Litter decomposition and Ectomycorrhiza in Amazonian forests

1. A comparison of litter decomposing and ectomycorrhizal Basidiomycetes in latosol-terra-firme rain forest and white podzol campinarana

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Abstract

Application of a mycosociological method (adaptation of the Lange method) in Central Amazonia produced the following results: In the white-sand podzol campinarana type of forests the dominant trees are obligatorily ectotrophically mycorrhizal; litter is accumulated as raw humus as a consequence of ectotroph dominance; fewer leaf inhabiting litter fungi occur in the dry as well as the wet seasons than are counted in the latosol terra-firme rain forest, and the fungi of that category are most strongly represented ("F-dominance") by other species here than in the terra-firme stands tested. The ectomycorrhizal trees and fungi are enumerated. On the other hand, in the terra-firme forest, ectotrophically mycorrhizal fungi did not occur in the test plots. The trees are almost all non-ectomycorrhizal in primary terra-firme forest; here, litter does not appreciably accumulate as a deep raw humus layer because the considerably higher number of leaf inhabiting litter fungi (ratios of 4:1 to 4.2:1 in favor of terra-firme) and greater diversification (a larger number of species) is potentially capable of reducing more than the yearly leaf-fall. In this study, a group of fungi was mainly considered which is not represented in laboratory litter decomposition experiments. However, a comparison with unpublished and published data shows that our results satisfactorily match the experimental and phytosociological data obtained both with other classes of microorganisms and with observations in other regions. The quantity of litter decomposing fungi in the foliicolous group depends mainly on the amount of precipitation during the last few days before counting. This does not hold for all lignicolous fungi. The reasons for this as well as the mechanisms by which the ectomycorrhizae may reduce litter decomposition rates and influence the nutrient cycling patterns are discussed. The most important genera of Basidiomycetes involved in litter decomposition in the Lower Rio Negro forest associations are enumerated. Possible economic significance of introducing ectotrophs in the terra-firme forest is indicated.

INTRODUCTION

It had been assumed that ectomycorrhiza in the neotropics is restricted to 1) secondary forest and partially destroyed or damaged tropical and subtropical forests (cicatrizing mycorrhiza), 2) to the natural vegetation above a certain altitude in the Andes and pre-Andine tropical-montane zone, 3) plantations of introduced ectomycorrhizal trees, inoculated with ectomycorrhiza or carryng spores or mycelium with seeds or seedlings, 4) possible scattered occurrences restricted to certain genera of Cormophyta (Salix was suggested), not being dominant in the tropical rain forest (Singer, 1963; Singer & Morello, 1960). This assumption, if correct, would mean that the neotropical humid lowland cannot be expected to produce anything in the way of a true ectotroph forest excepting secondary forests (capoeira), plantations and possibly forests containing scattered non-dominant ectotrophic elements. This would mean that there is a basic difference in the composition of the neotropical and the paleotropical lowland rain forests.

However, recent observations by Kreisel (1971) and Fiard (personal communication) indicate that in the Gulf area certain types of forest contain ectotrophically mycorrhizal elements (Coccoloba in Cuba, Torrubia in Martinique).

Our own recent investigations in the Lower Rio Negro region of Central Amazonia show, that certain vegetation types (campina, campinarana, igapó) are rich in ectomycorrrhiza-forming fungi, e. g. Boletaceae (Singer, 1978a). Thus, in both hemispheres, certain tropical soils require for the formation of any kind of forest the presence of ectomycorrhiza. Conse-

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quently, the anectotrophic "hylaea" is intermittent, with interspersed islands of ectotroph forests where climatic or edaphic (in Amazonia mainly the latter) conditions make it impossible for anectotrophic trees to obtain sufficient mineral nutrition unless ectotrophs dominate to such a degree as to change the microbiology of the soil completely and introduce what has come to be called direct cycling (Went & Stark, 1968) or "short-cycling" (Harley, 1977) of mineral nutrients.

