A survey of micorrhizal infection in an amazonian rain forest

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Abstract

A survey of mycorrhizal infection and depth of rootlets was carried out on a hectare of primary rain forest in which all individuals over 15 cm in diameter had been identified and labeled. Non-mycorrhizal, lightly infected, moderately infected, and heavily infected species made up 16.7, 23.2, 14.8, and 16.7%, respectively, of the total plot's ecological importance value. Of the plot's total importance value, 59.9% were found to have fine roots in the 0- to 10-cm depth range, 7% to be in the 10-to 30-cm range, and 7.9% to have roots deeper than 30 cm. A strong association was found between root depth and mycorrhizal condition, with surface roots much more likely to be infected than deep roots. Rootlet depth was shown to be a consistent trait within a species and most often within a genus. The deep-rooted, non-mycorrhizal condition was interpreted as an ecological "strategy" for avoiding competition with more efficient mycorrhizal species.

Introduction

In spite of the known importance of mycorrhizal fungi in mineral nutrition of plants (Gerdemann, 1975; Bowen, 1973) and much speculation about the importance of these fungi in tropical ecosystems (McLean, 1919; Richards, 1953, Went & Stark, 1968), such basic ecological data as distribution and abundance of infection in tropical forests remain scarce. The nearest approach to this kind of information is in various surveys of tropical habitats: lists of species, including some natives (Janse, 1897); Johnson, 1949; Redhead, 1968); a short list of natives (Edmisten, 1970); or a determination based on unidentified root fragments (Stark, 1970). Only the last report allows the overall amundance of infection to be assessed, and its data apparently refer only to surface roots. A study of an area of primary tropical rain forest in which all individuals had been identified and labeled (Prance *et al.*, 1976) offered an opportunity to obtain such data in some detail. An index of importance value was calculated for each species as a means of identifying dominant or ecologically significant species in the forest. Species with high importance value were given priority in sampling. Each sampled species was assigned to one of four classes of infection by a semi-quantitative evaluation of intensity of infection. Finally, the depth at which each root sample was recovered was recorded.

Methods and materials

Importance value

Phytosociological data from Prance *et al.* (1976) were used t ogenerate an index of importance value for each species on the plot. We modified the importance value index of Curtis & McIntosh (1950) to exclude a measure of frequency. Since only one quadrat was used and all species occurred on it, the frequency values are all equal and this measure contributes nothing to the importance value index. Our index was converted to an **importance percentage** value as done by Risser & Rice (1971) Our index was $(N_i + BA_i)/2$. where N_i is the fraction of the total number of individuals comprised by species i, and BA_i is the fraction of the total basal area comprised by species i.) Species were selected in order of decreasing importance value, except that non-mycorrhizal taxa were more extensively sampled.

Collection of root samples

The study site was a hectare of lowland evergreen rainforest on a very heavy oxisol near Manaus, Brazil. It is described in detail by Prance *et al.* (1976). In every case, a root specimen was collected by following a root

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outward from the base of an identified plant until non-woody, ultimate-order rootlets of confirmed identity were encountered. Usually about 50 cm^3 (loosley arranged) of these roots were returned to the laboratory for preparation. The depth in the soil from which eac sample was taken was recorded.

PREPARATION AND EVALUATION OF ROOT SAMPLES

Root specimens were cleared and strained by the method of Phillips & Hayman (1970) and examined with a dissecting miccroscope. Subsamples thought likely to be infected were mounted in glycerin on slides and examined under a compound microscope. The usual basis for judging infection was the presence of characteristic internal hyphae. Vesicles were not common and arbuscules were almost never evident in field-collected native plants. Occasional root specimens were so opaque that satisfactory clearing was not achieved with these techniques; in such cases, judgement was based on external hyphae of the characteristic endogonaceous type.

Plants rated "non-mycorrhizal" were never found to support infection. Those rated **lightly infected** had occasional, isolated infection points. Those "moderately infected" had many parts infected, and those **heavily infected** had most of the roots infested with hyphae or other V-A mycorrhizal structures. Ectomycorrhizae were determined by the presence of a hyphal mantle on ultimate-order rootlets. Only three ectomycorrhizal species were found. Two of these were *Neea* spp. (Nytaginaceae), which Dr. Rolf Singer had already found to be ectomycorrhizal on other sites (personal communication). The third was *Gnetum* sp.; the ectomycorrhizal condition of this specimen was confirmed by Dr. Singer.

