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Roots of pioneer trees in Amazonian rain forest

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Abstract

On low fluvial terraces of the Caquetá River, Araracuara region, Colombia, tree root systems have been examined with regard to their structure, underground stratification and biomass distribution. Excavations of skeleton roots and microscopic observation of terminal fine roots included ten species belonging to the *Cecropia*, *Vismia*, *Miconia*, *Goupia*, *Clathrotropis* and *Brosimum* genera. Roots of particular species varied in the external features of their periderm and structure of freshly cut slash. Coarse skeleton roots differed in the shape and position of the plagiotropic branches and positively geotropic taproots or sinkers. None of the observed species could be identified as shallow-rooted tree, in spite of the general fine root concentration in the upper soil horizon. In the two seasons of study, the terminal roots displayed prevalingly secondary anatomical structure and did not maintain much primary anatomical tissues in their apices. Neither ectomycorrhizas nor endomycorrhizas were detected in the samples. In a set of regeneration stages the amount of tree roots linearly increased with the age of the growths, however, fine roots below 2 mm thickness shared between 80 to 90% of all roots in the upper 20 cm layer of all sample plots. In an old-growth forest, the total tree root biomass amounted 39 t/ha, thus being comparable with the underground biomass observed in similar tropical forests.

key words: tree roots – tropical rain forest – Colombian Amazonia

Introduction

The summaries dealing with the structure of tropical rain forests (HALLÉ et al. 1978: 71-73; GOLLEY 1983: 23; LONGMAN & JENÍK 1987: 166-170; RICHARDS 1996) refer to the scarcity of data with regard to tree roots. Many observations refer to aerial roots, such as stilt roots, spine roots, buttresses and pneumorhizae (JENÍK 1993) whose visible forms frequently dominate the illustrations of tropical forest interior. Underground organs of tropical trees, however, are little known organs and their structure and distribution in soil horizons remain rather obscure. In agreement with the soil stratification, general shallow-rootedness of tropical trees is frequently assumed, though contradictory observations have also been recorded (MENSAH & JENÍK 1968). However, shallow humus horizon and corresponding flat tree root systems cannot be taken for granted, and scattered observations confirm an array of adaptations and diversified underground organs for emergency water supply and nutrition in rain forest soils (JENÍK 1976, KAHN 1977, OLDEMAN 1990, BRUENIG 1996). Layering of underground biomass in humid tropical forests is little understood (JENÍK 1971) but pioneer data are available (KLINGE 1973a,b, 1976; JORDAN & ESCALANTE 1980; SANFORD & CUEVAS 1996; CAIRNS et al. 1997).

Shortage of data referring to root morphology is due to inherent methodical difficulties of “rhizology” and outstanding species diversity in tropical trees. In contrast to the systematically described architecture of aboveground organs (HALLÉ et al. 1978), tentative classifications of tropical tree root systems (JENÍK 1976, KAHN 1977, OLDEMAN 1990) did

not cover, so far, the variety of structures and growth processes expected in tropical forests of the Neotropical realm. Data are particularly missing with regard to the behaviour of underground organs during successional events in natural clearings and “eco-units” (sensu OLDEMAN 1990), and after the slash-and-burn operations performed in tropical forests (SALDARRIAGA 1994).

Study area

North-western Amazonian rain forests belong to the tree species-richest biomes of the world (DUIVENVOORDEN & LIPS 1998, GENTRY 1996, SAENZ 1997). This diversity is explained by a particular coincidence of high rates of speciation in native families and genera, with temporal isolation and linkage of forest refuges during the peaks of glacial periods (HAFFER 1982; PRANCE 1983). Recent research activity of both botanists and foresters in this region is being enhanced by continual interest in sustainable management of these species-rich tropical forests.

Field work of our study was conducted in the vicinity of Araracuara, a town situated on the Caquetá River (named Japurá on the Brazil's territory) in the Colombian Amazon (0° 37' S and 72° 27' W). This river is by far the largest river in this area, and the only one with a catchment in the Andes. With an annual mean air temperature of 25.7 °C, and annual total precipitation of 3059 mm (DUIVENVOORDEN & LIPS 1995) this region belongs to equatorial, humid (Afi) climate type according to Köppen's classification (CRITCHFIELD 1966). The wettest month is May with 400 mm of rain; average precipitation of the other months is circa 250 mm, but in January and February the monthly rainfall drops to 150 mm only.

