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Chapter 8
Fine Root Systems and Mycorrhizal Associations in Two Central Amazonian Inundation Forests: Igapó and Várzea

Ulrike Meyer, Wolfgang J. Junk, and Christine Linck

Contents

Abstract Fine root systems and mycorrhizal associations were examined in the central Amazonian várzea and igapó floodplain forests. While the várzea forest is located on fertile soil, infertile soil conditions prevail in the igapó region. Quantitative root analyses comprised of fine root length density within 8.5 cm soil depth (as a measure of root concentration) and fine root production rate within 43 cm soil depth. Fine root branching patterns and root symbioses with arbuscular/ endomycorrhiza (AM)

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or ectomycorrhiza (EM) were determined qualitatively. Fine root systems showed marked differences between the forest types. Fine root length densities, for both living and dead roots, were higher in the igapó as compared to the várzea. In spite of the greater fine root concentration within the topsoil, the fine root production rate was lower in the igapó relative to the várzea. It therefore appears that root longevity was greater and dead root decomposition lower in the igapó than in the várzea. While the majority of fine roots were concentrated within the surface horizon of the igapó, they extended to greater soil depth (43 cm) in the várzea. Root branching was characterised by higher ‘numbers of short roots’ in the igapó, while the ‘relative total root lengths’ were much higher in the várzea. In general, igapó roots were better equipped to retain nutrients within the soil-plant ecosystem through greater root concentration, greater root longevity and more intensive branching. Both forests associated predominantly with AM. EM symbiosis was only detected on Aldina latifolia in the igapó. The proposal by Singer and Araujo (1986) that the igapó forest should be viewed as an ectotrophic forest could not be confirmed by this study, as most of the tree species were symbiotically associated with the AM-type in both forests.

8.1 Introduction

The central Amazonian floodplain forests are subject to prolonged inundation periods. The várzea forest is situated in close proximity to the white-water Solimões River, whose electrolyte-rich sediment load serves as an annual nutrient input to the fertile alluvial soils (Klinge and Ohle 1964; Irion et al. 1984; Furch 1997, 2000; Furch and Junk 1997a; Junk and Piedade 2010). In contrast, sediments deposited by the electrolyte-poor, black-water Negro River contribute little to the nutrient status of the highly-weathered, infertile igapó soils (Furch 2000).

The flora and fauna of both forest types are largely controlled by the flood pulse (Junk et al. 1989). This pulse encompasses an annual alternation of an aquatic (submerged) phase and a terrestrial, temporarily dry (emerse) phase. Important in the context of forest development is that tree growth is considerably reduced in the submerged phase (Parolin et al. 2010c). Short optimal growth conditions coupled with a nutrient-poor soil environment may result in a different relative importance of nutrient cycling in the igapó as compared to the várzea forest.

Tree roots commonly form symbiotic relationships with mycorrhiza for improvement of nutrient uptake (Moyersoen et al. 2001). The two types of mycorrhizal symbioses include: ectomycorrhiza (EM) and endomycorrhiza/arbuscular mycorrhiza (AM). While EM are characterised by the formation of hyphae surrounding epidermal root cells (Hartig Net), AM are in more direct contact with roots, through penetration of host cells (Jackson and Mason 1984). Most tropical tree species associate with the AM type, which improve uptake of inorganic phosphorus (Alexander 1989). However, EM may dominate in some tropical forests, especially if they are located on infertile soils with seasonal dry periods and low nitrification rates (Janos 1983). This is in line with results of Singer and Araujo (1986), who suggested that the igapó forest should be described as an ‘ectotrophic’ forest.

The aim of this study was to examine and compare the fine root length densities, root production rates and root branching patterns of the igapó and várzea forests. Mycorrhizal associations with fine roots were investigated in both forests.

8.2 Study Area and Site Descriptions

The igapó and várzea forests are situated in central Amazonia, Brazil. The igapó forest is located adjacent to a confluent (Igarapé Nova Invéja) of the Tarumă Mirim River, which flows into the Negro River 20 km upstream of Manaus (3°S, 60°W). The várzea forest is found on the first island upriver of the confluence of the Negro River with the Solimões River (Ilha de Marchantaria) and is approximately 15 km south to the town of Manaus.

The study region is characterised by a seasonal alteration of a dry period lasting from June to November and a rainy period between December and March/May (Ribeiro and Adis 1984). A rise in water table commences approximately 4–6 weeks after the onset of the rainy season (De Simone et al. 2003a). The average annual rainfall is 2,542 mm year^{-1} (Ribeiro and Adis 1984). The average temperature range is 27.9°C in the dry period and 25.8°C during the rainy period (Junk and Furch 1985). The underlying geology of the igapó region consists of Pleistocene terraces. The várzea study area is characterised by Holocene alluvial deposits (Fittkau 1982).

Sampling was conducted in 1987 at the onset of the emerse phase. In both forest areas, three sampling plots (30 × 20 m) were selected. The plots were situated along a catena of a sloping river bank. Differences in plot elevations corresponded to variations in inundation periods. The sampling plots of the igapó forest were termed TA (2.7), TH (3.9) and TN (4.9), where numbers in brackets denote 'months of inundation'. The várzea plots were, according to increasing inundation length/declining elevation, in the following order: MA (3.5), MB (5.4) and MH (7.1).