The proposal (Singer, 1964) to reclassify the forest types of the world in such a way that they are first and basically divided into two main groups ([1]) — ectotroph and anectotrophic forests — has been ignored by forest ecologists, first because of misunderstandings with regard to the term "ectotroph" on the part of some mycorrhiza-specialists (Meyer, 1973) and secondly because understandably the mycological literature is not adequately accessible to all forest ecologists and phytosociologists ([2]).

The necessity to accept the importance of basidiomycetous components of the ecosystems and the usefulness of terms describing unequivocally the fungus-cormophyte symbiotic associations at the level of the individual (ectotroph) and the plant-fungus community (ectrotroph forest) has, in the meantime, become ever more obvious and the present study will show that, without them, an understanding of the phenomena observed is nearly impossible.

With regard to litter decomposition, the role of the Basidiomycetes is generally understood but rarely presented in quantitative form, principally because earlier investigators were hampered by the intricacies of the taxonomy involved. On the other hand the experimental methods tend to minimize the part played by Basidiomycetes since in litter samples their growth under laboratory conditions is suppressed. A convincing study, or even estimate of the relative numbers and efficiency of litter decomposing organisms (Basidiomycetes, other Eu-Mycetes including Hypho-and En-

domycetes, Zygomycetes, etc., as well as bacteria, Myxomycetes, and Actinomycetes. worms, Arthropods, higher animals) under various conditions of tropical forests has, as far as we are aware, never been made, and with the methods available, meets with some difficulties.

Under these circumstances it was felt that a method had to be found that at least provides quantitative data on the Basidiomycetes, their numbers, diversity, habitat requirements and dependency on meteorological conditions, their capacity of forming ectomycorrhiza, their fruiting periodicity, in fact all data that could not be obtained in laboratory studies. This method had already been introduced (Moser-method in Europe, North, and South America; Lange-method in Europe) and had now to be adapted to the conditions of the lowland tropical rain forest. The method chosen — the Lange method — was expected to provide the desired data and permit comparisons between the latosol — terra firme rain forest and the podzol white-sand campinarana.

MATERIALS AND METHODS

The Lange method (1948) was introduced for the study of fungus sociology in Danish Sphagneta whereby, in contrast to the Moser method (1959), permanent 1x1 m squares were marked and fructifications periodically counted. In our case one 5x5 m square was marked in the primary latosol terra firme forest 30 km north of Manaus (immediately adjacent to a hectare of a fully studied (Prance et. al., 1976) forest reserve at EMBRAPA) and regularly observed (in 6-11 day intervals) 37 times during a whole year. Furthermore two 5x1 m rectangular test lots, one in latosol terra firme forest at km 45 of the Manaus-Caracaraí Road and another immediately adjacent in the Reserva Biológica de Campina INPA-SUFRAMA, with three countings (two, at different seasons of the year coordinated with countings, the same day, in the latosol terra firme forest). The campinarana forest, the relatively most

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(1) — An ectotroph forest is one in which the dominant trees are obligatorily ectomycorrhizal. An anectotrophic forest is one in which the dominant trees are not obligatorily ectomycorrhizal.
(2) — "Despite this massive documentation plant scientists commonly seem to little heed the phenomenon [mycorrhiza] and its implications unless they are studying mycorrhizae per se" J. M. Trappe & R. D. Fogel (1977).

thoroughly studied one in the Lower Rio Negro (Anderson, 1978; Anderson *et al.*, 1975; Lisbôa, 1975; Prance, 1975) is located between the entrance to the Reserva and the transition to the more open, true campina-vegetation further east. In the following text we shall refer to this lot and the corresponding campinarana vegetation in other Rio Negro localities as CR and to the latosol terra firme rain forest as TF.

The fungi were counted according to the carpophores observed and were without difficulty divided into six main categories, viz. those inhabiting dead dicotyledonous leaves (foliicolous), those inhabiting dead pieces of dicotyledonous wood and fallen branches and sections of fallen tree trunks (lignicolous); those inhabiting monocotyledonous trash; those growing on the basic mineral soil without recognizable organic tissue (terricolous); those growing in association with tree roots (ectomycorrhizal); those growing in association with algae (basidiolichens).