The average altitude is about 160 m above sea-level. Two non-flooded fluvial terrace systems of the Caquetá River were described by Van der HAMMEN et al. (1992): the low terraces and high terraces, at 10–15 and 25–55 m above the low water level, respectively. In terms of Amazonian ecology these terraces belong to the "terra firma" (PRANCE 1979). The low terraces bordering the alluvial plain are characterised by oval ground plan stretched along the river, and by almost flat surface; they were created in the Middle Pleniglacial, 65,000–26,000 years BP.

Soils of the study area were extensively described by DUIVENVOORDEN & LIPS (1993). They are basically subdivided according to their (1) topographical position in the floodplain or uplands (the latter area is not flooded by river water, but its soils are sometimes poorly drained and inundated due to high phreatic water levels), (2) drainage (waterlogged "swamp" soils versus well-drained soils), and (3) features of podzolization (i.e., "white sand" soils, generally waterlogged, covering less than about 5 percent of the uplands, and confined to sandstone outcrops, and non-dissected high terraces of the Caquetá River and the Tertiary sedimentary plain). Moderately fertile soils, with base saturation above 50 % are found only in the recurrently inundated floodplain. In less frequently inundated parts of the floodplain and over the upland area, soils are strongly leached and moderately to extremely poor in nutrients. Two groups of well-drained upland soils have been recognised by LIPS & DUIVENVOORDEN (1996): (1) Soils classified as Alisol and Acrisol (according to FAO-UNESCO system, 1971–1981) develop mostly on sediments of Andean origin on the low terraces, and on sediments of the Tertiary Pebas formation; they are characterised by fine textured reddish B horizons, and contain relatively high concentrations of major nutrient. (2) Soils classified as Acrisol and Ferralsol are mostly developed on the Guyana-Shield-derived medium to coarse textured Tertiary deposits or on Palaeozoic sandstone outcrops. These soils are characterised by medium textured, yellowish B horizons within 100 cm depth, and show very low total major nutrient concentrations.

In terms of HOLDRIDGE (1987) the pertinent zonal biome of the study area has been classified as tropical moist forest. On well-drained parts of the low river terraces DUIVENVOORDEN & LIPS (1995) described the *Goupia glabra*–*Clathrotropis macrocarpa*-

Type whose 26 m height and about 350 t/ ha aboveground biomass correspond to a high forest structural type (according to OVERMAN et al. 1992). Similar forests are found also on well drained soils of the high terraces and on the adjacent Tertiary sedimentary plain.

Archaeological research estimated human settlement of the Amazon Basin, including the Araracuara region, for about 5000 years (ANDRADE et al. 1992). Current human population density is far below 0.2 person km⁻² and traditional indigenous agricultural system seldom disturbed the prevalingly virgin stands. Traditional farming technique in the Colombian Amazon is a kind of shifting cultivation, but its destructive impact on the closed-canopy forest land is moderated by planted useful trees which are left after the abandonment of the plots. People living along the Caquetá River preferably use well drained soils on the low terraces. At the beginning of the „dry“ season trees of the primary forest are girdled on plots 0.2 – 2 ha in size, then left to dry and burnt. Soon after burning, the cultivation and planting follow of preferential *Manihot*, *Erythroxylum* or *Capsicum* species, but as many as 30 different crops are cultivated in the area (Van der HAMMEN et al. 1992). After two years the „chagra“ is gradually abandoned and secondary succession takes place. Patches shortly used for agriculture are readily invaded by pioneer trees and forbs and trees of the primary forest successively return. While the changes of visible aboveground structures in the course of secondary succession have been described (SALDARRIAGA 1994, VESTER & CLEEF 1997), little is known about the hidden structure and layering of the root systems of the invading woody *r*-strategists, such as the various species of the *Cecropiaceae*, *Guttiferae*, *Melastomataceae* and *Moraceae*. In view of the increasing area of secondary forests, the information gap about roots is retarding the adoption of rational silviculture and sustainable management in the Colombian Amazon.

Materials and methods

In two periods of 1997 (from March to May, and from October to November) rhizological studies in the Araracuara region have been conducted as a follow-up project of earlier secondary forest investigations by HEES & MEEL (1993), VESTER & SALDARRIAGA (1993), DUIVENVOORDEN & LIPS, (1995), OVERMAN et al. (1990) and VESTER (1997). Observations took place in age-differentiated plots, situated on well-drained soils of the low terraces of the Caquetá River, in stands developed on former agricultural plots and in the nearby primary forest. Four regrowth stages (locally called 'rastros') developed after 6, 14, 18 and 37 years following the slash-and-burn operations were chosen and described with regard to their habitat features, species composition, architectural age of individuals, and details of preceding agricultural treatment (PAVLIŠ 1998).