According to the U.S. Soil Taxonomy Classification (1990), the soil orders identified for the igapó and várzea regions were Entisols and Inceptisols, respectively. The subhorizons of the humus profiles were termed according to Babel (1971). Intergrades, e.g. Lv(FAhh), were termed by addition of the pertaining symbols, with symbols in brackets representing a lower portion of the respective components.

8.3 Materials and Methods

8.3.1 Soil Analyses and Tree Species Composition

Bulk soil samples were collected from each soil layer comprising the soil profile. Soil pH was measured in 0.02 N $CaCl_2$ after 2.5 h with a standard glass electrode. C_{total} (C_t) was determined by the potassium dichromate oxidation procedure (Schlichting et al. 1995). N_{total} (N_t) was analysed by the Kjedahl method (Schlichting et al. 1995). P_{total} (P_t) and K_{total} (K_t) were extracted from soil with 30% HCl. P_t was measured spectrophotometrically after the addition of molybdate-vanadate solution at a wavelength of 440 nm. Caesium-aluminium buffer was added to the extract for determination of K_t by AAS.

Tree species composition was recorded for each sampling plot using trees >5 cm stem diameter at breast height. Epiphytes were not accounted for in this study.

8.3.2 Root Analyses

Investigation of the fine root systems included: root length density within 8.5 cm soil depth; root production within 43 cm soil depth; root branching patterns and mycorrhizal associations. While root length density and root production investigation involved quantitative analyses, root branching patterns and mycorrhizal associations were examined qualitatively.

8.3.2.1 Fine Root Length Density

Fine root length (per soil area) and fine root length density (per soil volume) were examined on soil blocks with polished vertical surfaces (preparations after soil impregnation with polyester resin, Babel 1979). An advantage of this method is that roots can be assigned exactly to the individual layers of the humus profile, which sometimes are merely a few millimetres thick. The values obtained by this method are higher than those derived from washing and sieving methods. This is true for living roots and still more pronounced for dead roots as no losses occur by breaking off parts of the root systems.

The number of section profiles of fine roots (<1 mm) (Q) per test area (A) was counted under a stereomicroscope with magnification 25×. At least six test squares (5 × 5 mm) were placed at random in each subhorizon of each of 5 blocks (60 × 120 mm) per sampling date. The root length densities J_v (cm cm^{-3}) were calculated as follows (Weibel 1979):

$$J_v = 2\,Q / A$$

The factor 2, which is only valid for isotrophism, was found to be a sufficiently good approximation in this study.

Fine root length (cm cm^{-2}) was calculated by multiplication of J_v with the soil horizon thickness.

The fine roots were classified into two categories:

- Living roots – rhizodermis turgescent or slightly shrunken, cortex parenchyma and central cylinder bright to slightly brownish.
- Dead roots – cortex and central cylinder dark, or cortex milky, no central cylinder, exodermis wrinkled.

8.3.2.2 Fine Root Production

The vertical distribution of newly developed fine roots and their production rates were examined in situ in the medium-elevated plots of the igapó (TH) and várzea (MB) forests over time. Six glass tubes (43 cm length), containing a mini-rhizotron (Wolf GmbH, Knittlingen) each, were vertically inserted into soil per plot. Adequately sized holes were drilled beforehand to ensure close contact between the glass tubes and the surrounding soils. One month after installation, a camera (Olympus OM 4) was attached to the mini-rhizotron to scan the surfaces of the glass tubes at certain depth intervals. The numbers of newly developed fine roots were counted per 1 cm soil depth using a surface area of 4 cm^2. This procedure was repeated five times on a monthly basis.

The fine root production rate was calculated from the sum of the positive differences of the fine root numbers between the six dates (Hansen and Steen 1984; Vogt et al. 1986). The production rate was expressed as root length density ($cm\ cm^{-3}$), assuming that a fine root touching the surface of the mini-rhizotron tube can be handled like a root section profile in a soil section plane.

8.3.2.3 Fine Root Branching Pattern

Investigation of fine root branching patterns was only feasible for trees exhibiting highly branched root systems within close distance to the stem and the soil surface. Trees with long tap roots were not included in this study.

The whole root system, from the stem to the final branches, was uncovered. Root first order end sections (25 cm) with all their branches (including third/last order branching) were removed. The roots were conserved with AFE-solution. The fine root branching systems were later analysed with the aid of a semi-automatic image analyser (MOP-MO2, Kontron). The analyser calculated mean values of the lengths and numbers of root segments. Schematic drawings were produced from the values obtained according to the method of Kottke (1986) taking 10 cm root first order as the reference length (Fig. 8.1). In addition, the following ratios were calculated for numerical characterisation of the branching types:

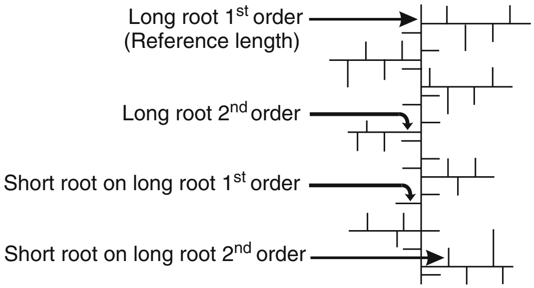


Fig. 8.1 Terminology of root segments

- Relative number of short roots (cm^{-1}): number of short roots on long roots first and second order per centimeter of long roots first and second order.
- Relative total root length: length of all long and short roots (cm) per cm of long roots first order.

