

First observations on the root morphology and symbioses of 21 major tree species in the primary tropical rain forest of French Guyana

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Summary — A wide diversity of root morphology and symbiotic associations have been catalogued in 21 tree species in the tropical rain forest of French Guyana. Some unusual structures are described, such as nodular short roots containing hyphal coils. Endomycorrhizal symbiosis prevails in this type of forest. Parasitic nematodes (*Meloidogyne* sp) on young seedling roots of *Dicorynia guianensis* and *Peltogyne venosa* probably interfere with their regeneration.

tropical rain forest / Caesalpinioideae / root type / symbiotic status / French Guyana

Résumé — Premières observations sur la morphologie des racines et les symbioses racinaires de 21 espèces principales d'arbres en forêt tropicale humide primaire de Guyane française.

Dans la forêt tropicale humide de Guyane française, une grande diversité de morphologie racinaire et d'associations symbiotiques a été observée sur 21 espèces d'arbres. Certaines structures inhabituelles sont décrites, comme des racines courtes noduleuses contenant des hyphes en pelotons. Les endomycorhizes constituent l'association symbiotique dominante dans ce type de forêt. Des galles à nématodes (*Meloidogyne* sp) fréquentes sur les racines des semis de *Dicorynia guianensis* et de *Peltogyne venosa* jouent probablement un rôle dans la régénération de ces espèces.

forêt tropicale humide / Caesalpinioideae / morphologie racinaire symbiose / Guyane française

INTRODUCTION

The primary tropical rain forest of French Guyana has been extensively studied for its structure and regeneration dynamics (Riera *et al*, 1990; Sabatier and Prevost, 1990). Most previous studies have concerned the part of the stands above ground, and little attention has been paid to the interactions between trees within the soil. This should be an important part of any modelling of the spatial distribution of species and their regeneration patterns. More generally, very little is known about the rooting habits and symbiotic status of trees in the neotropics (Souza Moreira *et al*, 1992).

The occurrence of different types of root symbioses and parasitism seems to be particularly relevant in this respect, because symbionts determine different modes of nutrient mobilization and uptake, and parasites can alter the efficiency of roots. Moreover, the spatial distribution and dispersive mechanisms of microbial symbionts or parasites might contribute to the complexity of those mechanisms in trees.

This paper presents some preliminary descriptive results showing the wide diversity of root morphology and their symbiotic or parasitic status in this type of rain forest. We also discuss some unusual structures.

MATERIALS AND METHODS

The observations were carried out in 3 sites that are relatively close to each other (ca 20 km apart, centred around Sinnamary, 5° 20' N, 52° 50' W, 110 km west of Cayenne on the Atlantic coast). These sites are representative of the wide diversity of soil conditions and forest structure prevailing in the region and are found:

- along the Saint Elie track in the ECEREX research zone (Sarrailh, 1984). The soils here are developed on the Bonidoro shales (Boulet, 1990);

- in the experimental plots of Paracou (Bariteau and Geoffroy, 1989). The soils here are developed on migmatite and shales (Boulet and Brunet, 1983);

- along the Anse de Sinnamary road on a sandy detritic coastal flat.

Table I lists the 21 tree species observed. They were chosen from 13 families (among the 68 in French Guyana), which include 61% of the species, and for their economic importance (more than half provide valuable timber). Some species are economically interesting or putatively ectomycorrhizal, according to their taxonomic position (the sub-family Caesalpinioideae in the Leguminosae) and to other studies in Africa (*eg*, Alexander and Högberg, 1986; Fassi and Moser, 1991). The Caesalpinioideae sub-family is the dominant group of trees in the Guyanas, in diversity, density and biomass (Puig *et al*, 1990). The species *Dicorynia guianensis*, *Peltogyne venosa*, *Sclerolobium melinonii*, *Eperua falcata* and *E grandiflora*, *Hymenea courbaril* were thus more extensively sampled at the seedling stage (> 100 individuals).