The following frequent and most dominant tree species of different diameter breast height (d.b.h.) have been selected for detailed rhizological observation: *Cecropia distachya* Huber, *C. ficifolia* Snethl, *C. sciadophylla* Mart.; *Vismia glaziovii* Ruhland, *V. japurensis* Reichardt, *V. macrophylla* Kuntze; *Miconia poeppigii* Triana; *Goupia glabra* Aublet; *Clathrotropis macrocarpa* Ducke; *Brosimum rubescens* Taub. and *B. utile* (Ducke) C.C. Berg.

“Eco-morphological” comparative method based on careful excavation and identification of root forms (JENÍK & SEN 1964; SUTTON & TINUS 1983; OLDEMAN 1990) and methods for assessment of root biomass in pertinent soil blocks (BÖHM 1979) have been applied. Emphasis has been made on (1) assessment of morphological and histological traits of individual coarse and fine roots in selected tree species, (2) detection of characteristic root branching in trees of various age, with regard to soil horizon and depth, and (3) estimate of total root biomass at various soil depth in age-differentiated stands. Individual roots and vertical structure of their systems were assessed on smooth walls of the soil pits excavated in the form of either a wedge situated at the tree base between two plagiotropic skeleton roots, or a straight ditch across the broader surroundings of the selected tree. The horizontal

arrangement of skeleton and fine roots was observed after successive removal of litter and fermentation/humus soil. Drawings, photographs and samples stored in FAA of the exposed root systems have been subsequently analysed and described in terms of JENÍK (1973) and SUTTON & TINUS (1983).

Root stratification was ascertained at random positions outside the large skeleton roots, down to 50 cm by (1) 15 x 15 x 10 cm rectangular blocks cut from the soil layers and (2) cores sampled by a root auger. As mentioned below, in the shallow litter stratum of Ali-Acrisols roots scarcely occur; similarly - below 50 cm depth the presence of roots was next to negligible. Separation of roots by washing was performed in the forest, further manipulation was carried out in the field laboratory. Roots were divided in 3 categories according to their diameter: <2 mm, 2 to 5 mm, and > 5 mm. Dead and live roots were not distinguished, since fine roots readily disintegrate and cause a minor error. The dry biomass was assessed after 12 hours of drying at 110 °C.

The soil horizons described in Table 1 were distinguished according to FAO-UNESCO classification. Soil samples were collected by means of an Eijkelkamp soil auger sized 8 cm in diameter. Analyses of soil texture and nutrients have been performed by standard methods used in the Laboratory of Nature and Landscape Preservation Agency in Brno: (1) content of accessible soil elements by Melich II method, (2) content of clay/argillaceous particles (by the pipette methodology), (3) content of potassium by flame photometry, (4) percentage of phosphorus colorimetrically, (5) calcium and magnesium content by atomic absorption spectrometry.

Results and discussion

Structure of roots and root systems

Aerial stilt roots of various models (JENÍK 1973) have been encountered in trees of the *Apocynaceae*, *Cecropiaceae*, *Guttiferae* (*Clusia* sp.), *Lauraceae*, *Melastomataceae* (*Miconia* sp.), *Moraceae*, and *Palmae* (*Iriartea* sp., *Socratea* sp.). None of these aerial roots develop by successive raising of the tree, as assumed by KUNKEL (1965), but all successively develop by growth of adventitious organs on the bole. Remarkably, except for the observation of aerial roots in *Cecropia* (HERRERA 1989, LAMOTTE 1992, ATGER & EDELIN 1994) details about the underground roots of the above named pioneer trees are missing.

