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Species and site characteristics that permit the association of fast-growing trees with crops: the case of *Eucalyptus deglupta* as coffee shade in Costa Rica

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Abstract

The benefits that tropical farmers derive from associating trees with crops may be reduced or outweighed by competition for light and soil resources, and the use of incompetent trees in agroforestry associations is therefore a standard recommendation. However, under certain conditions tropical farmers use very fast-growing and presumably competitive trees in tree–crop associations. We studied the factors which allow the use of *Eucalyptus deglupta* as coffee shade in parts of Costa Rica, considering three possible explanations: (a) the availability of soil resources matches the requirements of the two species so that competition cannot arise; (b) complementary resource use reduces competition; and (c) coffee plants possess sufficiently competitive root systems to cope with the competition of fast-growing trees. We measured coffee and tree growth, soil nutrient availability, root distribution and dynamics of 4- to 5-year-old coffee and *E. deglupta* shade trees on a private coffee farm with recommended fertilization in a high-rainfall area in Costa Rica. There was no evidence of a negative effect of the trees on coffee growth, yields and mineral nutrition despite fast tree growth. However, a significant small-scale partitioning of the soil space between the root systems, with most of the coffee roots close to the coffee rows and most of the tree roots in the interrow spaces, was evidence for root interactions between the two species, resulting in complementary use of soil resources. Apparently, the root system of coffee was sufficiently competitive to restrict the rooting space of the trees. Trees and coffee also differed in the depth distribution of their roots, with the trees having the shallower root systems. The compatibility of coffee with fast-growing shade trees at this and similar sites can be explained with a combination of all three hypothesized mechanisms.

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1. Introduction

Tropical farmers conserve or actively plant trees in their agricultural fields for a variety of reasons, reaching

from the production of timber, firewood, fruits and resins through microclimatic protection and soil conservation to esthetic reasons. However, when trees are associated with agricultural crops, these benefits can partly be offset by competition between the trees and crops for light and soil resources and consequent losses in crop yields. A typical recommendation for

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agroforestry associations is therefore to use uncompetitive tree species (Schroth, 1995). In apparent defiance of this rule, tropical farmers integrate under certain conditions surprisingly fast-growing and presumably competitive tree species in their agroforestry systems. In parts of Indonesia, farmers associate the extremely fast-growing *Paraserianthes falcataria* (L.) I.C. Nielsen with coffee (*Coffea* sp.; G. Schroth, pers. obs.). Similarly, agronomists have been surprised by the increasing adoption of *Eucalyptus deglupta* Blume, one of the fastest-growing tropical timber trees, as coffee shade by Costa Rican farmers during the past 10 years. The objective of this research was to understand the conditions under which such associations can be successful.

In Central America, coffee (*Coffea arabica* L.) is traditionally grown under shade trees. Most of these are legumes such as *Gliricidia sepium* (Jacq.) Kunth ex Walp., *Inga* spp. or *Erythrina* spp., which are managed principally for the benefit of the coffee, although they may produce some secondary products such as firewood. Responding to insecure coffee prices, an increasing number of Central American coffee farmers have diversified their plantations in recent years by replacing these traditional legume shade trees with native or exotic timber species (Galloway and Beer, 1997). The timber trees can increase the overall profitability of the system and reduce financial risks (Hernández et al., 1997; Mehta and Leuschner, 1997). Furthermore, unlike most legume shade trees certain timber species do not require regular pruning, which is labor-intensive. Damage to the coffee from the timber harvest can be minimized if tree felling coincides with the renewal or pruning of the coffee (Somarriba, 1992).

E. deglupta as a coffee shade tree appeals to farmers because of its fast growth and therefore rapid provision of shade, adaptability to a wide range of site conditions, relatively homogeneous, light shade, which is considered ideal for coffee, and little need for pruning (Grijpma, 1969; Tavares et al., 1999). The species was also promoted in Costa Rica by tree planting incentives (Viera et al., 1999). On sites with favorable water and nutrient supply, it grows exceedingly fast with up to 5 m of annual height growth during the first 8 years (Ugalde, 1997). Root competition between shade trees and coffee for water and nutrients might therefore be expected, especially in regions with a pronounced dry season and/or infertile

soil. Strong competition between *Eucalyptus* spp. and associated crops has reportedly discouraged farmers from using these trees in agroforestry associations in other countries (Saxena, 1991; Khybri et al., 1992; Narain et al., 1998). In contrast to these experiences, no serious negative effects of *E. deglupta* on associated coffee have so far been reported from the southern Pacific zone of Costa Rica (dry season of approximately 4 months and ferrallitic soils) and the Turrialba region on the Atlantic side, where the present study was carried out. The dry season is usually negligible in this region. In both the seasonally dry and permanently humid coffee regions of Costa Rica, high fertilizer rates are common, especially on larger farms (ICAFE, 1998).