Non-mycorrhizal species, unless rare, were collected at least twice. The most common species were collected several times, usually from different trees, regardless of mycorrhizal condition.

Permanent mounts were made of at least one collection of each species.

DATA MANIPULATION

Calculation of importance value, sums of I.V., and counts of species in each category were carried out with the aid of the computer facility (CDC 6000) of Colorado State University, Fort Collins, Colorado U.S.A.

Extrapolation of results was done by assuming that mycorrhizal condition of in-sampled species is the same as the closest relative actually sampled.

RESULTS

Mycorrhizal infection was assessed in 71.4% (86 species) and fine-root depth in 74.8% (89 species) of the total importance value (greater than 15-cm diameter) of the plot. The fraction of total importance value in each category of infection is shown in Table 1. The fraction in each of three classes of root depth is shown in Table 1. Values for each species are given in the Appendix.

TABLE 1 — Percent of total importance value in each category of infection and root depth

	VAM infection			
	Non-mycorrhizal	Lightly infected	Moderately infected	Heavily infected
Actual	16.7 (24 spp)	23.2 (17 spp)	14.8 (25 spp)	16.7 (18 spp)
Extrapolated to whole plot	23.0 (48 spp)	25.2 (26 spp)	27.5 (96 spp)	20.9 (45 spp)

	Root depth		
	0-10 cm	10-30 cm	> 30 cm
Actual	59.5 (74 spp)	6.6 (6 spp)	10.5 (11 spp)
Extrapolated to whole plot	79.3 (190 spp)	6.6 (6 spp)	13.2 (23 spp)

DISCUSSION

Although the mycorrhizal categories to which different individuals of the same species were assigned varied somewhat, they never differed by more than one category. If additional examples were collected, the appropriate category for a given species could always be

decided. At the generic level, mycorrhizal condition was constant in some genera and varied in others. Three representatives of each of the genera *Protium* and *Brosimum* were all heavily infected. Three species of *Swartzia* (including one from a different site) were all non-mycorrhizal. Of seven representatives of *Eschweilera,* all but one were lightly infected. Certain genera showed wider variation: *Couepia* had both a heavily and a lightly infected representative, and *Pouteria* had two non-mycorrhizal and a moderately infected species. Constancy within genus seems to be the usual condition, however. At the family level, some of the families are constant and others quite variable. All three legume families consistently have either moderate or heavy infection, ecept *Swartzia* of the Caesalpiniaceae. Lauraceae, Vochysiaceae, and Lecythidaceae also show little variability, while the important families Moraceae and Sapotaceae are notable for wide variation.

From these observations, mycorrhizal condition of about 97% of the plot's importance value can be estimated from congeners and family reprpesentatives actually examined. Clearly, such extrapolation is more reliable for consistent generaand families; but since these are more frequent than inconsistent ones, the estimate should be reasonably accurate. The fraction of total importance value estimated to occur in each category of infection intensity is shown in Table 1. It differs somewhat from that actually sampled because non-mycorrhizal plants, many of high importance value, are over represented in the sample actually examined. The Lecythidaceae in particular was over reprepresented in the field work because it offered an opportunity to substantiate the somewhat surprising finding that many species were non-mycorrhizal or only lightly infected. In view of this over representation, the whole forest may well be characterized better by the extrapolated data than by the actual sample.

The depth of fine roots was a very consistent characteristic of a species. Different individuals of the same species differed by more than a few cm in only one case. Thus, depth of ultimate-order laterals is clearly a genetically controlled trait in this forest, not simply a response to local environmental variables, and may reasonably be considered an important component of a species ecological niche in this environment of intense competition for limited nutrients. At the generic level, rooting depth was again remarkably uniform, as exemplified by *Protium, Eschweilera, Brosimum*, and *Pouteria*. Some variability is found in *Couepia*, *Salacia,* and *Saccoglottis*. Again, some families are constant (legumes excep *Swartzia,* Lauraceae, Moraceae and Vochysiaceae) and others variable (Lecythidaceae, Meliaceae), but uniformity is more frequent and the entire forest may be characterized better by the extrapolated root-depth data (Table 1) than by the original sample.