***Cecropia distachya*, *C. ficifolia* and *C. sciadophylla* (Cecropiaceae)**

(9 specimens with d.b.h. > 5 cm excavated, Figs.1 and 2)

In the study area, there was no essential difference in the root structure of these 3 pioneer species. Their root system is characteristic by the presence of distinct aerial stilt roots. They are all adventitious organs which develop on young saplings and later emerge at the higher level of near lenticels of the stem. These organs create an arch-like structure and become rooted in the soil at a distance of even more than 1 metre (Fig.1). They successively acquire great part of radial growth and their total volume surpasses the volume of the original stem near the ground, however, on the contrary d.b.h. increment does not slow alike in HERRERA (1989) findings for the Cuban *Cecropia* species. Stilt roots reinforce the anchorage of trees which could be easily approved in specimens which fell down after the removal of these organs. Upon reaching the ground surface, several aerial roots (2 to 4) spread close to the ground far from the stem and beyond the projection of the crown (Fig.2). Some of these "invasive" roots reached a 25 m length. They do not branch except at the end where they are terminated by a cluster of fine roots. Young invasive roots show up early in

the stage of tree seedlings whose taproot stops growing and remains dwarfed or can change into invasive root, too.

Underground root skeleton are marked by grey-ecru colour of the periderm and pink-red colour of their slash. Their vertical structure lacks positively geotropic roots. Even the tap root does not develop into the depth, and remains either dwarfed or curved into plagiotropic direction. Root grafts within the same tree and between the neighbouring specimens are a common feature in *Cecropia* species. Fine roots occupy the upper 0.1 m layer and clusters of terminal roots appear far beyond the crown projection. By means of invasive roots the cecropias frequently penetrate into the area of thick roots of neighbouring *Miconia poeppigii* and *Clusia* trees. A pronounced dimorphism of brachyrhizas and macrorhizas (sensu JENÍK & SEN 1964) was not detected.

Vismia glaziovii, *V. japurensis* and *V. macrophylla* (Guttiferae)
(8 specimens with d.b.h. > 5 cm excavated, Figs.3 and 4)

In the study area on low fluvial terraces, only less essential difference have been observed in the root structure of the 3 above named species. Older roots display red-brown peeling strips of periderm and orange exudates upon slashing - both features similar to those of the bark of the trunk (GENTRY 1996). Since the seedling stage of these species there occur a pattern of radially stretched roots but in older specimens a few plagiotropic skeleton roots dominate the system (Fig.3). Juvenile taproots hardly penetrate below the depth of 0.3 m, but in mature trees they can reach down to 1m. Positively geotropic roots penetrate deeper in *V. macrophylla* than in *Vismia japurensis* which invests more energy into the formation of plagiotropic skeleton roots. These skeleton roots (Fig. 4) frequently expand more than 5 meters outside the crown projection, which may be the response to roots of palms (*Astrocaryum sciophyllum*, *Attalea racemosa*) occasionally occupying the base of *Vismia* trees. The root system in *Vismia* species is generally poor in branching and is characterised by geotropic laterals growing from the coarse plagiotropic skeleton roots. Toward the soil surface, the same skeleton roots develop numerous thin lateral branches bearing the system of slender brachyrhizas. Presence of typical macrorhizas was observed neither by naked eye and lens, nor by microscopic study of the root specimens. In the excavated trees maximum root concentration was in the upper 0.2 m.

Miconia poeppigii (Melastomataceae)
(7 specimens with d.b.h. from 5 up-to 30 cm excavated, Figs.5 and 6)

Skeleton roots of this late pioneer species generally possess smooth grey-brown bark and slash becoming blackish after a while. Early from the seedling stage the root system develops the heart root type (sensu "heart" root system of European foresters) featured by both horizontally and transversally growing branches (Fig.5). Five or more coarse plagiotropic skeleton roots radiate from the stem and create distinct root spurs at their proximal part (Fig.6). Older specimens often display thickened plagiotropic roots which spread on the soil surface and at their distal end (even after 7 m) curve down into the soil and serve as sinkers improving the mechanical stability of the tree. Less pronounced taproot (<5 cm in diameter) penetrates down to 1.2 m depth. From the sapling stage there occurs a dense fine root network around the proximal root skeleton. In comparison with above described species, *Miconia poeppigii* forms denser root mat of brachyrhizas growing in the humus horizon, but strictly superficial horizontal roots are less frequent. Center of rooting lays underneath the crown shade, although superficial horizontal roots reach even 7 m distance from the stem. Distal brachyrhizas are concentrated mainly in the upper 0.3 m of the soil. Symbiotic fungi were found neither on the surface nor inside the primary cortex of the brachyrhizas.