8.3.3 *Mycorrhizal Association*

Mycorrhizal association types with fine roots were examined using the AFE-conserved root samples. The root sections were stained with Trypan blue in lactophenol (Phillips and Hayman 1970) and examined microscopically (40×–100×) for intracellular hyphae and possibly vesicles (AM). EM associations were examined microscopically by the use of permanent slides containing non-dyed root segments embedded in glycerine.

8.4 Results

8.4.1 *Soil Chemical Parameters and Tree Species Composition*

Table 8.1 depicts the chemical parameters corresponding to the soil layers of the igapó and várzea soil profiles. In general, organic matter accumulation, as indicated by C_t contents, was greater in the topsoils of the igapó relative to the várzea forest. C_t increased in both forests with increasing inundation lengths. Similarly, N_t was usually higher in the topsoils of the igapó plots. In contrast, P_t and K_t concentrations were, at each soil depth interval, higher in the várzea than in the respective igapó plots. In both forests, nutrient concentrations (C_t, N_t, P_t, K_t) declined with increasing soil depth.

The várzea and igapó forests were heterogeneous in terms of tree species composition and numbers of individual species (Table 8.2). In this study, a total of 67 tree species were detected in the investigated igapó plots and 31 species were identified in the plots of the várzea forest. Three species were common to both forests. Both forests showed a distinct zoning of tree species composition according to plot location along the catena (Table 8.2).

A greater above-ground biomass production was observed in the várzea as compared to the igapó forest. Trees rarely exceeded a stem diameter of 15 cm in the igapó forest, while thicker trees were often noticed in the várzea plots (data not shown).

8.4.2 *Fine Root Length Density*

Fine root length densities (cm cm^{-3}), for both living and dead roots, were significantly higher in the igapó as compared to the várzea topsoils (analysis of

Table 8.1 Chemical soil characteristics according to plot location in the igapó and várzea forests

Forest type	Plot	Soil horizon	Horizon thickness (cm)	pH ($CaCl_2$)	C_t (%)	N_t (%)	C/N	P_t (ppm)	K_t (%)
Igapó	TA	L	2	4.0	50.7	1.60	32	334	0.13
		Ahh	3	3.5	7.0	0.40	18	223	0.05
		(Ah)Gr	15	3.8	0.8	0.06	13	62	0.02
		G(o)r	30	4.3	1.0	0.05	22	90	0.02
		GoBv	52	4.1	0.5	0.04	14	82	0.03
	TH	L	2	3.7	49.0	1.10	45	242	0.09
		(F)Ahh	4	3.4	11.5	0.60	19	239	0.11
		(Ah)Gr	10	3.7	2.5	0.20	16	86	0.09
		G(o)r	10	3.7	0.9	0.10	9	76	0.09
		Go	76	3.8	0.8	0.07	11	99	0.12
	TN	L	1	4.3	51.9	1.00	52	234	0.39
		F(Ahh)	2	3.4	35.6	1.60	22	546	0.26
		(F)Ahh	2	3.5	16.9	0.90	19	400	0.21
		Ah(Gr)	3	3.6	6.2	0.50	12	219	0.14
		(Ah)Gr	11	3.7	2.2	0.20	11	109	0.12
		G(o)r	17	3.7	1.2	0.09	14	82	0.13
		Gro	65	3.8	0.6	0.05	13	170	0.11
Várzea	MA	L	1	5.1	41.5	1.50	28	921	0.36
		Ahh	4	4.2	6.2	0.40	16	561	0.78
		(Ah)Gor	5	4.2	1.2	0.10	12	255	0.77
		Gro	14	4.2	0.9	0.09	10	286	0.77
		II BvGo	44	5.3	0.2	0.02	10	439	0.28
		Gro	33	5.8	0.5	0.04	13	516	0.41
	MB	L	1.5	4.6	44.3	1.30	34	812	0.27
		Fahh	1	4.0	18.7	1.30	15	800	0.60
		Ahh	3	3.9	4.2	0.30	14	495	0.71
		Gro	6	4.1	0.8	0.10	8	231	0.79
		Go	25.5	4.5	0.5	0.10	5	336	0.64
		II BvGo	64.5	5.3	0.2	0.02	10	448	0.25
	MH	L	2	5.0	43.9	1.60	27	1,210	0.89
		Fahh	1.5	4.0	22.0	1.30	17	797	0.67
		Ahh	3	4.1	4.4	0.30	15	509	0.91
		Gro	7	4.2	1.0	0.10	10	251	0.82
		Go	35	5.1	0.8	0.07	11	393	0.96
		II Gro	46.5	6.1	0.6	0.05	12	545	0.61

variance, 5% Confidence Interval (C.I.) (Fig. 8.2). Specifically, the fine root lengths (cm cm^{-2}) of living roots were 1.8–4.8 times greater in the igapó than in the respective várzea plots. Root lengths determined for dead roots were 1.3–3.0 times higher in the igapó relative to the várzea plots. For both forests, highest root length densities were associated with the humus-rich loose Ahh horizons, which were mixed with organic materials from the humus cover by animal perturbation.