Sampling was performed all year long, on either roots of mature trees (roots were traced from the base of the tree) or seedlings at different distances from the corresponding mother trees. Fine roots were carefully washed and observed fresh under the stereomicroscope. Putative ectomycorrhizas were examined following the methods described by Ingleby *et al* (1990). Hand-cut sections and crushed roots were observed unstained under the light microscope (500 x). Part of the fine roots were cleaned and stained according to the technique described by Phillips and Hayman (1970) for the observation of endomycorrhizas with the light microscope (120 x – 500 x).

The occasional presence of sporocarps of putative ectomycorrhizal higher basidiomycetes was noted.

RESULTS

The general architecture of the fine roots varies greatly in both diameter and branching, from 0.3 mm and a very dense mat of fine roots for *D guianensis* and *P venosa* (fig 1), to 1 mm and a poorly branched sys-

Table I. List of the tree species studied and sampling pattern.

| Family (sub-family) and species | Sampling site * | Mature tree | Seedling |
|--|-----------------|-------------|----------|
| Leguminosae ** | | | |
| (Caesalpinioideae) | | | |
| <i>Dicorynia guianensis</i> Amshoff | 1.2 | + | + |
| <i>Eperua falcata</i> Aublet | 1.2 | + | + |
| <i>Eperua grandiflora</i> (Aublet) Bentham | 1.2 | + | + |
| <i>Hymenea courbaril</i> Linnaeus | 3 | + | + |
| <i>Peltogyne venosa</i> Bentham | 1 | + | + |
| <i>Recordoxylon speciosum</i> (R Ben) Norm and Mor | 2 | + | + |
| <i>Sclerolobium melinonii</i> Harms | 2 | + | + |
| <i>Vouacapoua americana</i> Aublet | 2 | + | + |
| (Papilionoideae) | | | |
| <i>Andira coriacea</i> Pulle | 2 | + | + |
| <i>Bocoa prouacensis</i> Aublet | 2 | | + |
| Clusiaceae | | | |
| <i>Platonia insignis</i> Martius | 2 | | + |
| <i>Symphonia globulifera</i> Linnaeus L f | 2 | | + |
| <i>Vismia guianensis</i> (Aublet) Choisy | 2 | | + |
| Lauraceae | | | |
| <i>Ocotea rubra</i> (Aublet) Choisy | 2 | | + |
| Lecythidaceae | | | |
| <i>Eschweilera odora</i> (Poeppig) Miers | 2 | | + |
| Meliaceae | | | |
| <i>Carapa procera</i> AP de Candolle | 2 | | + |
| Moraceae | | | |
| <i>Brosimum rubescens</i> Taubert | 2 | | + |
| <i>Cecropia sciadophylla</i> Martius | 2 | | + |
| Sapotaceae | | | |
| <i>Regala sanguinolenta</i> (Pierre) Aublet | 2 | | + |
| Sterculiaceae | | | |
| <i>Sterculia excelsa</i> Martius | 2 | | + |
| Vochysiaceae | | | |
| <i>Qualea rosea</i> Aublet | 2 | | + |

* 1: Saint Elie; 2: Paracou; 3: Anse de Sinnamary. ** According to the taxonomy of Polhill and Raven (1981).

tem for *E falcata* (fig 2) and *E grandiflora*. The length distribution of fine roots is also variable, from very short roots (0.5–5 mm, fig 2) on long axes (10 cm and over with no long laterals) for the 2 *Eperua* sp, to the evenly branched systems of *Sterculia*

excelsa, *Qualea rosea*, *P venosa* (fig 1). Typical bacterial nodules of the *Rhizobium* or *Bradyrhizobium* type, containing bacteria and infection threads, were found on 3 Caesalpinioideae (*D guianensis*, *R speciosum*, fig 3; *S melinonii*, (fig 4) and the 2