Goupia glabra (Celastraceae)

(2 specimens with d.b.h. > 20 cm excavated, Figs.7 and 8)

This climax species possesses robust stump base and adjacent root spurs. Old roots are covered by ridged periderm resembling the stem bark. Typical plagiotropic branching was detected since young seedlings stage. Similarly, in the two mature specimens the root skeleton is situated in the upper layer of the soil profile and consists of thick plagiotropic and positively geotropic roots (Fig. 7). Plagiotropic roots spread far beyond the crown projection (Fig. 8). Larger plagiotropic branches bear 3-4 sinkers which extend down to a depth of 0.7 m in the proximal area of the system. These sinkers keep branching even at a greater depth. Plagiotropic skeleton roots distributed in the upper horizon are regularly branched along their length and there are abundant clusters of terminal brachyrhizas, bearing clouds of end-roots in the upper 0.2 m soil horizon. On the surface and within the tissues of primary roots no symbiotic fungi were observed.

Clathrotropis macrocarpa (Leguminosae/Papilionoideae)

(3 specimens with d.b.h. > 15 cm excavated, Figs.9 and 10)

This climax tree is marked by the yellow periderm and slash of thin roots and by their aroma of fresh cucumbers. Deeply penetrating tap-root richly branched in its upper section dominates the root system of young saplings. Thin laterals bear numerous nodules of N₂ fixing *Rhizobia*. With the increasing age a dominant tap-root prevails (1.3 m max. depth) and becomes ramified into (1) few horizontally oriented skeleton roots and (2) thinner transversally penetrating roots. The upper plagiotropic roots gradually change into thickened skeleton roots important for the mechanical stability. They stretch far in the distal direction (observed maximum 11 m) and densely branch into fine roots with sparse root nodules. Dense concentration of roots appear in the upper 30 cm. Microscopic slides did not confirm occurrence of symbiotic fungi. Remarkable parallel growth (up-to 4m) of *Clathrotropis* roots with roots of the neighbouring *Miconia poeppigii* and *Goupia glabra* was observed.

Brosimum rubescens and *B. utile* (Moraceae)

(2 specimens with d.b.h. > 20 cm excavated, Fig. 11)

Roots of this climax species have bright red periderm and the coarse branches are marked by rings of lenticels. In the juvenile stage a slender taproot was observed, but with the increasing age the roots system develops a great number of the transversal and vertical skeleton roots creating a heart-root system similar to that of European beech. Vigorous roots penetrate deeper than those of *Miconia poeppigii*. A bunch of sinkers penetrates below the maximum observed in other tree species (our observations indicate 1.5 m depth). Coarse plagiotropic skeleton roots spread in the wide surroundings of the tree and create a superficial mat of bright red-yellow fine roots. Thick concentration of roots occupies a space covering an area of 20 to 30 m in diameter. The fine roots with numerous brachyrhizae readily occupy half-rotten stumps, fallen limbs and trunks. Rich ramification of *Brosimum* roots on the bank of a stream suggested an affinity to open water.

Root/soil stratification and root biomass

The texture of the soils examined plots in the Araracuara region varied between silt loam and loamy sand in the upper horizon (A), changing to clay loam in the lower horizon (Bt), in some places to silty clay and others silt loam, showing an increase in clay from the A to the Bt horizon. In the excavated pits, the profiles showed an accumulation of iron (Fe) but the intensity and depth varied, indicating differences in drainage. In the same area, leaf litter fall was found by LIPS & DUIVENVOORDEN (1996) poor in Ca, Mg, K and P nutrients, comparably to oligotrophic central Amazonian upland forest (HERRERA et al. 1978). VESTER

& CLEEF (1997) also found these soils poor in nutrients, with a cation exchange capacity of 8.5 me/100 g in the 5–60 cm column. The base saturation is about 7 % at this depth.

Charcoal bits together with an increased content of phosphorus (up to 15 ppm in samples taken from the upper 30 cm layer) are currently encountered in soil of the primary forest, suggesting that humans have occupied this site many centuries ago. In order to estimate the recent human influence, soil was sampled by means of an auger down to 100 cm depth in two regeneration stages (6-year-old regrowth, 18-year-old regrowth) and primary forest; features of litter analysed in detail by LIPS & DUIVENVOORDEN (1996) were not studied.

In Table 1 contents of nutrients and clay fractions of the analyses are given according to the genetical horizons specified after FAO-UNESCO classification. Due to differences in the stratification no direct counterparts could be compared, but no substantial differences were ascertained in the nutrient content of soils in the chosen age-differentiated plots. This can be explained either by a less drastic degradation of soils by local traditional farming and by a rather fast uptake of nutrients by roots, and/or by recovery of the modest fertility through decomposing litter and root biomass.

