the layers 2–6 and 6–10 cm formed a significantly different horizon between the 0–2 cm and deeper layers. Fine root biomass density of inga was significantly higher in the 0–

Table 3 Percentage of superficial coarse roots of *I. edulis* and *T. cacao* in an organically grown shaded cocoa plantation under humid tropical conditions in Guácimo, Costa Rica

Species	Shallowness threshold (%)	
	≤10°	≤45°
Inga edulis	86.1	96.3
Theobroma cacao	93.6	100.0

Roots with insertion angle to root collar smaller or equal than the shallowness threshold were considered superficial
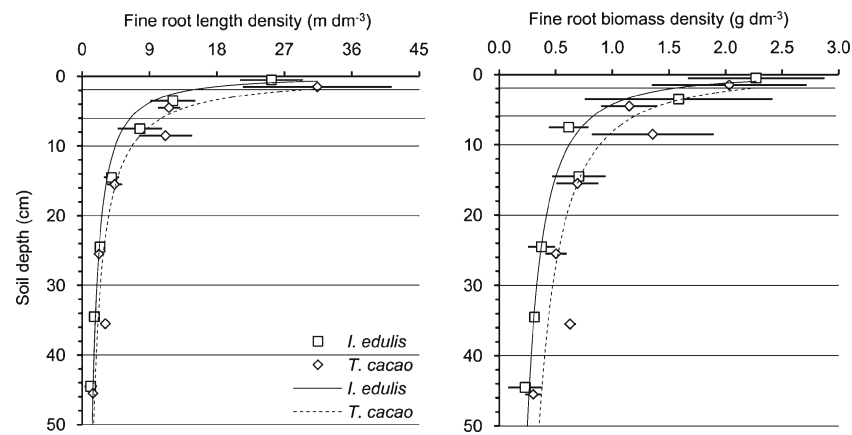
Fig. 4 Mean fine root length and biomass density of *I. edulis* (31 trees ha^{-1}) and *T. cacao* (680 trees ha^{-1}) in different soil depths in an organically grown cocoa plantation. Each marker denotes the mean for the soil layer delimited by the *horizontal lines*. *Error bars* indicate the SD. The trend lines for fine root length density (ρ_L) as a function of mean depth of each soil layer in cm (d_s) are $\rho_L = 25.746 \times d_s^{-0.640}$ ($R^2 = 0.98$) for *I. edulis* and $\rho_L = 31.464 \times d_s^{-0.665}$ ($R^2 = 0.98$) for *T. cacao*. The trend lines for fine root biomass density (ρ_M) are $\rho_M = 2.3670 \times d_s^{-0.502}$ ($R^2 = 0.92$) for *I. edulis* and $\rho_M = 2.0688 \times d_s^{-0.370}$ ($R^2 = 0.89$) for *T. cacao*. All trend lines are significant at least with $P = 0.0002$

2 cm layer than in the layers below 6 cm; the 2–6 cm layer was intermediate. In cocoa, the fine root biomass density was significantly higher in the 0–2 cm layer than in horizons deeper than 10 cm; the 2–6 and 6–10 cm layers were intermediate. No significant differences between the species were observed in any soil layer. Trend lines with negative power relationship between soil depth and fine root length and biomass density were fit with good accuracy (Fig. 4).

Nitrogen concentration in the fine roots of inga was significantly higher in the 0–2 cm layer than in the deeper layers (Table 4). The same trend was observed in cocoa, but differences between soil layers were not significant. Following the decrease in N concentration with depth, the C/N ratio of fine roots increased with soil depth.

3.3 Root systems in the cocoa plantation

We simulated the total coarse root length and biomass for three spatial arrangements of a cocoa plantation shaded by inga (Table 5): (1) inga at 9×9 m spacing with full density of cocoa; (2) inga at 9×9 m spacing with observed cocoa density (after natural plant turnover) in the coarse root measurement plot; (3) inga at 18×18 m with full density

of cocoa; and (4) inga at 18×18 m with observed cocoa density in the fine root sampling plot. In all cases, cocoa was assumed to be at 3×3 m spacing so that each inga replaced a cocoa. The probable range was covered by making the simulation with the optimised and observed coarse root turnover factor (Table 2). The N content in coarse roots was computed using the mean N concentrations observed in the plantation used for fine root sampling (Nygren and Leblanc 2009), with 8.0 and 8.3 mg [N]g^{-1} [biomass] in inga and cocoa, respectively.