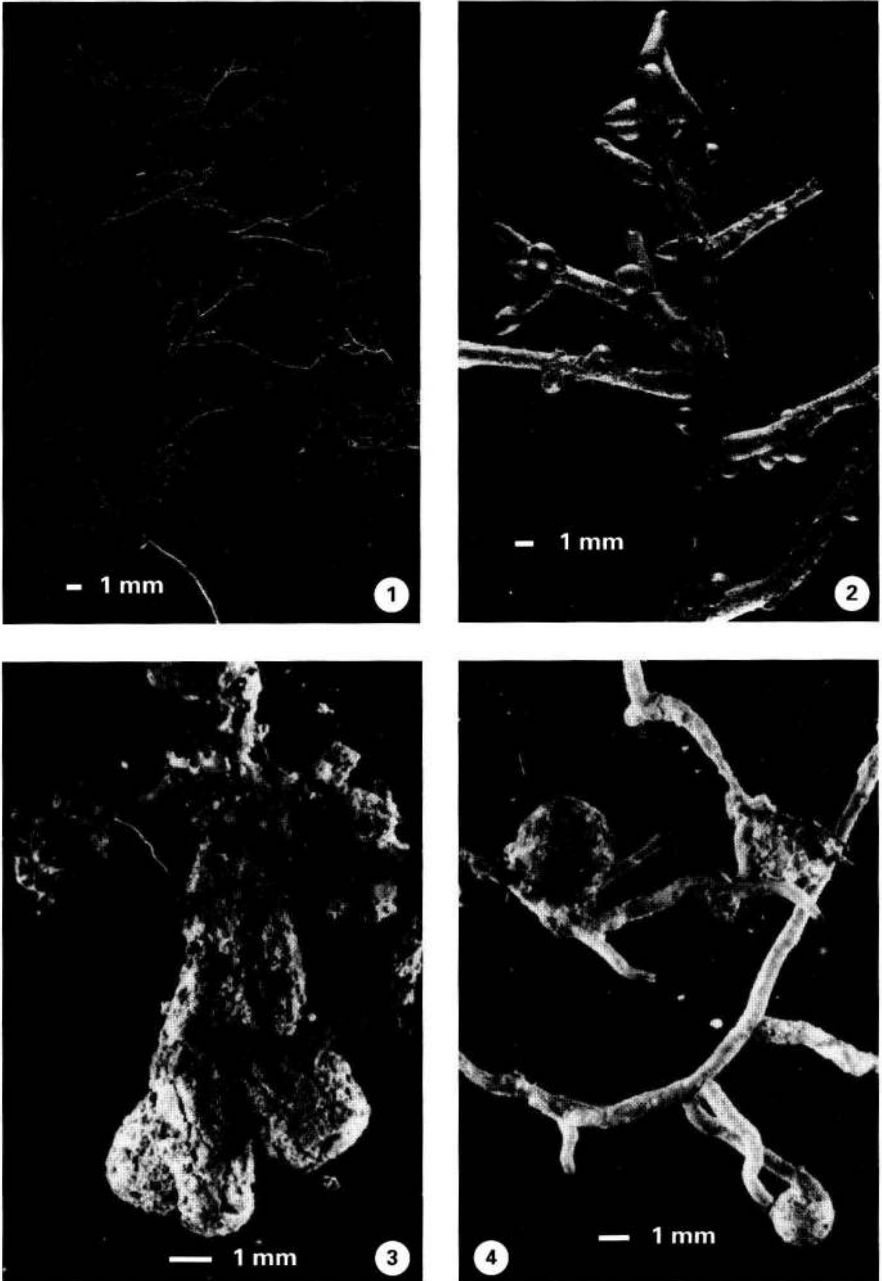


Fig 1. Roots of a *Peltogyne venosa* seedling, from just under the litter. The roots are small in diameter (0.3 mm) and highly branched.

Fig 2. Roots of a mature *Eperua falcata*, from just under the litter. The roots are large in diameter (1 mm and more) and poorly branched.

Fig 3. Lobed bacterial nodules of *Recordoxylon speciosum* (seedling).

Fig 4. Globular bacterial nodules of *Sclerolobium melinonii* (seedling).