We hypothesized that the apparent compatibility of coffee and *E. deglupta* shade trees on these sites could be due to one or several of the following factors: (a) the availability of soil resources matches or exceeds the combined requirements of the two species throughout the year so that competition cannot arise; (b) the two species exploit the soil resources in a complementary manner, thereby reducing competition; (c) the coffee plant, which has evolved in the understory of tropical forests, possesses a sufficiently competitive root system to cope with the competition of fast-growing trees.

In order to test these hypotheses, we measured coffee and tree growth, soil nutrient availability, root distribution and dynamics of 4- to 5-year-old coffee and *E. deglupta* shade trees on a private coffee farm in Costa Rica. We suggest that an improved understanding of the mechanisms which allow crops to grow and produce satisfactorily in association with competitive tree species should help in the design of productive agroforestry associations, the definition of criteria for shade tree selection in accord with site characteristics, and the development of management measures for alleviating competition problems where these occur.

2. Materials and methods

2.1. Study site and experimental design

The study was carried out between March 1998 and January 2000 in a commercial coffee plantation, shaded by 4- to 5-year-old *E. deglupta* trees, in Juan Viñas in the province of Cartago, Costa Rica (9°55'N,

Table 1

Nutrient concentrations in the soil at 1.5 and 5.5 m distance from *E. deglupta* shade trees in a coffee (*C. arabica*) plantation at Juan Viñas, Costa Rica^a

Distance (m)	Depth (cm)	pH (H ₂ O)	N (g kg ⁻¹)	P ^b (mg kg ⁻¹)	K ^b (mmol ^c kg ⁻¹)	Ca ^b (mmol ^c kg ⁻¹)	Mg ^b (mmol ^c kg ⁻¹)	Fe ^b (mg kg ⁻¹)	Mn ^b (mg kg ⁻¹)	Zn ^b (mg kg ⁻¹)	CEC (mmol ^c kg ⁻¹)	BS (%)
1.5	0–10	5.0 (0.1)	4.7 (0.7)	28.6 (9.3)	6.4 (1.0)	60.1* (7.2)	7.8* (0.5)	72 (9)	32 (5)	2 (0.3)	83.6* (6.8)	86 (4)
5.5	0–10	4.8 (0.1)	4.9 (0.7)	24.8 (8.7)	5.7 (0.8)	43.2* (7.1)	5.7* (0.5)	72 (4)	33 (3)	2 (0.2)	67.5* (6.3)	80 (4)
1.5	10–20	4.6 (0.1)	4.0 (0.6)	10.3 (4.0)	4.6 (0.6)	21.9 (3.4)	3.3 (0.2)	64 (6)	33 (6)	2 (0.3)	46.9 (3.7)	63 (6)
5.5	10–20	4.6 (0.1)	4.1 (0.6)	11.5 (4.6)	4.2 (0.6)	20.4 (2.6)	2.8 (0.2)	62 (3)	36 (7)	2 (0.3)	48.5 (4.8)	57 (4)

^a Values in brackets are standard errors ($n = 4$). CEC, cation exchange capacity; BS, base saturation as percentage of the CEC.

^b Extracted with Mehlich 3 extractant.

* Differences between distances are significant at $p < 0.05$.

83°43'W; 1185 m above sea level; humid tropical climate with approximately 4000 mm annual rainfall without a pronounced dry season). The soil is a Haplic Andosol (FAO–UNESCO, 1990). Soil nutrient concentrations are adequate (Bertsch, 1987) because of regular fertilization of the coffee (Table 1).

Coffee (*C. arabica* variety Catimor 5175) and shade trees were planted in May 1994 in an area which had been used for coffee production for many years. Coffee spacing was $2 \times 1 \text{ m}^2$ and tree spacing was $8 \times 8 \text{ m}^2$ with the trees planted between the coffee rows. The trees were fertilized at planting and the coffee was fertilized three to four times per year, receiving approximately 200 g fertilizer per coffee bush per year (in kg ha^{-1} per year: N, 193; P, 17; K, 66; Mg, 16; B, 13; Zn, 13). Fertilization followed the recommendations of the national coffee institute (ICAFE, 1998).