Table 8.2 Description of vegetation in the igapó and várzea[a]

Forest type	Plot location and size	Number of tree species	Number of individuals	Diversity (Shannon-Weaver)
Igapó	TA (600 m^2)	29	85	3.09
	TH (600 m^2)	33	73	3.25
	TN (600 m^2)	36	119	2.97
	TA+TH+TN (1,800 m^2)	67	277	3.81
Várzea	MA (600 m^2)	15	64	2.34
	MB (600 m^2)	16	35	2.35
	MH (600 m^2)	14	65	2.01
	MA + MB + MH (1,800 m^2)	31	164	2.93

[a] Species names in Meyer (1991)

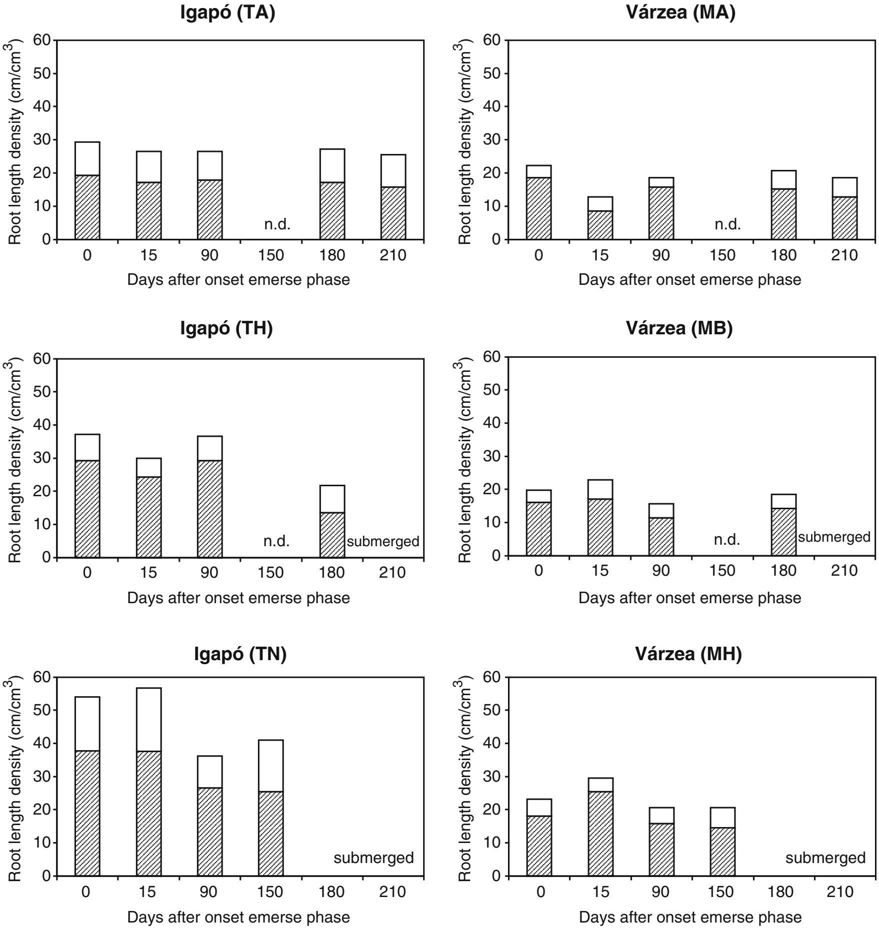


Fig. 8.2 Root length densities of dead (striped bars) and living roots (white bars) within 8.5 cm soil depth in the Igapó and Várzea plots (n = 5); n.d. = not determined

Differences in root length densities were negligible for the shortest inundated plots of both forests (TA. MA) (Fig. 8.2). An increase in the amount of fine roots with increasing inundation length was prominent in the igapó, but less pronounced for the várzea forest. In particular, fine root lengths determined for the igapó forest were 35% higher for living and 45% higher for dead roots in the longest inundated TN plot relative to the shortest inundated TA plot.

Minor fluctuations in root length densities were observed for both dead and alive roots in all plots during the emerse phase (Fig. 8.2). Thus, the proportion of living roots remained relatively constant in both forests between the beginning and end of the emerse phase.

8.4.3 Fine Root Production

Depth distribution of newly-formed fine roots and their production rates were only examined in the medium-elevated plots of the igapó (TH) and várzea (MB) forests. Comparison of both plots revealed marked differences in the vertical distribution of fine roots. With respect to the igapó forest, the maximum concentration of young fine roots was found within 0–16 cm soil depth (Fig. 8.3). This rooting depth coincided with the extent of the AhGr horizon. Below, a humus-free mineral horizon was located, which contained noticeably fewer roots (16–25 cm depth). Only few roots were occasionally detected up to 43 cm soil depth. In contrast, two peaks in fine root concentrations were identified in the soil profile of the várzea forest (Fig. 8.3). The first peak corresponded to the Ahh/AhGOR horizon within 4–8 cm soil depth. Fine root development was then sparse between 12 and 38 cm soil depth. The second peak and highest concentration of fine roots was observed within 38–43 cm of the várzea soil profile.

The production rates of new fine roots were, for the soil depth intervals 0–8 cm and 33–43 cm, significantly higher in the várzea than in the igapó plot (T-test, 5% CI) (Fig. 8.4). With respect to the latter depth interval, the fine root production rate determined for the igapó plot accounted only for 6% of the one identified in the várzea. Similar production rates were, however, determined for both plots between 8 and 32 cm soil depth.