Papilionoideae examined (*Andira coriacea* and *Bocoa prouacensis*). These nodules were either spheroid (*S melinonii*, fig 4) or lobed (other species), with colours ranging from off-white to brown. However, no nitrogen fixation test was performed and we have no proof that these nodules are functional and effective.

Typical vesicular-arbuscular endomycorrhizas with entry points, intercellular mycelium and arbuscules, and/or vesicles (fig 5) were found in the fine long roots of all the species examined. Another endomycorrhiza-like structure, with intracellular hyphal coils instead of arbuscules, with or without vesicles, was found on *D guianensis* (fig 6), *P venosa*, *Platonia insignis*, *Symphonia globulifera*, *Ocotea rubra*, *S excelsa*, *R speciosum*, and *Brosimum rubescens*.

Many of the Caesalpinioideae tree species examined (eg, *D guianensis*, *P venosa* and *E falcata*) had brown, swollen, short roots, which were more or less branched, and very similar to smooth ectomycorrhizas at the first glance (fig 2). However, sections revealed that none of these short roots (out of several hundred trials) were ectomycorrhizas. In contrast, they displayed a dark outer layer of cells with thickened walls and a voluminous cortical parenchyma with isodiametric, thin-walled cells (fig 7). When stained with the Philips and Hayman (1970) technique, the parenchyma contained conspicuous endomycorrhiza-like structures with vesicles and coils. The formation of the thick outer layer occurs very rapidly after the apparition of the short root, close to the elongating tip of the long root. The most spectacular diversity was found on *Vouacapoua americana* and on the 2 *Eperua* species (*E falcata* and *E grandiflora*) with shapes ranging from spheres to cones, clubs and beaded short roots (fig 2). In these species, the outer layer was also thicker than in *D guianensis* and *P venosa* (fig 8). This types of structure will be

referred to below as 'polymorphous short roots'. A dense accumulation of such roots belonging to *Eperua* sp was found in the litter around the base of neighbouring trees. This suggests that these roots are particularly well adapted to this special ecological niche with high water and nutrient fluxes due to stem flow, litter accumulation and mineralization.

Another unusual feature was found on 3 Caesalpinioideae (*D guianensis*, *R speciosum*, and *V americana*). Small (0.5–1 mm in diameter), jet-black, smooth and glossy, spherical or slightly elongated nodules were directly attached to the long roots (fig 9). The presence of a stele connected to the main vascular system of the long roots indicates that nodules are transformed short roots, like the previously described 'polymorphous short roots' (fig 10). They differ in their dense and smooth black surface and by the fact that their parenchyma contains no hyphal coils or vesicles.

The fine roots of *D guianensis*, *P venosa* and occasionally other species were sometimes covered by a loose white or cream-coloured fungal mantle, often associated with hyphal strands (fig 11). However, the absence of a Hartig net indicates that these structures are only non-symbiotic peritrophic associations. As these associations are usually observed on the surface of dead leaves, or are found growing through dead leaves in litter occupied by the white mycelia of decomposers, it is probable that they are caused by these saprophytic fungi (although the root tissues are clearly alive).

The seedlings of 2 Caesalpinioideae species (*P venosa* and more particularly *D guianensis*) always had galls (fig 12) due to an endoparasitic nematode identified as *Meloidogyne* sp (fig 13). These parasitic structures mostly occupied the superficial roots growing in the litter from the collar of the plants, which were severely affected by the infection (reduced number and length of roots).