Coarse root length density estimate for cocoa was higher than for inga at 18×18 m spacing, both with the theoretical and observed cocoa densities (Table 5). Coarse root biomass of inga was about the same or higher than that of cocoa. The coarse root biomass estimate calculated using Eq. 6 resulted in total biomass of 1,561 kg ha^{-1} in the 18×18 m spacing or close to the upper end of the FracRoot estimates (Table 5). Under 9×9 m spacing of inga, its coarse root system was both longer and had considerably higher biomass than cocoa. Visualisation of coarse root systems in a plantation with inga at 9×9 m spacing and cocoa at full density and inga at 18×18 m and cocoas in the positions observed in the fine root sampling plot (680 trees ha^{-1}) are shown in Fig. 5. The

Table 4 Mean±SD of nitrogen concentration and C/N ratio in the fine roots of *T. cacao* and *I. edulis* in different soil depths in an organically grown cocoa plantation

Depth (cm)	*Inga edulis*			*Theobroma cacao*		
	n	N (mg g^{-1})	C/N	n	N (mg g^{-1})	C/N
0–2	5	24.4±2.54a	19.0±3.07a	8	16.0±4.03a	30.6±6.34a
10–20	9	19.9±3.45b	23.7±3.92b	8	13.3±3.29a	35.7±7.87a
40–50	4	16.5±0.39b	27.8±1.37b	6	12.3±3.42a	39.5±10.7a

Means followed by the same letter within columns do not differ significantly (Student–Neuman–Keuls test at 5 %)

Table 5 Simulated range of coarse root length, biomass and N content of *T. cacao* and *I. edulis* in shaded cocoa plantations planted at 3×3 m spacing with two theoretical densities of the component species and the densities observed in the organically grown study plantation

Density of *I. edulis*	Species	Plant number per hectare	Length (km ha^{-1})	Biomass (kg ha^{-1})	N content (kg ha^{-1})
9×9 m	*I. edulis*	123[a]	272–353	5,161–5,488	41.29–43.90
	T. cacao	988[b]	160–286	1,191–1,424	9.88–11.82
	T. cacao	855[c]	138–248	1,031–1,232	8.56–10.22
18×18 m	*I. edulis*	31[a]	68.5–89.0	1,301–1,382	10.41–11.06
	T. cacao	1,080[b]	175–313	1,302–1,556	10.81–12.91
	T. cacao	680[c]	110–197	820–980	6.81–8.13

The low and high limits of the range are estimated using the optimised and observed turnover factor, respectively (Table 2)

[a] Theoretical and observed tree number in the experimental plantation

[b] Theoretical tree number without plant turnover

[c] Observed tree number in the experimental plantation

visualisations were done with the optimised turnover factors for both species. In the first case, the coarse root systems of the two species of the agroforestry system fill the available soil space (Fig. 5a), while in the latter case, the coarse root cover seems to be patchy (Fig. 5b). Assuming that the average influence area of an inga is 219.2 m^2, the influence areas of 123 ingas at 9×9 m would total to 26,960 m^2. Thus, the ratio of influence areas to available land (here, 1 ha), a soil occupation index (SOI) analogous to the leaf area index, is 2.70. With 31 ingas ha^{-1}, the SOI is 0.68. In the case of 680 cocoas ha^{-1}, the sum of influence areas is 45,220 m^2, or

the SOI for cocoa is 4.52. The combined SOI for 31 ingas and 680 cocoas ha^{-1} (Fig. 5b) is 5.20, and for 123 ingas and 988 cocoas ha^{-1} (Fig. 5a), the combined SOI is 9.27.