In order to study the effects of farming on the rhizosphere, underground biomass was examined in 7 age-differentiated plots: old grassy plot, traditional agricultural field, 4 regeneration stages (regrowths) developed 6, 18, 25, 37 years after their abandonment by indigenous farmers, and old-growth primary forest. At five randomly situated points for each plot, soil blocks (0-30 cm) and columns (from 30 down to 50 cm) were withdrawn. Results of the fresh and dry biomass dynamics (Fig. 12) suggest a linear increase in the totals of all size categories of roots.

Comparing the total root dry biomass of 39.24 tons in the old-growth forest on the low terraces of the Caquetá River with other tropical rain forests, we find 10 to 61 t/ha (i.e. 1000 - 6100 g/m²); e.g. OGAWA et al. (1961) state for Thailand 33 t/ha, GOLLEY et al. (1975) summarised 40 t/ha for Panama, KLINGE (1976) estimated 45 t/ha for the Manaus region and SANFORD (1989) count 61 t/ha in Venezuela. The value of root dry biomass per hectare in the studied primary forest thus appears comparable to those in other areas.

In the forests on the well-drained uplands of the Araracuara region the only available data of DUIVENVOORDEN & LIPS (1995) refer to fresh weight. They estimated the total fresh weight of fine roots up to 5 mm in thickness in the range between 49 t and 52.4 t/ha, and related their differences to various soil types. Soils of the Ali-Acrisol group with a shallow humus layer contained few fine roots, whereas soils of the Acri-Ferralsol group with relatively thick humus layer were inhabited by a dense network of fine root. Taking into account that the fresh weight amounted in our sampling about a double of the dry weight biomass, the amount of small roots given by the above authors is comparable with our results.

Understandably stratification of the underground biomass of roots of various size categories can better reflect the differences between regeneration stages (regrowths) and old-growth rain forest. This vertical arrangement is affected also by the structure of root systems of individual species (see Figs. 1 to 11), but quantitative assessment of the biomass could not be readily identified - in spite that root surface tissue might enable to distinguish between various species. Stratification and decline of root biomass connected with depth is summarised in Fig. 13.

In all sample plots fine roots below 2 mm thickness represent between 80 to 90 % of all roots in the upper 20 cm layer (Table 2), however, none of these plots displayed a root mat created by more or less loosely stretched roots in the litter, above the mineral-organic horizon. Remarkably in the grassy plot and abandoned field the fine roots of graminoid and woody species remain clearly concentrated in the upper 10 cm layer (Fig. 13A,B). In the primary forest proportion of thicker skeleton roots increases to 50 % (Table 3) but there are 78% of fine roots under 2 mm in size in the upper 20 cm layer (Table 2) and fine roots still

create about 28 % of this category in the uppermost layer (Fig. 13G). In the 25 and 37-year-old regrowths higher representation of thicker roots in the upper layer reflects the presence of plagiotropic skeleton roots (Fig. 13 E,F); some of these roots stretch far beyond the crown projection and reach up-to 30 meters distance from the foot of the trunks.

Roots of trees are opportunistic organs and their maximum penetration depends both on hereditary features of species (see above) and soil properties. Availability of nutrients and aeration in the soil profile essentially induce the depth of tap and sinker roots. Their increasing presence is obvious with the increasing age of the examined forests (Fig. 13D-G). Maximum vertical root penetration observed in the clayey soil reached 1.5 meters, but occasionally deeper roots can be expected.

Morphological description of the tree roots and their stratification in Araracuara region bring about the long-lasting issue of the shallow-rootedness in tropical rain forest (SCHNELL 1950, JENÍK 1971, MABBERLEY 1992). In discussion of this problem, two terms are rather ambivalently used: root mat and root plate. Unlike MABBERLY's usage referring to the whole system of plagiotropic roots, we use the term root mat in the sense of a superficial layer of fine roots and slender plagiotropic skeleton roots which stretch above the consolidated organic-mineral layer, and are exposed to air on their upper surface. Tree species examined on the lower river terraces of the Caquetá River do not develop that kind of roots, but similar organs are represented in old-growth rain forest on the upper terraces. Root plate refer to shallow-situated system of plagiotropic roots with negligible occurrence of weak sinkers, which occasionally may get exposed in windfalls; none of the studied species developed this system. Windfalls do exist on the lower terrace of the Caquetá, but the exposed root systems possess bulky tap or sinker roots torn out of the lower layers of soil. In the traditional notion of the foresters the heartroot and taproot systems are prevailing.