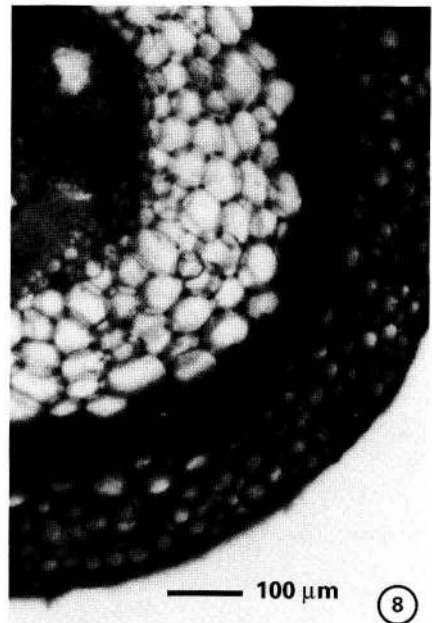
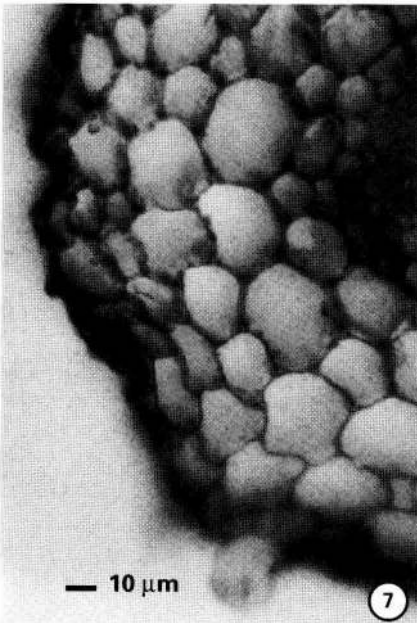
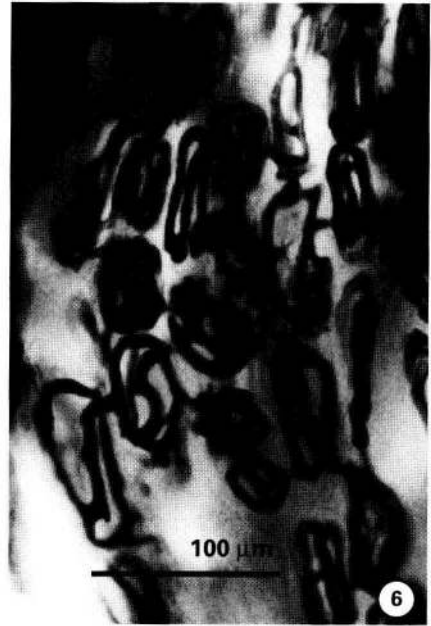
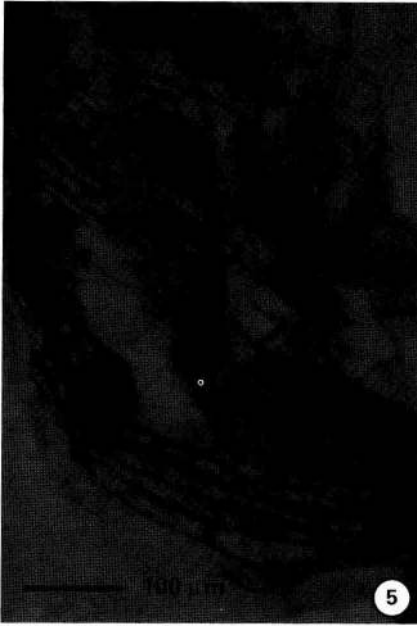


Fig 5. Endomycorrhiza of *Vismia guianensis* (seedling). The vesicles and the thick mycelium are typical of vesicular-arbuscular endomycorrhizas. The root was cleared and the fungus stained with acid fuchsin.

Fig 6. Hyphal coils of endomycorrhiza-like structures in *Dicorynia guianensis* roots (seedling). The root was cleared and the fungus stained with acid fuchsin.

Fig 7. Unstained hand-section of a *Dicorynia guianensis* short root (seedling). The cortical cells are thin-walled.

Fig 8. Unstained hand-section of an *Eperua falcata* short root (seedling). The cells of the inner cortex are thin-walled and those of the outer cortex have thick dark walls.