8.4.4 Fine Root Branching Pattern

Fine root branching patterns were investigated using 43 and 29 tree species of the igapó and várzea forests, respectively. For each species, one individual tree was examined in order to gain a more complete overview of the different root branching types, rather than investigating fewer tree species more intensely. Both forests showed distinct differences in root branching types. Figures 8.5 and 8.6 illustrate

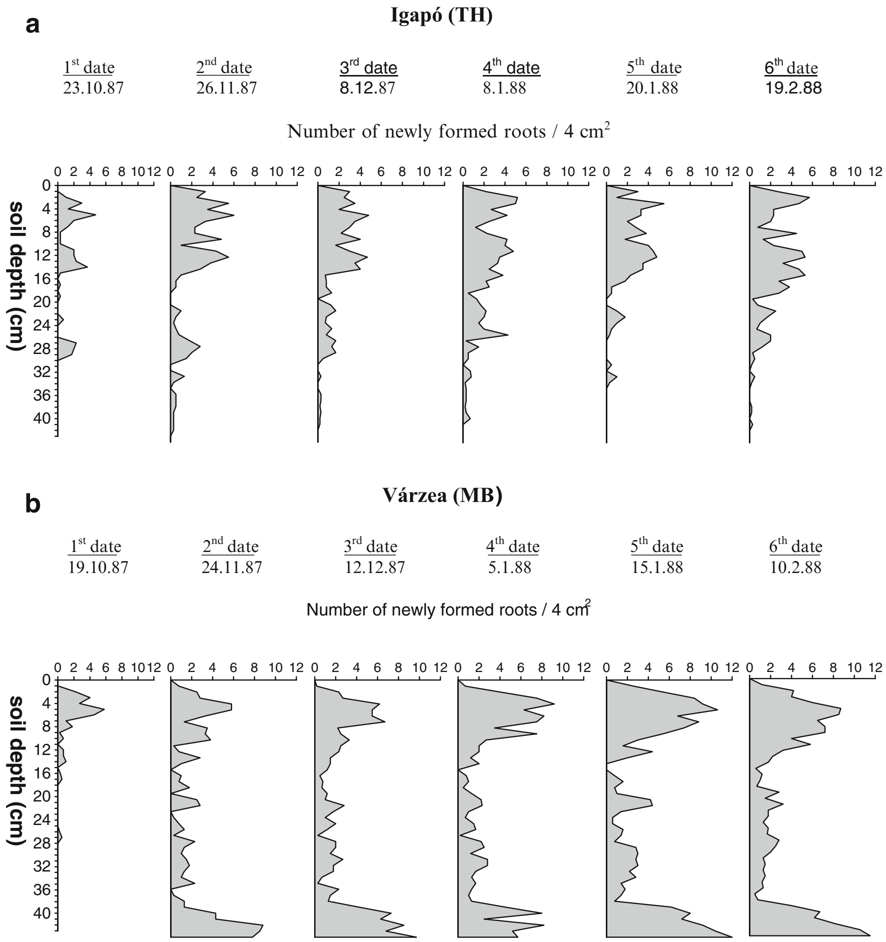


Fig. 8.3 Depth distributions of fine roots at different times during the emerse phase in the igapó (**a**) and várzea (**b**)

examples of root branching patterns identified for tree species in the igapó and várzea forests, respectively. The 'relative numbers of short roots' were considerably higher in the igapó than in the várzea plots. While many of the igapó tree species produced exceptionally high 'relative numbers of short roots' (up to 19 short roots cm^{-1}) in the different plots, none of such extreme root branching patterns were established by várzea tree species. In contrast, the 'relative total root lengths' were significantly higher in the várzea forest. Typical of the igapó forest was the species *Cynometra spruceana* (Fig. 8.5), while *Labatia glomerata* was prevalent in the várzea (Fig. 8.6).

Variations in inundation periods did generally not impact on root branching types in both forests. The tree species *Triplaris surinamensis*, which was explicitly

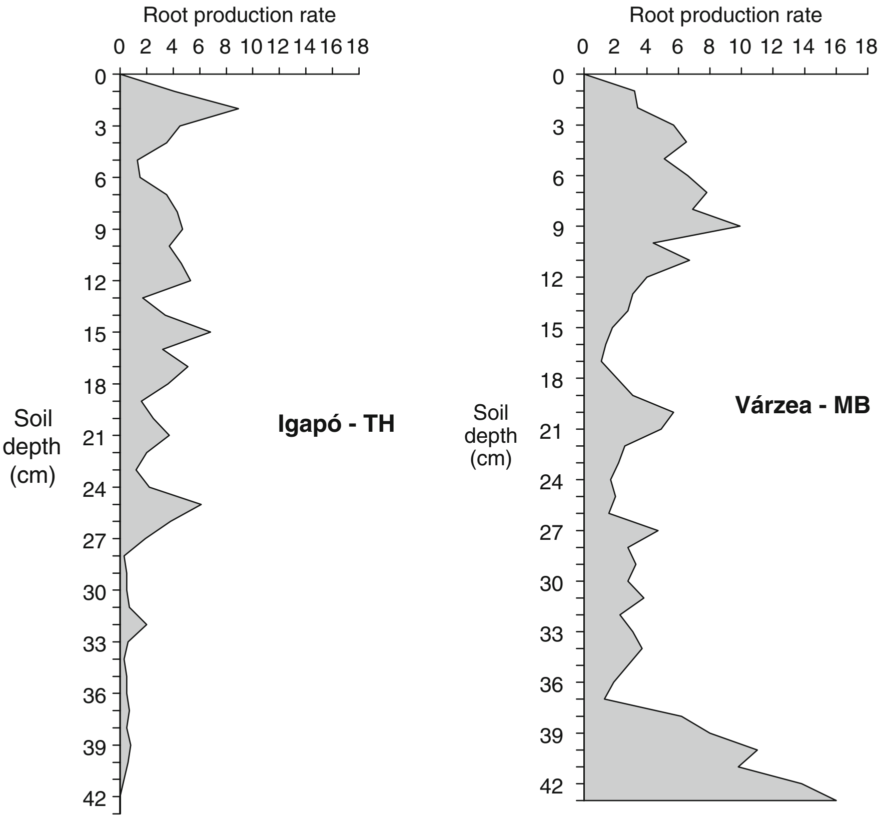


Fig. 8.4 Fine root production rates (number of newly formed roots/4 cm^2/5 months) during the emerse phase in the plots TH (igapó) and MB (várzea)

examined using two individual trees at different plot locations in the várzea forest (MA and MB), developed a fairly constant geometry of its root system regardless of differing inundation lengths.