In order to obtain data on a homogeneous group of litter decomposing fungi, all Discomycetes and carpophore-producing Basidiomycetes were counted excepting the lignicolous category and the fungi associated with algae; in the lignicolous category Aphyllophorales were excluded, and in the lichens all but Basidiolichens were excluded. The fungi counted are exactly those that are probably overlooked in traditional phytosociological work as well as in laboratory experiments. They were identified, as far as possible to the species, and in all cases to the genus; specimens of each species were deposited at the Herbarium of INPA, Manaus.

The meteorological data corresponding to a 1-, 2-, 3-, and 6-day period preceding the actual count (in the morning between 8AM and 11.30 PM) were restricted to precipitation since in the interior of the forest precise data on soil temperature and humidity of the air immediately above the soil were not available and did not appear to influence fungus growth equally in all strata and substrata involved nor did they vary appreciably except as a function of precipitation. Wind velocity never reached sufficient force or duration inside the forest during the observation period. Nevertheless

days with exceptional temperatures or air humidity measured were marked as such for later reference. The precipitation data for the test lot at EMBRAPA were obtained from the meteorological station of EMBRAPA (less than 1 km away) until October 1977, and from then on from that of Ducke Forest (INPA), little more than 3 km away. During this latter period very minor rainfall may have been local, but any major rainfall and most minor ones were sufficiently widespread so that the figures registered at Ducke Forest should be considered valid for the test lot.

The presence and distribution of ectotrophically mycorrhizal fungi was determined by the following method: Inside the test plots intensive search was undertaken in order to detect 1) short roots suspected of being ectomycorrhizal (these were preserved in alcohol and tested anatomically), 2) carpophores belonging to any of the genera known to be ectomycorrhizal (the surrounding rootlets were then investigated as above). This search for ectomycorrhizal fungi was not restricted to the test lots but was extended to the whole surrounding area so far as it belonged to the same type of primary forest. The search outside the test plots was supplemented by occasional observations and collections by A. B. Anderson and T. V. St-John.

RESULTS

A. The latosol terra firme forest (TF) — The Cormophyta individuals which contributed to the litter of the TF test plot I (30 km N of Manaus) and/or penetrated the lot which their roots are the following:
Araceae: *Anthurium* sp.
Bignoniaceae species
Bombacaceae: Probably *Bombacopsis nervosa* (Vitt.) Robyns
       "   : *Scleronema micranthum* Ducke
Chrysobalanaceae: *Licania* sp.
Duckeodendraceae: *Duckeodendron cestroides* Kuhlm.
Euphorbiaceae: *Mabea* sp.
Lecythidaceae: *Eschweilera* sp.
       "   : *Corythophora rimosa* W. Rodr.
Leguminosae (Caesalpiniaceae): *Eperua* sp.
       "   (Mimosaceae) : *Pithecollobium racemosum* Ducke

Melastomaceae: *Miconia* sp.
Meliaceae: *Trichilia* sp.
Moraceae: *Brosimum* sp.
Myristicaceae: *Virola ? elongata* Warb.
Myrtaceae species
Palmae: *Bactris* sp.
    "   : *Astrocaryum acaule* Mart. and *A.* sp.
Rubiaceae: *? Coussarea* sp.
Sapotaceae: *Eremoluma* sp.
    "   : *Pouteria* sp.

The Cormophyta of the latosol TF test lot II (km 45 of the road Manaus-Caracaraí) with roots reaching into and/or contributing to the litter on the surface are the following:
Araceae: *Philodendron* sp.
Burseraceae: *Protium* sp.
Chrysobalanaceae: *Licania latifolia* Benth. ex
               Hook.
    "   : *Parinari* sp.
Leguminosae (Papilionaceae): *Derris floribun-*
                   da Benth.
Linaceae: *Roucheria punctata* Ducke
Melastomaceae: *Miconia* sp.
Myristicaceae: *Virola* sp.
Myrtaceae species
Musaceae: *Heliconia psittacorum* L. f.
Rubiaceae species (incl. *Psychotria* sp.)
Sapotaceae species
    "   : *Micropholis* sp.