Table II. Occurrence of the different root structures observed in Leguminosae.

| (Sub-family) tribe, species | Bacterial nodule | Endomy corrhizas | Peritrophic association | Nematode galls | Unidentified structures | |
|-------------------------------|---------------------|---------------------|----------------------------|-------------------|----------------------------|----|
| | | | | | 1* | 2* |
| (Caesalpinioideae) | | | | | | |
| Caesalpinieae | | | | | | |
| <i>Recordoxylon speciosum</i> | + | + | | | + | |
| <i>Sclerobium melinonii</i> | + | + | + | | | |
| <i>Vouacapoua americana</i> | | + | | | + | |
| Cassieae | | | | | | |
| <i>Dicorynia guianensis</i> | + | + | + | + | + | + |
| Detarieae | | | | | | |
| <i>Eperua falcata</i> | | + | + | | | + |
| <i>Eperua grandiflora</i> | | + | | | | + |
| <i>Hymenea courbaril</i> | | + | | | | |
| <i>Peltogyne venosa</i> | | + | + | + | | |
| (Papilionoideae) | | | | | | |
| Swartzieae | | | | | | |
| <i>Bocoa prouacensis</i> | + | + | | | | |
| Dalbergieae | | | | | | |
| <i>Andira coriacea</i> | + | + | | | | |

* 1: black glossy nodules; 2: polymorphous short roots (see text).

Table II presents the distribution of the different structures described in the Leguminosae (all other observed species had only vesicular-arbuscular endomycorrhizas).

DISCUSSION AND CONCLUSIONS

The different tree species in the tropical rain forest of the French Guyana obviously display a wide range of strategies in exploring the soil and using its water and mineral resources. Some, for example *Dicorynia guianensis*, form dense mats of thin and highly branched roots, intercepting fluxes of low intensity on large areas, whereas others, such as *Eperua* spp, send long but poorly branched roots to microsites where

these fluxes are concentrated, for instance, around the base of other trees.

No ectomycorrhiza were found, even on Caesalpinioideae, a tree group proposed as potentially ectomycorrhizal in the literature. In Africa, genera such as *Gilbertiodendron*, *Azelia* and *Dalbergia* have often been reported to be ectomycorrhizal (eg, Khasa *et al*, 1990; Fassi, 1991). In South America (Venezuela), Moyersoen (1991) found typical ectomycorrhizas only on *Aldina kunhardtiana* (Papilionoideae, Swartieae), and none on *Eperua* sp, which is consistent with our results. Thus, ectomycorrhizal symbioses seem to be less frequent in Venezuela and the Guyanas than in other tropical rain forests, in spite of the fact that the soil fertility is particularly low in these

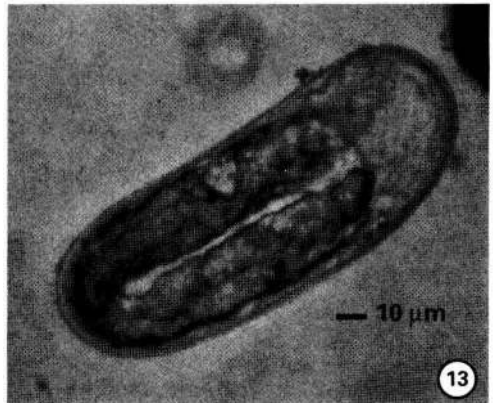
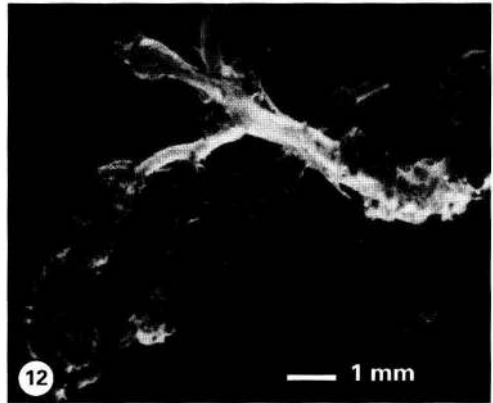
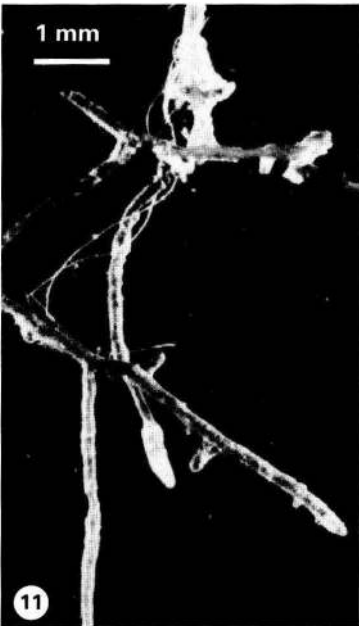
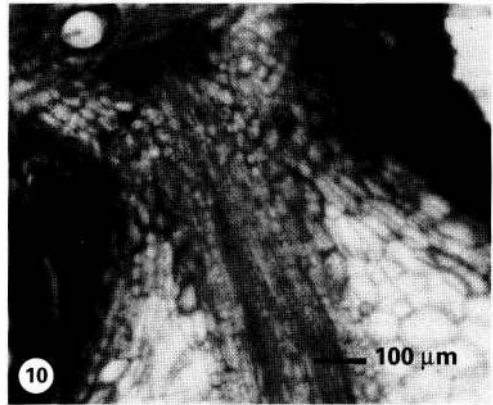