In 1998, four measurement plots with trees of average growth as the four plot corners, were identified within the plantation. Two of the plots were lost when the farm management felled some trees at the end of 1998 to reduce fungal leaf diseases of the coffee and were replaced by two new plots. Average slope of the plots was 2% except for one plot with 25% slope, and drainage was good.

The experimental design did not include a control treatment without trees, because unshaded coffee did not occur on the farm and is unusual in the region. Also, shading affects the physiology, nutrient requirements, and pest and disease dynamics of coffee, so that comparisons between shaded and unshaded coffee involve several confounding factors. Instead of using separate control treatments, we therefore compared coffee plants at different distances (up to 5.5 m) from

the shade trees within the shaded coffee plots, assuming that tree competition, if it occurred, would result in significant gradients of the measured variables (coffee size and yield, root distribution) with increasing tree distance.

2.2. Growth measurements

Tree height and stem diameter at breast height (dbh at 130 cm) of 16 trees (four plots) were measured in September 1998. The dbh of five randomly chosen trees amongst the 16 trees was measured with a dendrometer during the period of the root dynamic study (March 1999–January 2000; see below). In August 1999, height and diameter at the stem base (10 cm from the ground) of 16 coffee bushes per plot, eight of which were at 1.5 m and eight at 5.5 m distance from the trees, were measured.

2.3. Root sampling and processing

Fine root length density (RLD) ($d < 2 \text{ mm}$) of shade trees and coffee was studied with respect to the following factors: (1) distance from the nearest shade tree; (2) position with respect to the coffee rows and the localized application of fertilizer to the coffee; (3) soil depth; (4) season (Fig. 1). Roots in the soil were sampled with a cylindrical auger of 8 cm internal diameter. Roots in the litter layer were sampled with a similar device, which was inserted into the litter layer and the first millimeters of the topsoil after removing carefully from the soil surface freshly fallen, undecomposed leaves which were free of roots.

To measure the effect of the distance from the nearest shade tree on the root systems, the first set

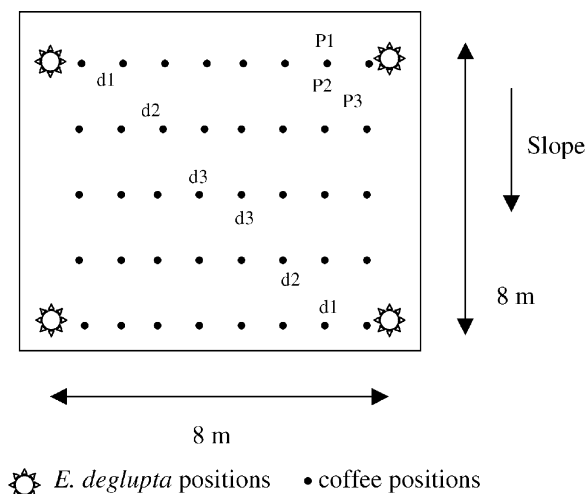


Fig. 1. Root sampling positions in a *C. arabica* plantation with *E. deglupta* shade trees at Juan Viñas, Costa Rica. The positions P1, P2 and P3 are only shown for one tree distance (for symbol meanings see text).

of samples (February/March 1998) was collected from 0–10 and 10–20 cm soil depth, measured from the top of the mineral soil, on the diagonal across each plot at 1.5, 3 and 5.5 m (plot center) from the trees. To obtain a representative sample for each distance and depth, soil cores from the following three positions were collected and mixed: “P1”, 40 cm uphill from a coffee plant, where the fertilizer was applied (“fertilized position”); “P2”, downhill at the same distance from a coffee plant (“unfertilized position”); and “P3”, between coffee rows (1 m distance from each row = “interrow position”). The latter position was usually bare of litter due to management activities, whereas the soil in positions P1 and P2 was covered by a layer of 1–2 cm of coffee and some tree litter. This litter was included in the topsoil sample, without altering the depth of the mineral soil sample. The root concentration in litter and mineral soil was measured separately in another sampling (see below). For each distance and depth, a bulked sample was formed by pooling six individual soil cores (one core from each of the three positions P1, P2 and P3 from each of two opposite corners of a plot; see Fig. 1).

To study the effect of the position with respect to the coffee rows, fertilizer placement and coffee litter, a second set of samples was taken in March–April 1998 for the first four replicates and in March 1999 for the

two additional replicates from the litter layer and from 0 to 10 cm soil depth at 1.5 m distance from the shade trees, where most of the tree and coffee roots had been found in the previous study. Soil from the three positions P1, P2 and P3 was analyzed separately (and not pooled per distance as in the previous experiment), and bulked samples for each position were obtained by mixing the corresponding four soil cores or litter samples from the four trees of a plot. Litter and mineral soil were processed separately.