Sterculiaceae: *Theobroma* sp.

In the test plot at km 30 (test area I) in TF, the year-round survey of litter decomposers yielded the results given in table I.

In the test plot at km 45 (test area II) in TF, two surveys were made with the specific aim of comparing, under equal conditions, the survey of test area III on CR (see chapter B, below). This result can be found in table III.

B. The campinarana (CR) — The Cormophyta whose roots crossed or entered test plot III in CR or contributed to its litter are the following:
Annonaceae: *Annona nitida* Mart.
Apocynaceae: *Tabernaemontana rupicola* Benth.
Guttiferae: *Clusia* sp.
Leguminosae (Caesalpiniaceae): *Aldina hete-*
                  rophylla Spruce
                  ex Benth.
    "   : *Swartzia dolico-*
                  poda Cowan
Linaceae: *Roucheria punctata* Ducke
Myrsinaceae: *Conomorpha* sp.
Myrtaceae: *Myrcia servata* McVaugh
    "   : *Eugenia* sp.
Ochnaceae: *Ouratea spruceana* Engl.
Sapindaceae: *Matayba opaca* Radlk.
Simarubaceae: *Simarouba amara* Aubl.

The surveys of the litter decomposing fungi of test area III will be found in table II. Table III

TABLE II — Carpophore count in plot III. CR, carpophores per species (ca/sp.), and F-dominance — compared with a carpophore count in a Patagonian ectotroph forest (Singer, 1971).

	1. 28 II 1978 (main rainy season)	2. 5 IV 1978 (main rainy season)	3. 10 VIII 1978 (dry season)	Average CR	Nothofagetum (N. pumilio) 1964 [1]
Foliic.	33	25	8	22	20.9
Lignic.	11	11	8	10	5.1
Ectomyc.	0	1	0	0.3	8.9
Total	44	37	16	32	39.2
Foliic. ca/sp.	3.3	3.6	4		
Lignic. ca/sp.	1.8	1.8	2		
Foliic. F-dominance	Mycena osmundicola var. (14)	Mycena osmundicola var. (16)			Mycena microleuca (15.2)
Lignic. F-dominance	Hemimycena spec. (14)	Hemimycena spec. (5)			Crepidotus sphaerosporus (6.6)

1) Data here adjusted to 5 m2 surface as used in plot III.

shows the data obtained when test area III (CR) was compared with test plot II (TF) in order to obtain, under equal meteorological conditions comparable figures for both CR and TF.

C. Dependence of fungus growth on precipitation — Our chart (fig. 1) clearly shows that there is a strong dependence of fungus growth, as measured by carpophore production, on the amounts of precipitation. There is no proportional rise of carpophore production but mostly an increase with higher, a decrease with lower amounts of precipitation. The clearest dependence can be demonstrated by the absolute number of carpophores and the number of carpophores per species in the foliicolous category (fig. 1). There are even here occasional irregularities which, however, in nearly all cases can be explained by some special factors entering in specific surveys such as exceptionally violent and abundant rainfall (which is contraproductive to fruiting especially during the "summer"; this does not necessarily mean that the mycelial activity during such periods is diminished), possibly · also exceptionally high air humidity in the test area (which is favorable for fructification). There is also some influence of precipitation on the number of carpophores produced by lignicolous and terricolous fungi but in this case the dependence is not, as in the foliicolous fungi, primarily on the amount of rainfall during the preceding day, but on that of a longer period preceding the appearance of the carpophores. The reason for this will be discussed in Critic. But dependence on available humidity in and on the substratum

TABLE III — Comparation data on carpophore and species counts in adjacent CR (plot III) and TF (plot II) test areas.