Fig 9. Black glossy root nodules on *Recordoxylon speciosum* (seedling).

Fig 10. Hand-section across a *Recordoxylon* seedling root (top) with a black glossy nodule (bottom). The vascular bundle in the nodule is connected with the stele of the root.

Fig 11. Roots of *Peltogyne venosa* with a loose fungal sheath and mycelial strands (seedling).

Fig 12. Nematode galls (*Meloidogyne* sp) on the roots of a seedling of *Dicorynia guianensis*.

Fig 13. Nematode (*Meloidogyne* sp) egg (incubation stage) from a gall on a root of a *Dicorynia guianensis* seedling.

regions, and that ectotrophy is commonly proposed as an adaptation to low fertility conditions (Janos, 1983). Observations of sporocarps of putative ectomycorrhizal fungi in Amazonia seem to be in contradiction with this conclusion (Singer and Araujo, 1979, 1986). However, these authors did not put forward any direct proof that ectomycorrhizas were actually present on the roots. It is also important to note that in our studies in French Guyana, no local factor is responsible for the rarity of ectomycorrhizas. Introduced pines and eucalypts in nearby plantations were massively ectomycorrhizal. Our results are thus consistent with the remark by Fassi and Moser (1991), according to which plant formations with dominant ectomycorrhizal species do not appear to constitute climatic climaxes in the neotropics.

All the sampled roots had arbuscular endomycorrhizas, which are thus by far the most dominant symbiotic association in this type of rain forest. Some tree species also had endomycorrhizas with intracellular hyphal coils. In *Eperua* sp it is not known if this type of symbiosis is host-specific or not, but it is clearly associated with structures atypical for Angiosperms in some Caesalpinioideae species. What we called 'polymorphous short roots' are somewhat similar (mostly those with a nodular shape) to the roots of Podocarpaceae and Araucariaceae (Gymnosperms) described by Baylis *et al* (1963) and Baylis (1972). They have a thickened outer cortex and endomycorrhizal infection (coil-type in our case) in the swollen inner cortex.

The black glossy nodules, which were only found on *R speciosum*, *V americana* and *D guianensis*, are unusual and their origin and function remain unknown.

Bacterial nodules of *Rhizobium* or *Bradyrhizobium* occur on several genera of Caesalpinioideae belonging to the Cassieae and Caesalpinieae, but not on Detarieae. This is consistent with the data

of Allen and Allen (1981) and Faria *et al* (1989). Souza Moreira *et al* (1992) recently published the first report of nodulation in the genus *Dicorynia*. Our results confirm this finding and the presence of nodules on *D guianensis*.

The systematic occurrence of nematode galls due to *Meloidogyne* sp on young seedlings of *D guianensis* and *P venosa* suggests that this parasite probably plays a major role in the seedling mortality, and thus in the regeneration dynamics of these species. Indeed, *D guianensis* is one of the species with the highest mortality rate in the experimental plots in Paracou (Schmitt and Bariteau, 1990).

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