The vertical distribution of the root systems was studied by collecting additional samples, also in March 1999, from position P1 at 1.5 m from the four shade trees down to 40 cm depth in 10 cm increments (Fig. 1). Sampling at greater depths was restricted by the presence of rocks. Each bulked sample was formed from four soil cores or litter samples from the four trees of a plot.

To characterize the temporal dynamics of coffee and tree root growth, samples from the litter layer and from 0 to 10 cm depth were taken in March 1999 (driest month), June 1999 (after onset of rainy season and second fertilization) and January 2000 (after harvest) in position P1 at 1.5 m distance from the trees (Fig. 1). The sampling positions were changed by 10–15 cm between the three sampling dates to avoid resampling of disturbed soil. Each bulked sample was formed by pooling four soil cores or litter samples from the four trees of a plot.

After sampling, the soil cores were stored at 10 °C and were processed within a week. The bulked samples were thoroughly mixed, cutting larger roots into pieces of 2–3 cm, and a subsample of approximately 5–10% by weight was taken for the quantification of fine roots ($d < 2$ mm only) as described by Schroth and Kolbe (1994). For the litter samples a subsample of approximately 25% was taken. The subsample was soaked in water overnight, then washed with tap water on a 0.5 mm sieve. Roots were separated from organic debris and sorted according to species using a stereomicroscope. *E. deglupta* and coffee roots were distinguished by color, branching characteristics and surface structure. Dead roots of both species were differentiated from living roots by their darker color and lower turgidity. RLDs were obtained by scanning the roots at 600 dpi and processing the data with a root image-scanning program (Winrhizo, V.3.9, Regent Instruments).

2.4. Soil and leaf analyses

Soil analyses were carried out on the samples collected for the “distance” (1.5 and 5.5 m only) and “position” root studies after air-drying and sieving to pass 2 mm. Total N was measured by Kjeldahl digestion. P, K, Ca, Mg and micronutrients were extracted with the Mehlich 3 solution at a soil:solution ratio of 1:10 (Tran and Simard, 1993) and measured by atomic absorption spectrometry except for P, which was measured colorimetrically with a segmented flow analyzer. Exchangeable acidity was measured in a 1 M KCl extract at a soil:solution ratio of 1:15 after 10 min shaking and a NaOH titration of a 25 ml subsample against a phenolphthalein indicator. The cation exchange capacity was calculated by summing the basic cations and the exchangeable acidity. The base saturation was expressed as the percentage of basic cations in the total cation exchange capacity. The pH was measured with a glass electrode at a soil:solution ratio of 1:2.5 in distilled water.

Leaf samples from the 16 coffee plants whose dimensions were measured were collected for nutrient analyses, taking two to four fully developed young leaves per coffee bush from the upper third of the crown (Carvajal, 1984). The samples were digested with nitric and perchloric acid. Cations were measured by atomic absorption spectrometry and P was measured colorimetrically with the ammonium molybdate method. Total N was measured by Kjeldahl digestion.

2.5. Statistical analysis

The data were analyzed by analysis of variance for a randomized complete block design, treating the six plots as replicates and sampling positions within the plots as treatments. Sampling time was analyzed as a repeated measurements factor. In case of significance of the *F*-test at $p < 0.05$, treatment means were compared by least significant difference tests at the same level of probability.

3. Results

3.1. Tree and coffee growth and productivity

In September 1998 at an age of 52 months, the *E. deglupta* trees were 15.9 m high (S.E. = 0.5 m) with a

dbh of 22.0 cm (S.E. = 0.8 cm). The dbh of the five trees fitted with dendrometers increased by 2.5 cm on average during the measurement period of 9 months, with monthly increments of 0.22–0.34 cm.