The estimate of the total fine root length in the plantation with 680 cocoa and 31 inga trees ha^{-1} was 26,762 km ha^{-1} for cocoa and 22,026 km ha^{-1} for inga (Table 6). Twenty-four and 23 % of fine root length of cocoa and inga, respectively, were concentrated in the top 0–2 cm soil layer. Fine root biomass of both species exceeded the estimated coarse root biomass for the same spacing (Table 5), and N content in fine roots was about sevenfold higher than in
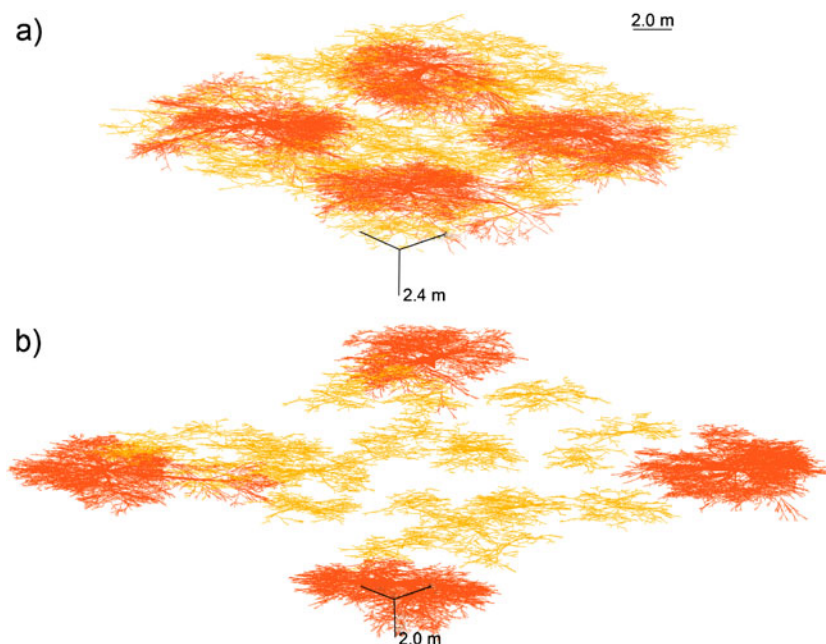
Fig. 5 Visualisation of coarse root systems of *I. edulis* (*dark shading*) and *T. cacao* (*light shading*) in a 18×18-m square in a shaded cocoa plantation with *T. cacao* at 3×3 m and *I. edulis* at 9×9 m spacing (**a**) and in the plot used for fine root sampling (**b**) with *I. edulis* at 18×18 m spacing—in each corner of the plot—and *T. cacao* initially planted at 3×3 m spacing (988 trees ha^{-1}) but naturally thinned to 680 trees ha^{-1} by plant mortality. Tree positions in **a** are theoretical for full density and in **b** correspond to the measured coordinates in the fine root study plot of the plantation. The approximate total coarse root length of *T. cacao* within the square is 4,690 m and biomass 35.3 kg in **a** and 3,264 m and 24.2 kg in **b**. The respective numbers for *I. edulis* are 9,694 m and 202.3 kg in **a** and 2,203 m and 48.1 kg in **b**

Table 6 Length, biomass, necromass and nitrogen content of fine roots of *T. cacao* and *I. edulis* in different soil depths in an organically grown cocoa plantation with 31 *I. edulis* and 680 *T. cacao* trees ha^{-1}

Depth (cm)	Length (kmha^{-1})		Biomass (kgha^{-1})		Necromass (kgha^{-1})		N content (kgha^{-1})[a]	
	T. cacao	*I. edulis*	*T. cacao*	*I. edulis*	*T. cacao*	*I. edulis*	*T. cacao*	*I. edulis*
0–2	6,334	4,984	412	461	48	40	7.36	12.22
2–6	4,647	4,834	455	634	72	81	8.43	17.45
6–10	4,443	3,080	542	246	18	33	7.45	5.55
10–20	4,320	3,923	693	703	45	150	9.82	16.97
20–30	2,448	2,410	503	375	50	65	7.35	8.76
30–40	3,110	1,645	625	310	35	40	8.12	5.78
40–50	1,460	1,150	320	230	45	60	4.49	4.79
Total								
0–50	26,762	22,026	3,550	2,959	313	469	53.02	71.51

[a] Assuming same N concentration in biomass and necromass

coarse roots. Standing necromass accounted for 8.1 and 13.7 % of the total recovered fine root mass of cocoa and inga, respectively (Table 6).

4 Discussion

The characteristics and limitations of the FracRoot model were discussed by Nygren et al. (2009). They found that the model is most sensitive to the turnover factor, while internal variation of parameter values within a root system does not have an important effect on the simulation accuracy. The model version used here gave the best root length estimation for young *Populus deltoides* Bartr. ex Marsh. out of six modifications tested (Nygren et al. 2009). The model estimates for a root system are assumed fairly reliable, while it has low accuracy to predict features of individual roots. The root systems of cocoa and young *P. deltoides* are similar, which suggests that the FracRoot version used may be more suitable for cocoa than inga. Inga was considerably larger than cocoa or *P. deltoides*. In root systems of big trees, there may be a zone of rapid tapering comprising proximal roots and second and third branching generations (Kalliokoski et al. 2010) where allocation parameter *p* may be much larger than in the rest of the root system. We tried to avoid this problem by not including proximal roots in the estimation of *p*. Measured proximal root data were given as input to the simulations.