| | CR | TF | CR/TF | CR | TF | CR/TF | CR | TF | CR/TF |
	5 IV 78	5 IV 78	5 IV 78	10 VIII 78	10 VIII 78	10 VIII 78	$\overline{X}$	$\overline{X}$	$\overline{X}$
Total carp.	36	163	1:4.5	16	40	1:2.5	52	203	1:3.9
" species	13	17		6	13				
" carp./species	2.8	9.6		2.7	3.1				
Foliicol. carp.	25	106	1:4.2	8	32	1:4.0	33	138	1:4.2
" species	7	8		2	8				
" carp./sp.	3.6	13.3		4	4				
" % of Total	69.45	64.98		50	82.5				
Foliicol + Terric. ca.	25	107	1:4.3	8	33	1:4.13	33	140	1:4.2
" " sp.	7	9		2	9				
" " ca/sp.	3.6	11.9		4	3.7				
" % of Total	69.45	65.03		50	82.5				
Lignicol. carp.	11	54	1:4.9	8	7	1:0.88	19	71	1:3.7
" species	6	7		4	4				
" carp./sp.	1.83	7.71		2	1.75				
" % of Total	30.56	33.1		50	17.5				
Terricol. carp.	0	1.0	0:1	0	1.0	0:1	0	2	0:2
Mycorrhizal carp.	1	0	1:0	0	0	0:0	1	0	1:0
Dominant species % of Total	44.4*	22.7+			22.5+				

(*) Mycena osmundicola
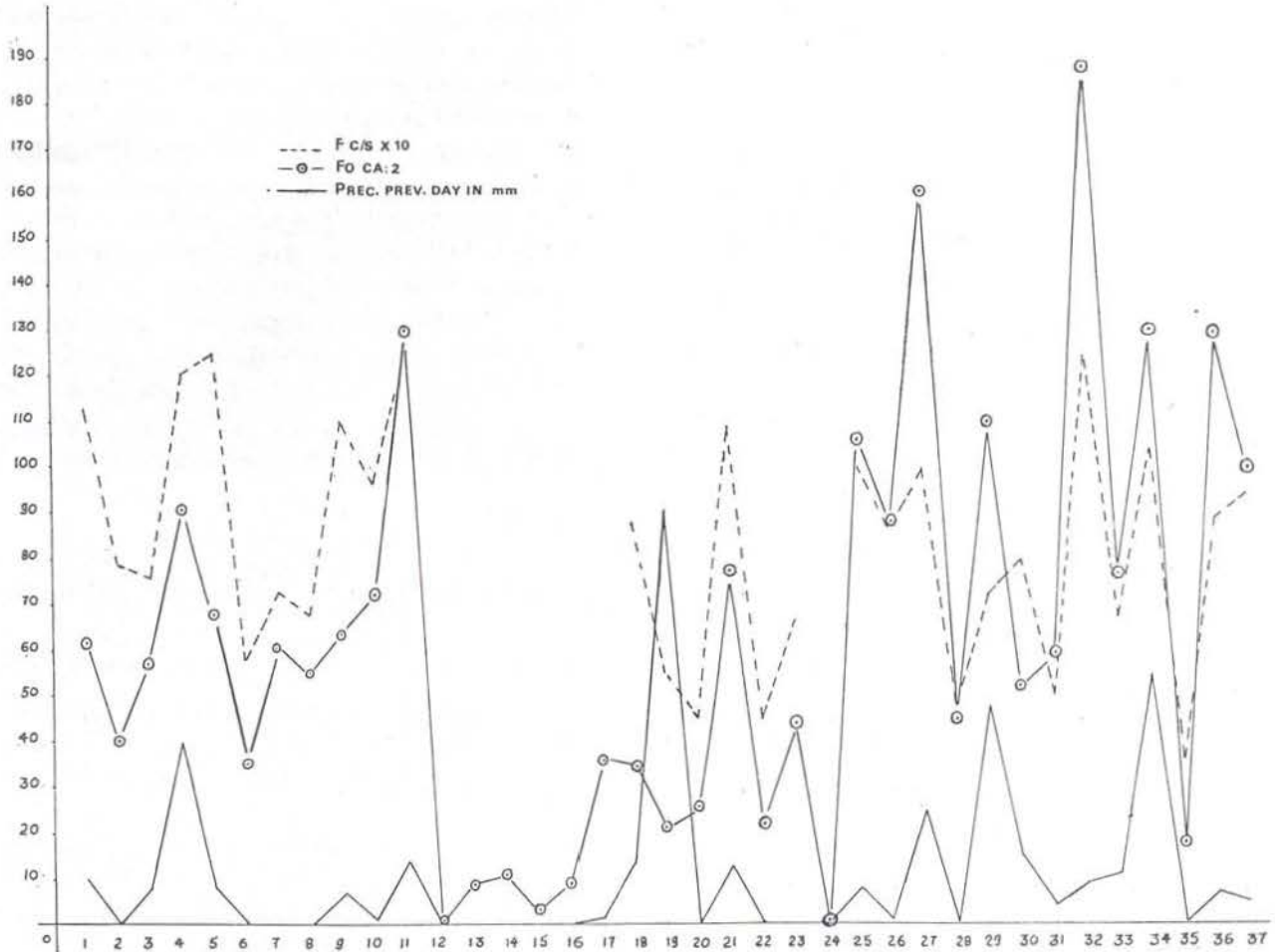(+) Mycena polyadelpha