Coffee production in the study plots, estimated from commercial harvests, was approximately 14,500 kg of green coffee berries per hectare per year during the first two harvests (1997/1998; O. Ortíz, pers. comm.). There was no difference in size between coffee plants close to the shade trees and at greater distance from the trees, with an average height of 2.63 m (S.E. = 0.04 m) and average diameter at the stem base of 4.42 cm (S.E. = 0.07 cm) at 1.5 m compared to 2.54 m (S.E. = 0.05 m) and 4.32 cm (S.E. = 0.09 cm) at 5.5 m distance. The nutrient concentrations in the coffee leaves were in the adequate range according to Müller (1966) and did also not differ significantly between tree distances (22–23 mg g⁻¹ N; 1.7 mg g⁻¹ P; 15–16 mg g⁻¹ K). The soil data showed that the shade trees did not cause nutrient depletion in their proximity in this fertilized soil. At 0–10 cm, Ca, Mg and CEC were significantly higher at 1.5 m than at 5.5 m from the trees ($p = 0.04$, 0.006 and 0.02, respectively; Table 1).

3.2. Influence of shade tree distance on coffee and tree roots

Coffee and shade trees had similar RLD in the topsoil (1–2 cm cm⁻³), but in the 10–20 cm layer, the RLD of coffee was significantly greater than that of the trees for the 1.5 and 5.5 m distances ($p = 0.003$ and 0.02, respectively, Fig. 2). The RLD of *E. deglupta* decreased significantly with increasing distance from the trees both at 0–10 and at 10–20 cm depth. The tendency of increased RLD of coffee close to the shade trees was not significant, in accordance with the aboveground growth data.

3.3. Influence of coffee rows and fertilizer placement on coffee and tree roots

The coffee roots were concentrated in the soil and litter in the proximity of the coffee rows and showed a marked decline to the interrow position where, due to the absence of litter, roots were only measured in the mineral soil (Fig. 3). Coffee RLD did not differ between the fertilized and the unfertilized side of

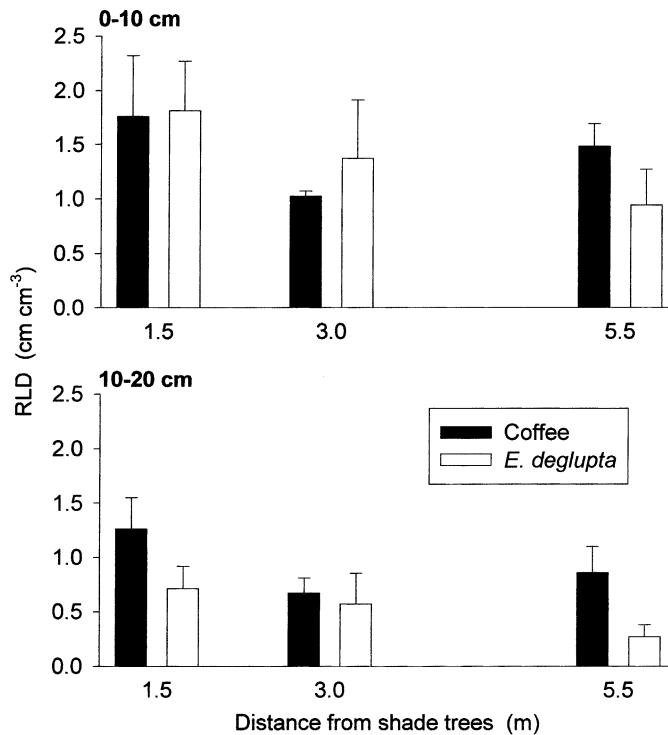


Fig. 2. Fine RLD (cm cm^{-3} ; $d < 2 \text{ mm}$) of *E. deglupta* shade trees and coffee (*C. arabica*) at different distances from the trees in a shaded coffee plantation at Juan Vías, Costa Rica (means and standard errors). The decrease of tree RLD with increasing tree distance was significant ($p < 0.05$). The effect of tree distance on coffee RLD was not significant.

the coffee rows. This was in agreement with non-significant differences in most soil chemical characteristics between these positions (data not shown), indicative of rapid uptake of fertilizer nutrients by coffee and shade trees and/or redistribution of nutrients in the plots by the frequent and heavy rainfall. Only the pH and values for Ca and CEC were significantly higher in the unfertilized position in comparison to the fertilized side, where fertilization had led to an acidification of the topsoil (pH of 5.4 vs. 4.6; $p = 0.001$). Bulk density for 0–10 cm was 0.84 g cm^{-3} (S.E. = 0.01 g cm^{-3}) on the average of the fertilized and interrow positions.

In contrast to coffee root distribution, the tree roots were concentrated in the unfertilized interrow areas, and their density at 0–10 cm depth declined by more than 50% in the proximity of the coffee rows (Fig. 3). The shade trees had higher RLD than the coffee in the interrows while the RLD of the coffee in the proximity of the coffee rows was higher than that of the trees

both in the litter and in the soil ($p = 0.004$). In the samples collected in 1998 (four replicate plots), the tree RLD in the litter was significantly higher on the fertilized than on the unfertilized side of the coffee rows ($p = 0.011$), indicating increased root proliferation of the trees in the fertilized soil. This effect was not observed in 1999.