Two of the investigated tree species were common to both forests: *Pterocarpus amazonum* resided in the highest-elevated plots (MA and TA) and *Macrolobium acaciaefolium* was present in the lowest-elevated plots (TN and MH). Both species developed the same basic type of root pattern in both forests (Figs. 8.5 and 8.6). However, they differed considerably in their relative total length, which was lower in the igapó than in the várzea (*P. amazonum* 31.4 and 59.2, *M. acaciaefolium* 44.6 and 52.2, respectively). Both species developed a higher number of short roots in the Igapó, the value for *M. acaciaefolium* being the highest one for all investigated root systems (*P. amazonum* 9.6 and 5.5, *M. acaciaefolium* 18.8 and 5.1, respectively).

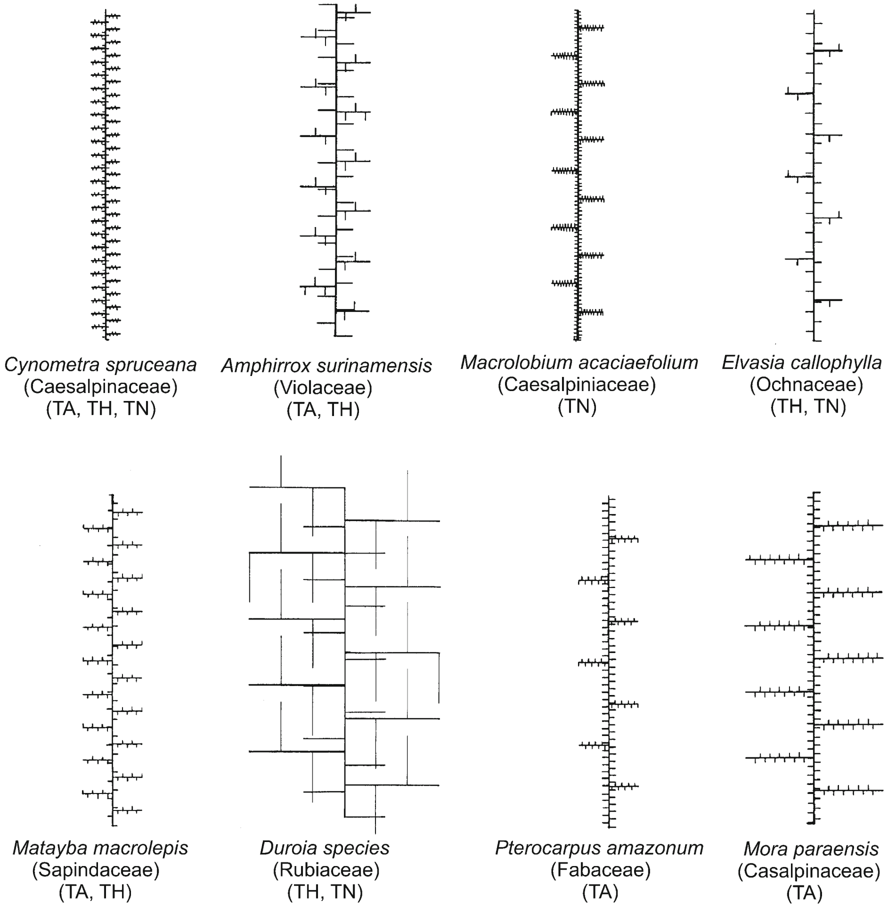
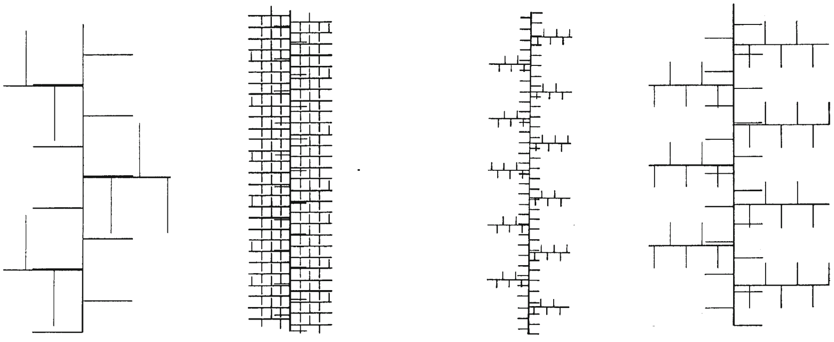