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Table 1. - Soil properties in three age-differentiated plots on the low terraces of the Caquetá river

6-year-old regrowth

<i>horizon</i>	unit	Ah (0-10cm)	A (10-22 cm)	AB (22-40 cm)	Bt ₁ (40-60 cm)	Bt ₂ (60-80 cm)	Bt _{cs} (below 80 cm)
<i>characteristics</i>							
pH/H ₂ O	-	3.8	3.9	4.5	4.7	4.6	4.7
C-ox	%	3.73	1.58	0.42	0.41	0.53	0.28
N	%	0.20	0.11	0.05	0.05	0.04	0.06
Ca	mg/kg	300 (?)	< 83	< 83	< 83	< 83	< 83
K	mg/kg	16	10	7	11	10	12
Mg	mg/kg	35	11	5	8	5	5
P	mg/kg	1	1	< 1	< 1	1	1
particles < 0.01mm	%	23.8	18.2	27.2	33.0	40.9	49.2

18-year-old regrowth

<i>horizon</i>	unit	Ah (0-8 cm)	A (8-30 cm)	AB (30-38 cm)	Bt ₁ (38-64 cm)	Bt ₂ (64-81 cm)	Bt _{cs} (below 81 cm)
<i>characteristics</i>							
pH/H ₂ O	-	3.9	4.1	4.6	4.7	4.7	4.8
C-ox	%	2.04	1.96	0.73	0.37	0.29	0.29
N	%	0.18	0.15	0.07	0.05	0.05	0.04
Ca	mg/kg	< 83	< 83	< 83	< 83	< 83	< 83
K	mg/kg	11	13	6	7	7	9
Mg	mg/kg	6	9	3	4	1	6
P	mg/kg	< 1	2	1	< 1	1	1
particles < 0.01mm	%	25.7	25.6	33.5	40.7	43.0	45.7

primary old-growth forest

<i>horizon</i>	unit	Ah (0-5 cm)	A (5-25 cm)	Bt ₁ (25-65 cm)	Bt ₂ (below 65 cm)
<i>characteristics</i>					
pH/H ₂ O	-	3.5	4.0	4.4	4.6
C-ox	%	2,50	1.30	0.84	0.30
N	%	0.19	0.10	0.05	0.06
Ca	mg/kg	< 83	< 83	< 83	< 83
K	mg/kg	14	6	6	9
Mg	mg/kg	14	6	4	6
P	mg/kg	1	< 1	1	1
particles<0.01mm	%	25.2	27.3	35.5	48.1

Table 2. Fine root biomass in age-differentiated sample plots (dry weight down to 50 cm in g/m²)

Old grassy plot	Traditional agric. field	6- year-old regrowth	18-year-old regrowth	25-year-old regrowth	37- year-old regrowth	old growth forest
455	878	938	1491	1371	2083	3924

Table 3. Proportion of dry weight of fine roots < 2mm in g/m² within the upper 20 cm layer of the soil, to the total weight of the same category down to 50 cm depth, in age-differentiated sample plots

Old grassy plot	Traditional agric. field	6- year-old regrowth	18-year-old regrowth	25-year-old regrowth	37- year-old regrowth	old growth forest
91 %	98 %	92 %	86 %	82 %	81 %	78 %

Table 4. Proportion of dry weight of fine roots < 2mm in g/m² within the soil column (down to 50 cm) in age-differentiated sample plots, to the total weight of all sampled categories

Old grassy plot	Traditional agric. field	6- year-old regrowth	18-year-old regrowth	25-year-old regrowth	37- year-old regrowth	old growth forest
82 %	76 %	74 %	62 %	56 %	56 %	50 %

Legends for figures

Fig.1. – Root system development in *Cecropia* species on the low terrace of the Caquetá River. **1** a, b, c – early development; **2** – *Cecropia distachya* (d.b.h. 12 cm, h 9 m) in a 6-year-old regrowth; **3** – *Cecropia ficifolia*. (d.b.h. 10 cm, h 12 m) in a 14-year-old regrowth; **4** – *Cecropia sciadophylla*. (d.b.h. 14 cm, h 17 m) in a 14-year-old regrowth; **5** – *Cecropia distachya* (d.b.h. 17 cm, h 12 m) in a 37-year-old regrowth. [Unless otherwise indicated, the scale divided at 10 cm refers to all figures.]