3.4. Vertical distribution of tree and coffee roots

Coffee had a relatively homogeneous root distribution in the upper 40 cm of soil in the fertilized positions (Fig. 4), where bulk density varied from 0.77 to 0.83 g cm^{-3} . Forty percent of the roots were concentrated in the litter and upper 10 cm of soil. The root system of *E. deglupta* was shallower than that of coffee, with 63% of the roots in the litter plus 0–10 cm stratum (Fig. 4). In the distance sampling, where the soil depths 0–10 and 10–20 cm were sampled separately, the percentage of coffee roots

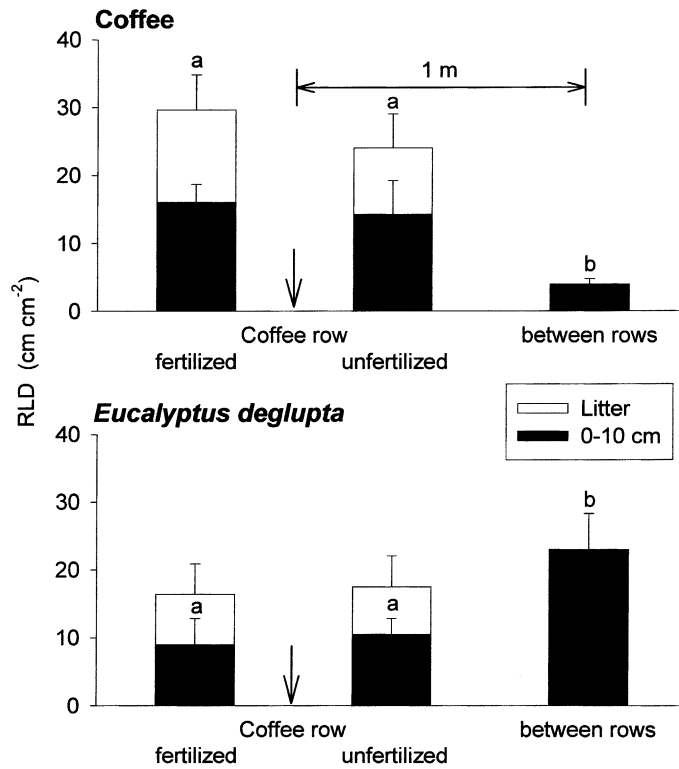


Fig. 3. Fine RLD (cm cm^{-2} ground area; $d < 2$ mm) of coffee (*C. arabica*) and *E. deglupta* shade trees at different positions between the coffee rows at Juan Viñas, Costa Rica (means and standard errors). Different letters indicate significant differences at $p < 0.05$.

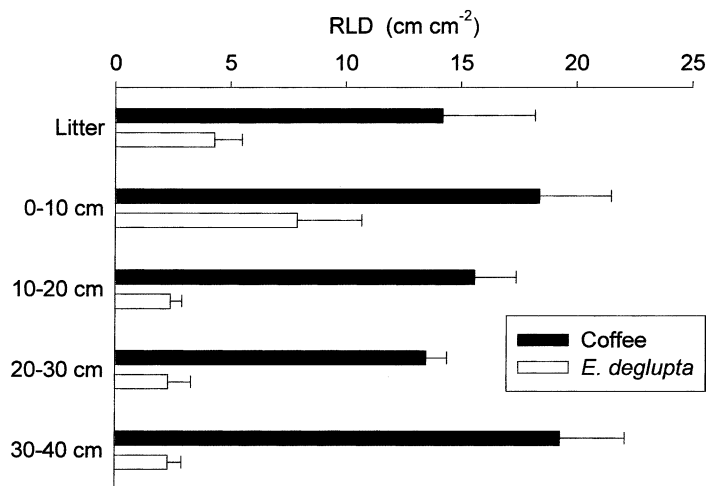


Fig. 4. Depth distribution of fine RLD (in cm cm^{-2} ground area; $d < 2$ mm; means and standard errors) of coffee (*C. arabica*) and *E. deglupta* shade trees at Juan Viñas, Costa Rica.