Fig. 8.5 Schematic depictions of root branching patterns in the igapó

8.4.5 Mycorrhizal Associations

In the igapó forest, 89% of the 44 investigated tree species were infected by AM-fungi, 2% were associated with EM, and 9% were symbiotically inactive. The ectomycorrhizal infection was diagnosed on the commonly occurring tree species *Aldina latifolia* (Fabaceae) (31% in TA, 6% in TH). These roots were almost inseparably attached to litter fragments (Fig. 8.7), a phenomenon not identified for AM roots. The non-mycorrhizal roots, detected only in the medium (TH) and lowest elevated (TN) plots, were characterised by little branching and relatively large root diameters (0.8–1.3 mm). The 26 tree species tested in the várzea forest predominantly associated with the AM-type (88%). The remainder of the várzea species were symbiotically inactive. One non-mycorrhizal tree species was present in each of the várzea plots; in the long inundated plot (MH) it

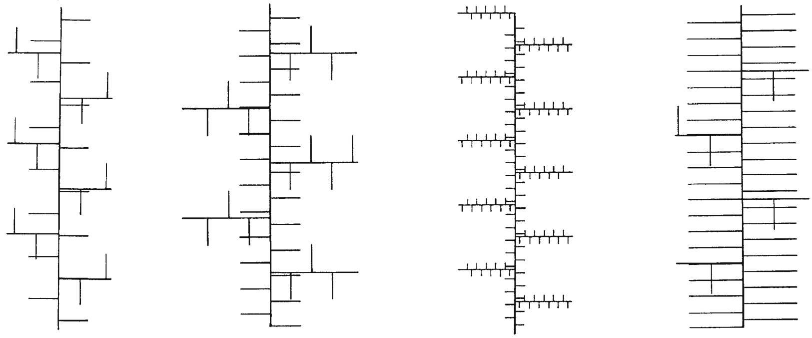


Labatia glomerata (Sapotaceae) (MA, MB, MH)

Triplaris surinamensis (Polygonaceae) (MA, MB)

Macrolobium acaciaefolium (Caesalpiniaceae) (MA, MH)

Gustavia augusta (Lecythidaceae) (MA)



Simaba guianensis (Simaroubaceae) (MH)

Alchornea schomburgkii (Eurphorbiaceae) (MH)

Pterocarpus amazonum (Fabaceae) (MA)

Pseudobombax munguba (Bombacaceae) (MA, MB,MH)

Fig. 8.6 Schematic depictions of root branching patterns in the várzea

was the frequently occurring species *Crataeva benthamii*. None of the examined várzea roots were infected by EM.

8.5 Discussion and Conclusions

The fine root systems of the várzea and igapó forests differed profoundly in their amount, depth distribution, production rates and root branching patterns. This points to different foraging strategies employed by tree roots to cope with conditions of low soil fertility. Mechanisms involved include an increase in root density within localised nutrient-rich soil patches (Blair and Perfecto 2001). The formation of superficial root mats has, for example, often been observed within organic-rich soil layers of tropical forests (Laclau et al. 2004). The proportion of fine roots may

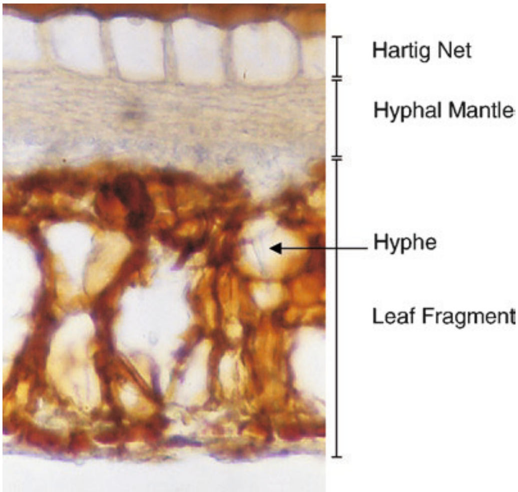


Fig. 8.7 Ectomycorrhizal symbiosis with *Aldina latifolia* (igapó)

further be enhanced, since fine roots are generally better suited to absorb nutrients than their thicker counterparts (Blair and Perfecto 2001).

While a lower above-ground tree biomass was observed in the igapó relative to the várzea forest, higher fine root concentrations were detected in the igapó topsoils (Fig. 8.2). This is in accordance with previous studies conducted on nutrient-poor tropical as well as temperate-zone forests (Meyer 1967; Scherfose 1990; Priess et al. 1999), since infertile soil conditions generally impose a selective pressure for maximization of the absorptive root surface area (Paz 2003).

Ecosystem stability under infertile soil conditions may be achieved through short circuited nutrient cycles (Vitousek 1982; Anderson and Swift 1983; Sayer et al. 2006). This nutrient cycling is often closely linked to the soil organic matter pool, which upon decomposition contributes greatly to the plant-available nutrient contents (Vitousek 1982). Leaching losses of nutrients may subsequently be diminished by means of an efficient root capturing system. Rapid ion uptake may further circumvent nutrient losses via leaching or fixation into plant-unavailable chemical forms. Such nutrient conserving mechanism is crucial for ecosystem stability in the igapó region, while short circuited nutrient cycling is not a matter of survival for the nutrient-rich várzea forest.

The vertical distribution of fine roots generally followed trends in soil fertility. Although highest nutrient concentrations corresponded to the litter layers of both forests, their availability was less relative to the underlying organic-rich soil horizons. This was due to lower mineralization rates, as indicated by higher C/N ratios, in the litter layers (Table 8.1). The preferred rooting depth was therefore associated with the organic-rich Ahh-horizons of both forests. Limited nutrient availability subsequently restricted the proliferation of fine roots into the lower soil mineral layers of the igapó forest (Fig. 8.3). In contrast, the fine root system of the nutrient-rich várzea forest extended to 43 cm soil depth (Fig. 8.3). The second peak in fine root concentration at 38–43 cm soil depth in the várzea forest did not coincide with an increased nutrient supply (Table 8.1), but was rather caused by a change in soil texture from loamy clay to silty sand (data not shown), the latter being more easily penetrated by roots.