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Fig. 1 — Comparison of precipitation during the day previous to counting date and fruiting (foliicolous carpophores — Fo Ca, and foliicolous carpophores per species — Fc/s) in TF.

is quite obvious inasmuch as during the driest periods of the year there is also a decrease in carpophore production in all categories. On the other hand, one of the interesting results of a year-round survey is the observation that in all test areas there is even in relatively dry periods of the year, interrupted in 1977 (as in many years) by a short secondary rainy season, never a complete stop of carpophore production which means that the mycelia, in all categories, continue their activity without interruption, even though in summer to a lesser degree and with the participation of species normally not fruiting in the main rainy season.

D. F — dominance[3] — This has been established at every single survey date for the two most important categories (foliicolous and lignicolous). Excepting those surveys that produced such a small number of carpophores in either of the categories that the data could not be considered statistically significant, there was a certain consistency in the F-dominance of *Mycena polyadelpha* in TF and *M. osmundicola* in CR, each species being most commonly encountered and most evenly distributed in the respective test areas, and their total numbers in all surveys together being higher than those of other species. Our data

[3] — We use, to be precise, the term F (ruiting)-dominance for the dominance in numbers and density, determined by the carpophores rather than by the extension of the mycelia in a given fungus association. F-dominance is not an identical but an analogous term compared to the term dominance of Cormophyta in phytosociology.

show that F-dominance is not constant during different periods of the year (different "aspects"), in different forest communities (TF and CR) cf. fig. 2 and table I.

E. Presence and absence of ectotrophic mycorrhizae — Our study shows that ectomycorrhizae are present in the test area in CR, absent in the test areas in TF. The negative result in the larger test area I (TF) suggests that TF does not contain ectotroph elements but a search through the entire I ha stand produced in two cases roots with ectomycorrhiza and in two more cases carpophores of genera believed to be generally ectomycorrhizal (Amanita craseoderma Bas and Russula puiggarii (Speg.) Sing.). One of the roots which macromorphologically and anatomically proved to be ectomycorrhizal belonged to a gymnosperm liana (Gnetum sp.) which is certainly not dominant, but on the contrary, scattered to rather rare in TF. The other root found to be ectomycorrhizal belonged to Neea sp.[4]. These data indicate that TF is, although scattered ectomycorrhizae occur, not an ectotroph forest but an anectotrophic forest.