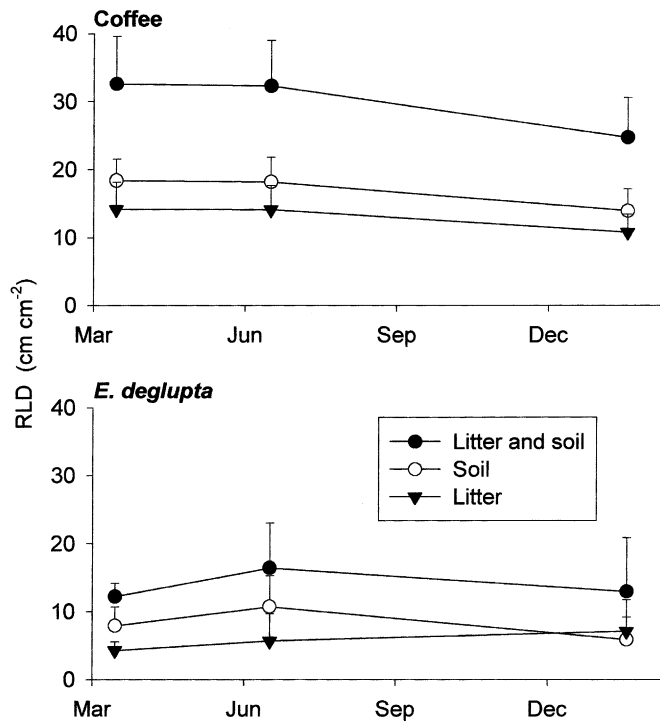


Fig. 5. Seasonal changes of coffee (*C. arabica*) and *E. deglupta* fine RLD (cm cm^{-2} ground area; $d < 2$ mm; means and standard errors) in litter and topsoil (0–10 cm) in a shaded coffee plantation in Juan Viñas, Costa Rica, during 1999. March, end of the drier period; June, rainy season; January, end of rainy season and coffee harvest.

in the top 10 cm were 56, 57 and 65% at 1.5, 3 and 5.5 m from the trees, respectively, without significant differences. This non-significant increase indicates that the vertical distribution of the coffee roots was not significantly influenced by distance from the shade trees and thus decreasing tree root density.

3.5. Temporal patterns of coffee and tree root growth

The RLD of the coffee did not differ between the drier period in March (when precipitation was, however, still 123 mm per month) and the rainy season in June 1999 and did not show a response to the fertilizer application in May (Fig. 5). In January 2000, when the carbohydrate reserves of the coffee plants should have been depleted from the previous harvest season (Cannell, 1985), their RLD was also not significantly reduced ($p = 0.487$). The absence of a seasonal pattern of the *E. deglupta* roots was in accord with the continuous aboveground growth of this evergreen species (Fig. 5).

4. Discussion

Despite the relatively fast growth of the shade trees, there was no obvious yield reduction of the associated coffee plants. With $14,500 \text{ kg ha}^{-1}$ per year on average for the first two harvests in 1997 and 1998, coffee production was adequate for this site and close to the yield of neighboring areas with traditional *Erythrina* shade trees ($15,000 \text{ kg ha}^{-1}$ per year; Rojas and Ramírez, 1988). Measurements on coffee plants at different distances from the shade trees within the plots also failed to reveal a suppressive effect of *E. deglupta* on growth or nutrient status of the coffee. Furthermore, although the RLD of the shade trees decreased with increasing distance from the trees, this did not result in increasing coffee RLD as might have been expected if coffee was released from tree root competition. The RLD of coffee even increased slightly in the proximity of the trees, possibly responding to higher litter input. A suppressive effect of *E. deglupta* on the regionally common root

rot “corchosis” (Bertrand et al., 2000) has also been suggested (O. Ortíz, pers. comm.), but no evidence for this could be collected in the field.

These data confirm the opinion held by many Costa Rican farmers that, despite its fast growth, *E. deglupta* is a suitable shade tree for coffee and does not cause coffee yield depressions at sites with relatively high-rainfall and fertilization. In contrast, in the Central Valley of Costa Rica, coffee associated with *E. deglupta* had lower soil water contents and suffered visibly more from drought stress during the 5 months dry season than coffee with regularly pollarded *Erythrina poeppigiana* shade trees or unshaded coffee (Jiménez and Alfaro, 1999). The successful use of *E. deglupta* as shade tree at our study site and other sites with sufficient rainfall and fertilization could thus be explained with hypothesis (a) given in Section 1, according to which the availability of soil resources was high enough to satisfy the combined demand of both species so that competition could not occur.