The statistically significant association ($p < 0.01$) between root depth and infection level (Table 2) is a warning to those who would do a survey of mycorrhizal infection and

TABLE 2 — Number of species in mycorrhizal categories at three classes of root depth

Depth (cm)	Non-mycorrhizal	Liphtly infected	Moderately infected	Heavily infected
0-10	22	19	65	34
10-30	0	3	6	0
> 30	14	0	0	0

$X^2 = 60.6$; $P < 0.01$.

could explain the differences between this and earlier tropical surveys: Because shallow-oroted species are much more likely than deep-rooted species to be infected and a single collection of deep-rooted species can take as long as a week, over emphasizing the **easy** species, an almost certain consequence of casual sampling, could prompt the conclusion that the amount of infection is unrealistically high. Table 2 also indicates that deep roots and the non-mycorrhizal condition are apparently associated components of an ecological **strategy**. Shallow-rooted, mycorrnizal species almost certainly obtain phosphorus (the nutrient most likely to limit growth in this soil) more efficiently than deep-rooted species Because they remain out of competition, deep-rooted species use a different soil volume and

are probably able either to obtain phosphorus without the aid of mycorrhizal fungi, as discussed by Baylis (1975) and for the Amazon region by St. John (1980), or to tolerate low internal concentrations of phosphorus, perhaps by mechanisms similar to those discussed by Beadle (1966), Benzing (1973), or Small (1972).

Although the association between root depth and mycorrhizal infection has been reported by others (Mejstrik & Dominik, 1969; St. John & Machado, 1978), this study shows that deep, non-mycorrhizal roots are a consistent feature of certain species in this environment.

A number of non-mycorrhizal species have shallow roots. The question of their competition with mycorrhizal species will be discussed in a forth-coming publication.

The division of the soil volume between species with different fine-root depths is clearly one **niche dimension** that, combined with mycorrhizal state and other parameters, may eventually enable us to demonstrate resource partitioning among tropical trees. Connell (1978) suggested that rain forest species do not differ sufficiently to occupy different niches; these data indicate that they do, however, and show the direction in which we may fruitfully seek measurable components of niche.

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Resumo

Foram feitas observações da intensidade de infecção por micorriza em radículas de plantas, sendo que todas com mais de 15 cm de diâmetro foram identificadas e etiquetadas, plantas estas situadas em um hectare de floresta primária chuvosa. Não micorrítica, pouco infectada, moderadamente infectada, e espécies abundantemente infectadas receberam o seguinte valor de importância ecológica em área circunscrita: 16,7%; 23,2%; 14,8% e 16,7%. Do valor de importância total 59,9%. Foi encontrado para finas raízes 0-10 cm de profundidade, 7% para 10-30 cm, e 7,9% para raízes profundas abaixo de 30 cm.

Uma grande correlação foi encontrada entre profundidade no cilindro radicular e condição micorrítica, com a superfície da raiz provavelmente mais infectada que zonas mais internas. Radículas profundas foi uma característica consistente em espécies e muitas vezes em gêneros. Raízes profundas não micorríticas foram interpretadas como uma **estratégia** ecológica para evitar competição com espécies micorríticas mais eficientes.

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APPENDIX — Root depth and mycorrhizal condition of 89 Amazonian tree species

	Root depth	Mycorrhizal
Annonaceae		
Unonopsis stipitata	0 cm (1)*	H † (1)
Apocynaceae		
Geissospermum argenteum	30 (2)	L § (1)
Arecaceae		
Oenocarpus bacaba	10 (1)	M ŋ (2)
Syagrus sp.	30 (2)	N £ (2)
Bombacaceae		
Scleronema micranthum	0 (1)	L (4)
Burseraceae		
Protium paraense	0 (1)	H (2)
P. pedicellatum	0 (1)	H (2)
P. sp.	0 (1)	H (2)
Tetragastris sp.	5 (1)	L (2)
Caesalpiniaceae		
Eperua bijuga	0 (1)	H (2)
Peltogyne paniculata	0 (1)	H (2)
Swartzia reticulata	80 (1)	N (1)
S. sp.	100 (3)	N (3)
Caryocaraceae		
Caryocar pallidum	0 (1)	H (1)
Chrysobalanaceae		
Couepia canomensis	20 (1)	L (1)
Couepia obovata	0 (1)	H (1)
Licania pallida	0 (1)	M (1)
Combretaceae		
Buchenavia sp.	0 (1)	H (1)
Connaraceae		
Rourea sp.	30 (1)	N (1)
Dichapetalaceae		
Tapura guianensis	10 (2)	L (2)
Duckeodendraceae		
Duckeodendron cestroides	20 (1)	L (2)
Eleocarpaceae		
Sloanea guianensis	0 (2)	M (3)
Fabaceae		
Andira unifoliolata	20 (1)	...
Dalbergia sp.	0 (1)	M (1)
Dipteryx odorata	0 (1)	H (1)
Flacourtiaceae		
Laetia procera	5 (1)	N (1)
Gnetaceae		
Gnetum sp.	0 (1)	ECTO (1)
Hippocrateaceae		
Salacia impressifolia	20 (1)	N (1)
S. sp.	0 (1)	N (1)

APPENDX (Continuação).