Despite lower root production rates (Fig. 8.4), the fine root length densities of both dead and living roots were higher in the igapó than in the várzea forest (Fig. 8.2). The elevated concentration of living roots pointed to a higher root longevity in the igapó forest, which was interpreted as an adaptation to low nutrient supply by means of an efficient use of energy. Similarly, long life spans of root systems have often been documented in nutrient-poor temporal forest ecosystems (Chapin and van Cleve 1981; Nadelhoffer et al. 1985; Trappe and Fogel 1977). The higher concentrations of dead roots in the igapó as compared to the várzea forest were caused by slower litter decomposition. It is noteworthy that the decomposition coefficients in the igapó were approximately half of those in the várzea (Meyer 1991). In contrast, the lower root concentrations, in spite of higher production rates, resulted from faster root turnover rates in the várzea relative to the igapó forest.

An increase in root length density with increasing inundation length was prominent in the igapó forest (Fig. 8.2). Prolonged flooding apparently favoured the formation of higher root concentrations to compensate for short optimal growth conditions. The zoning of vegetation along the catena suggested the selective establishment of certain tree species (Table 8.2), with differing root production abilities, according to inundation length.

The detection of a constant amount of living roots between the start and end of the emerse phase (Fig. 8.2) was interpreted as tolerance mechanism to flooding conditions. Such tolerance is generally of physiological nature and stems from the change of aerobic to anaerobic metabolism under waterlogged soil conditions (Schlüter 1989; Haase and Rätsch 2010).

The root systems in the igapó forest exhibited a higher geometric diversity than those of the várzea forest. Extremely high numbers of short roots were frequently detected in the igapó forest (Fig. 8.5), while the relative total lengths of várzea tree roots were significantly higher (Fig. 8.6). Since intensive branching allows for a more thorough exploitation of the soil nutrient reserves, igapó tree roots were better equipped to retain nutrients within the ecosystem. In addition, thinly-spaced branching enables roots to better influence the nearest rhizosphere chemically than can widely-spaced root systems, since root exudates are more diluted in the rhizosphere of the latter branching type (Gardner et al. 1983a,b; Fischer et al. 1989).

It should further be noted that the physiological root diversity was greater in the igapó forest. The totality of the different root branching types in the igapó forest thus, allowed for a more complete foraging of the soil nutrient pool. For instance, soil micro-sites unoccupied by highly branched root systems may be sought out by tree roots displaying other root branching types, such as the *Duroia* type (Fig. 8.5).

The fine root branching types identified for both forests were most probably genetically determined, since the general branching types remained similar for tree species common to both forests. Slight modifications of the branching types, however, resulted from differences in the soil nutrient regimes.

Most tree species associated with AM in both forests. The majority of AM symbioses with tropical trees has been documented in many studies (Redhead 1980; Janos 1983; da Silvia et al. 2001), however, some tropical trees may be infected by EM (Malloch et al. 1980; Janos 1983; Alexander and Höberg 1986; Högberg and Piearce 1986; Alexander 1989). In tropical forests located on infertile soils, EM may be more abundant than AM by virtue of their better nutrient scavenging abilities (Janos 1983). The proposal by Singer and Araujo (1986) that EM associate with the dominant tree species of the igapó forest was, however, not confirmed by this study. Only one tree species, *Aldina latifola*, was diagnosed to form ectomycorrhizal associations and was with a total of 11 individuals on the TA and TH plots not the principal tree species. While Singer and Araujo (1986) also detected EM on *Aldina latifolia*, they further documented ectomycorrhizal associations with *Swartzia polyphylla*. The latter tree species was in this study AM diagnosed. Likewise, Moyersoen et al. (2001) tested the hypothesis that EM may be more abundant than AM in tropical heath forests. In their study conducted on a Venezuelan caatinga, the most dominant tree species associated, however, with AM.

The co-occurrence of EM and AM tree species may be attributed to the occupation of different soil niches (Moyersoen et al. 2001). For instance, EM may have a selective advantage of accessing phosphorus from organic sources (Alexander 1989; Moyersoen et al. 2001), such as by secretion of chelators which increase P solubility (Cromack et al. 1979; Szaniszlo et al. 1981). The finding that EM were almost inseparably attached to litter fragments (Fig. 8.7) suggests the extraction of organically derived phosphorus.

Investigation of fine root length densities, branching systems and the production rates of fine roots in the nutrient-poor igapó as compared to the nutrient-rich várzea forest, lead to the following conclusions. The igapó has three strategies to meet the low nutrient reserves of its site:

- Firstly, it develops higher concentrations of fine roots in the soil relative to the várzea forest. This results in shorter pathways for nutrient uptake by roots.
- Secondly, the higher root longevity of igapó roots allows for an economic use of assimilates.
- Thirdly, the more diversified branching systems of fine roots result in a more thorough exploration of the soil nutrient reserves.

The proposal by Singer and Araujo (1986) that the igapó forest should be viewed as an ectotrophic forest could not be confirmed by this study, as most of the tree species were symbiotically associated with the AM-type in both forests.

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