It has been proposed that the turnover factor may be calibrated by comparing the measured and simulated root length because the model is sensitive to this factor and root length is a more sensitive output than the rather conservative root system mass (Nygren et al. 2009). We calibrated the turnover factor applying two criteria: (1) good fit of the regression between observed and simulated root length (Mayer and Butler 1993) and (2) by requesting the regression slope between observed and predicted values to be within a predetermined biologically acceptable accuracy

(Rita and Ekholm 2007), in our case 0.95–1.05 (Nygren et al. 2009). These criteria were achieved in both species. However, the model could be tested only with data including both natural turnover and digging loss. Thus, we simulated the coarse root systems using both the observed natural turnover and an optimised turnover factor for getting the most probable range of coarse root system length and mass. It should be noted that the larger difference between the observed and optimised turnover factor in cocoa than inga and poorer fit of the link length equation for cocoa may have been caused by the same measuring error: scars of missing bifurcations unnoticed during excavation caused both the overestimation of link length and underestimation of turnover factor.

The analysis of the relationship between stem basal diameter and root system length in inga (Eq. 5; Fig. 2) indicated that the turnover factor affected much more the length estimates than tree size. Root system mass had a linear relationship with stem basal diameter squared (Eq. 6). We interpret that these results imply that the maximum root system length of inga may be reached in quite an early phase of development, while root system mass may increase with shoot biomass increment. This may be related to the growth of proximal roots that provide mechanical support for big trees, but do not contribute to root system length (Kalliokoski et al. 2010). Although tree size probably did not bias the coarse root length estimates in the fine root measuring plot, the effect of the different inga spacing between the coarse and fine root measuring plots remained unknown. The roots in the sparse spacing and lighter spatial competition of the fine root plot may have grown farther away from the stem, thus increasing the influence area. However, because the nutrient availability was similar within the whole plantation (Mogollón Frasca 2007), we assume that the root system lengths and influence areas were quite similar in the two plots, yet we do not have the data to verify this assumption.

Because cocoa was maintained at the same size in all plots by periodic prunings, any size-related differences between the plots in the coarse root system length and, consequently, cocoa influence areas are unlikely.

Both the coarse (Table 3; Fig. 3) and fine root analyses (Fig. 4) indicated superficial root systems. Cocoa had practically no deep coarse roots, inga had only a few and the SOI computed based on influence areas was high for both species. Further, vertical distributions of fine roots were about the same for both species. Thus, we may conclude that there is a potential for strong competition between cocoa and the shade trees and inga does not form a deep root safety net (van Noordwijk et al. 1996) that would capture nutrients leaching through the cocoa rooting zone. On the other hand, the fine roots form such a dense system in the 0–2 cm soil layer that any nutrient leaching is improbable. Capturing nutrients released from the dense litter layer is the probable reason for the superficial root systems because soil bulk density was relatively low and, thus, did not restrict deep rooting. Groundwater depth was not measured, but observations made on a deep ditch at the side of the fine root plot suggest that it remained below 1.5 m in spite of the heavy rains of the study region.

Cocoa and inga are combined in agroforestry because they occupy different aboveground niches, with inga forming a shading canopy over cocoa and providing abundant N-rich litterfall. Inga is a confirmed N_2 fixer (Leblanc et al. 2007), which may add N to the system. However, the two species seem to occupy mostly the same belowground space, in which both capture nutrients released from the decomposing litter. The capacity of inga to fix N_2 alleviates competition for N, and the proximity of the root systems may promote positive interactions like the potential direct transfer of fixed N from inga to cocoa (Nygren and Leblanc 2009). The high N concentration in superficial fine roots of inga may be caused by N_2 fixation because all inga nodules were observed in topsoil.

Spacing of shade trees is a compromise between shade requirements, nutrient recycling in litterfall and avoidance of root competition. We do not have quantitative data on horizontal distribution of the fine roots. If we assume that the horizontal influence area estimated from coarse root distribution also describes the horizontal fine root distribution, the optimal inga spacing is probably between the 9×9 and 18×18 m spacing studied here because the former implies strong root competition (SOI of inga, 2.70) and the inga root system in the latter spacing is patchy (SOI, 0.68), leaving space for nutrient leaching and less possibilities for facilitative root interactions like N transfer.

5 Conclusions

Our results support the general perception that rhizosphere conditions determine the root system shape and size (Tobin

et al. 2007). In the humid tropical agroforestry system studied, roots of both inga and cocoa were superficial, probably because both captured nutrients from the thick litter layer over the soil. The thick superficial root mat efficiently captures nutrients and a deep safety net is not needed for efficient nutrient use. Water deficit is extremely rare in the study site and the wide lateral spread of the root system of inga provides the necessary mechanical stability needed by big trees. While competition for other nutrients may be envisioned, the proximity of the cocoa roots with the roots of the N_2-fixing inga may provide positive interactions for N nutrition of cocoa. The FracRoot model seems to be an adequate tool for describing coarse root systems in agroforestry.

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