	Root depth	Mycorrhizal Condition
Humiriaceae		
Saccoglottis ceratocarpa	0 (1)	L (1)
S. matogrossensis	20 (1)	M (1)
Lauraceae		
Aniba Duckei	0 (1)	M (1)
Licaria aurea	0 (1)	H (2)
L. sp.	7 (1)	M (1)
Nectanda rubra	0 (1)	H (2)
Lecythidaceae		
Corythophora alta	...	N (1)
C. rimosa	150 (2)	N (1)
Couratari guianensis	0 (3)	N (3)
Eschweilera amara	3 (2)	L (3)
E. odora	5 (3)	L (6)
E. polyantha	7 (1)	L (1)
E. sp. 2	0 (4)	L (5)
E. sp. 4	0 (2)	N (2)
E. sp. 5	0 (2)	L (3)
E. sp. 6	0 (2)	L (3)
Holopyxidium jaranum	100 (1)	...
H. latifolium	50 (2)	N (3)
H. sp. 2	50 (1)	N (1)
Leguminosae		
sp.	12 (1)	M (1)
Melastomataceae		
Mouriria lunatanthera	0 (1)	N (2)
Meliaceae		
Guarea duckei	50 (2)	...
Trichilia weddelii	0 (1)	M (1)
Mimosaceae		
Pithecolobium racemosum	0 (1)	M (1)
Monimiaceae		
Siparuna sp.	0 (1)	M (1)
Moraceae		
Brosimum parinariodes	0 (1)	H (1)
B. sp.	0 (1)	H (1)
B. utile	0 (5)	H (5)
Ficus sp.	0 (1)	N (1)
Helicostylis sp.	0 (1)	N (3)
H. tomentosa	0 (1)	N (2)
Naucleopsis caloneura	0 (2)	L (3)
sp.	5 (1)	N (1)
Myrtaceae		
Eugenia citrifolia	7 (1)	L (4)
E. egensis	0 (1)	H (1)
Nyctaginaceae		
Neea altissima	0 (2)	ECTO (3)
N. sp.	0 (2)	ECTO (3)

APPENDX (Continuação).

	Root depth	Mycorrhizal Condition
Ochnaceae		
Ouratea discophora	0 (2)	M (2)
Olaceceae		
Heisteria sp.	0 (1)	N (1)
Minquartia guianensis	0 (1)	M (3)
Quiinaceae		
Quiina pteridophylla	0 (1)	N (1)
Rhamnaceae		
sp.	0 (1)	N (1)
Rubiaceae		
Rudgea (coussarea) sp.	0 (3)	M (3)
sp.	0 (1)	L (1)
Sapindaceae		
sp.	5 (1)	N (1)
Sapotaceae		
Eremoluma sagotiana	0 (1)	M (2)
Pouteria caimito	0 (2)	N (2)
P. guianensis	0 (3)	N (2)
P. sp.	0 (1)	M (1)
Prieurella sp.	0 (2)	L (3)
Richardella cladantha	0 (1)	M (1)
sp.	0 (3)	N (5)

APPENDX (Continuação).

	Root depth	Mycorrhizal Condition
Simarubaceae		
Simaba cuspidata	150 (1)	...
Sterculiaceae		
Sterculia sf. Pruriens	0 (1)	M (1)
Theobroma sp.	0 (1)	M (1)
Tiliaceae		
Lueheopsis rosea	0 (1)	M (1)
Violaceae		
Rinorea sp.	0 (1)	H (1)
Vochysiaceae		
Erisma bicolor	0 (1)	M (1)
E. fuscum	0 (1)	M (2)
Qualea paraensis	0 (1)	M (2)
Q. sp.	0 (1)	M (1)

* Numbers in parentheses indicate number of collections examined.

† H = Heavily infected.

‖ M = Moderately infected.

§ L = Lightly infected.

ε N = Non-mycorrhizal.