However, if this hypothesis was entirely true, the root systems of both species in the association would practically not interact. The fine root distribution of either species would then not be expected to be influenced by the other species, but to follow a random pattern except for a general decrease of RLD with increasing distance from the respective plant. This expectation was contradicted by a clearly non-random distribution of the tree roots with respect to the coffee rows. While the coffee roots reached highest densities in the proximity of the coffee rows, the RLD of the trees was significantly higher in the alleys between the coffee rows (Fig. 3). Clearly, the tree roots avoided soil with highest densities of coffee roots. Whether in turn the trees also influenced the horizontal distribution of the coffee roots could not be tested without a crop-only control. It is remarkable that the pronounced complementarity in root distribution of coffee and trees led to a very homogeneous distribution of total RLD in the plots, with values between 2.5 and 2.7 cm cm⁻³ in all positions (Fig. 3), suggesting a complete and efficient exploitation of the soil resources by the association. The non-random distribution of the tree roots strongly suggests that complementarity was a result of competition between tree and crop roots, as has also been shown for associations between trees and herbaceous plants (Schroth, 1999). Complementary root distribution between trees and

crops could be an important mechanism for reducing root competition between coffee and fast-growing timber trees during dry spells and could also help to explain why *E. deglupta* is successfully being used as shade tree at sites with up to four months of dry season on the Pacific side of Costa Rica.

While the small scale, horizontal division of the rooting space between trees and crops certainly reduced root interactions in accord with hypothesis (b), the generally high resource availability at our study site may explain why other windows of complementarity between the root systems of the two species were not used, or only to a minor extent. The *E. deglupta* trees had very shallow root systems with which they colonized opportunistically local nutrient enrichments and litter accumulations in the topsoil (Schaller et al., 1999; Morales and Beer, 1998), while the coffee exploited the subsoil better with its roots than the shade trees (Fig. 4). Decreasing RLD of the trees by more than one half between 1.5 and 5 m tree distance (Fig. 2) would have given the coffee plants the opportunity for increased root proliferation in the fertile topsoil, but the observed effect on relative coffee root distribution between 0–10 and 10–20 cm depth was small and non-significant. In view of the magnitude of the reduction in tree root density, this could most likely be explained with little demand of the coffee for additional soil resources, and a larger response would be expected on a drier or less fertile site. If at other sites (or in other years) the decline of the coffee root systems after the harvest is more pronounced than in this study (Fig. 5), this might also result in temporally increased tree root proliferation, and thus temporal complementarity of resource use.

While high resource availability and complementary root distribution explain much of the success of the association of coffee with fast-growing timber trees on certain sites in Costa Rica, it cannot be completely understood without taking into consideration the high competitiveness of the coffee root system itself. At 40 cm distance from the coffee rows, the RLD of the coffee was approximately 1.5 cm cm⁻³. RLD is not a direct indicator of the competitive ability of a species, as root hairs, root exudates, mycorrhizae and specific uptake kinetics also play an important role for nutrient acquisition (Marschner, 1995; Schroth, 1999). However, the competitiveness of the coffee root

system was clearly high enough to force the tree roots into the interrow position, despite fertilizer application in the proximity of the coffee rows. Furthermore, the coffee roots dominated the subsoil in the plots, in contrast to the common perception of deep-rooted trees and shallow-rooted crops, and this could be especially important for the competitive balance between the two species on sites with a longer dry season. The competitiveness of the coffee root system may also explain why the growth of the *E. deglupta* trees was only in the medium range reported for this species (Ugalde, 1997), despite the favorable site conditions. These observations suggest that hypothesis (c) was also valid and that the use of very fast-growing timber trees in agroforestry associations may not be as successful with less competitive crops as it is with coffee.

5. Conclusion

Costa Rican farmers have found that *E. deglupta* is a suitable shade tree for coffee on sites with high precipitation and soil fertility, confirming experiences of coffee farmers in other tropical regions. Under these conditions, tree growth is fast, leading to early economic returns through timber production without evidence of simultaneous increase in competition with the coffee for soil resources. The compatibility of coffee with very fast-growing shade trees is due to a combination of high availability of soil resources, their complementary exploitation by trees and crops, especially through a small-scale horizontal and, to a lesser extent, vertical partitioning of the soil between coffee and tree roots, and high competitiveness of the coffee root system itself. On drier or less fertile sites, further windows of complementarity, such as complementary temporal dynamics of tree and crop root systems, may be increasingly exploited. These mechanisms are not sufficiently effective to avoid competition between coffee and shade trees on much drier sites, such as the central valley of Costa Rica, and less competitive tree species are required.

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