Fig.2. – Partly exposed surface horizontal roots in *Cecropia* spp. **1** – *Cecropia ficifolia* (d.b.h. 12 cm, h 15 m) in a 14-year-old regrowth; **2** – *Cecropia distachya* (d.b.h. 17 cm, h 12 m) in a 37-year-old regrowth

Fig.3. - Scheme of root system development in three species of the genus *Vismia*. **1** a, b, c, d – early development stage; **2** – *Vismia macrophylla* (d.b.h. 3, h 6) on 6-year-old regrowth; **3** – *Vismia macrophylla* (D.B.H. 5, h 7) on 6-year-old regrowth; **4** – *Vismia macrophylla* (d.b.h. 6, h 6) on 14-year-old regrowth; **5** - *Vismia japurensis* (d.b.h. 9, h 9) on 14-year-old regrowth; **6** - *Vismia glaziovii* (d.b.h. 12, h 13) on 18-year-old regrowth; **7** - *Vismia japurensis* (d.b.h. 15, h 13) on 14-year-old regrowth.

Fig. 4 - Partly exposed surface horizontal root systems of two *Vismia* species. **1** – *Vismia macrophylla* (d.b.h. 11, h 13) on 14-year-old regrowth; **2** – *Vismia japurensis* (d.b.h. 15, h 13) on 14-year-old regrowth.

Fig. 5. - Root system of *Miconia poeppigii* Triana. **1** a, b, c – early development stage; **2** – specimen in a 14-year-old regrowth (d.b.h. 9, h 16); **3** – specimen in a 14-year-old regrowth (d.b.h. 13, h 14); **4** – specimen in a 14-year-old regrowth (d.b.h. 20, h 15); **5** – specimen in a 18-year-old regrowth (d.b.h. 20, h 20).

Fig.6. - Partly exposed surface horizontal root systems of *Miconia poeppigii* Triana. **1** – individual on 14-year-old regrowth (d.b.h. 13, h 14); **2** – individual on 14-year-old regrowth (d.b.h. 20, h 15).

Fig.7. - Root system development of *Goupia glabra*. **1** a, b, c – early development stage; **2** – individual on 37-year-old regrowth (d.b.h. 17, h 16); **3** – individual on 37-year-old regrowth (d.b.h. 35, h 20).

Fig.8. - Partly exposed surface horizontal root systems of *Goupia glabra*. **1** – specimen in a 37-year-old regrowth (d.b.h. 35, h 20); **2** –specimen in a 37-year-old regrowth (d.b.h. 17, h 16).

Fig.9. - Root system development of *Clathrotropis macrocarpa*. **1** a, b, c – early development stage; **2** – specimen in a 37-year-old regrowth (d.b.h. 17, h 16); **3** - specimen in a 14-year-old regrowth (d.b.h. 18, h 14);**4** – specimen in a 37-year-old regrowth (d.b.h. 20, h 16).

Fig. 10. - Partly exposed surface horizontal root systems of *Clathrotropis macrocarpa*. **1** – specimen in a 18-year-old regrowth (d.b.h. 18, h 14); **2** – specimen in a 37-year-old regrowth (d.b.h. 20, h 16); **3** - specimen in a 37-year-old regrowth (d.b.h. 17, h 16).

Fig. 11. - Scheme of root system development of *Brosimum rubescens*. Vertical root distribution and penetration down to 1,5 m depth (d.b.h. 21, h 20)

Fig. 12. - Tree root biomass in various developmental stages of the rain forest in Araracuara region (**1**- old grassy plot; **2** - newly cut zone/traditional agricultural field under the use; **3** – 6-year-regrowth; **4** – 18-year-old regrowth; **5** – 25-year-old regrowth; **6** – 37-year-old regrowth; **7** – old-growth forest; **8** – average of data for tropical forests).

Fig. 13. - Dry weight biomass (in g/m^2) of roots of different size categories, according to their diameter, in the soil profile (soil horizons by 10 cm) on low terraces of Araracuara region (**A** - old grassy plot; **B** - traditional agricultural field under the use (2,5 years after felling); **C** – 6-year-old regrowth; **D** – 18-year-old regrowth; **E** – 25-year-old regrowth; **F** – 37-year-old regrowth; **G** – old-growth forest)