The characteristic, bright yellow clamp-bearing, mycelium forming the ectomycorrhiza in Gnetum sp., first collected by T. V. St-John, was subsequently also discovered in CR, and tentatively identified as belonging to Sclero-derma sinnamariense Mont.. Only physiological studies can determine whether this is a
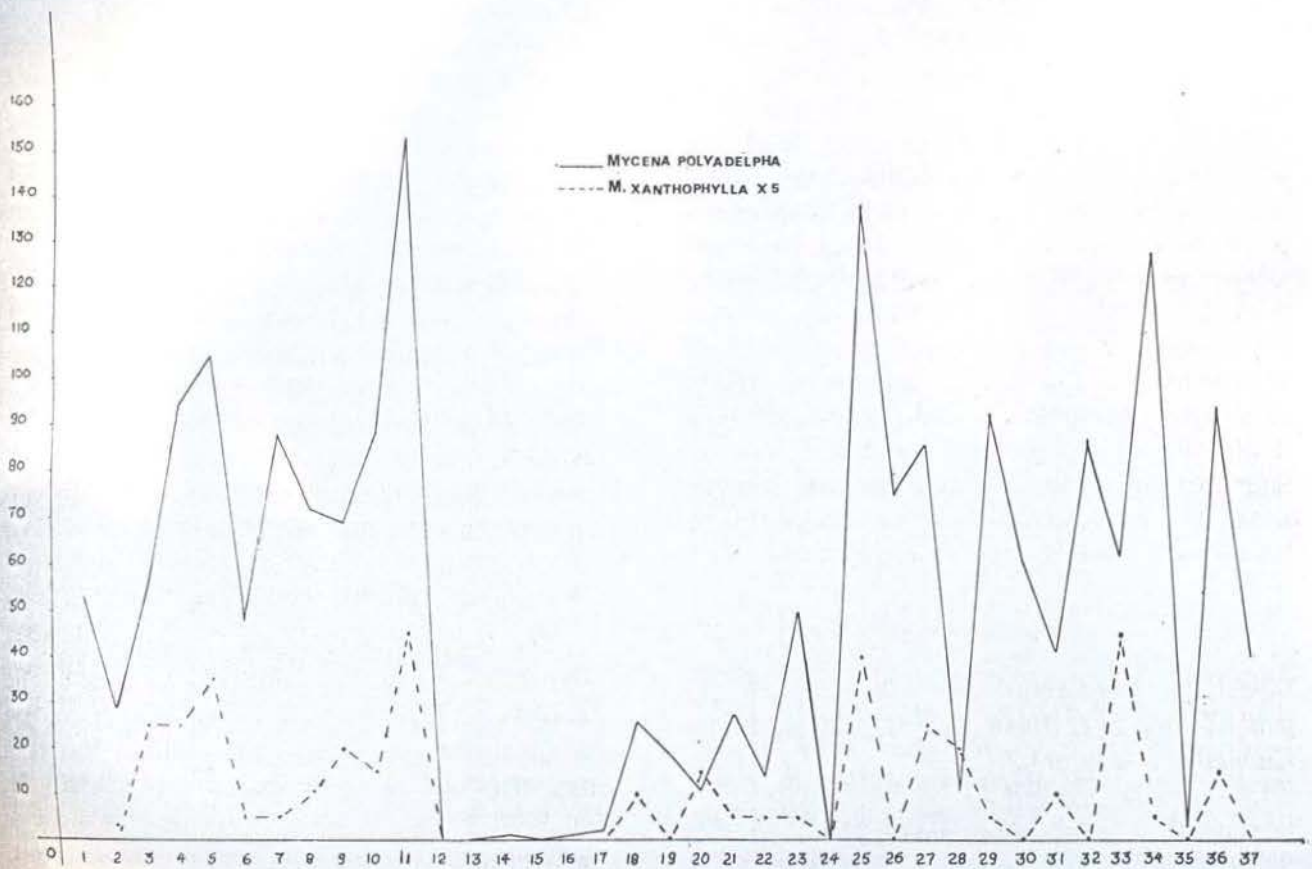

Fig. 2 — Number of carpophores of two representative species of foliicolous fungi during 37 counts in TF (for corresponding meteorological data compare fig. 1 and table I).

(4) — **Neea** (Nyctaginacae) forms cicatrizing mycorrhiza where root-damage occurs, especially in secondary latosol forests.

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mutualistic or a pseudomycorrhizal relationship but the apparently constant association Gnetum/Basidiomycete sp. in primary forest suggests the former. On the other hand, in the CR and shaded campina, obligatory ectomycorrhizae are not an isolated occurrence but are represented by numerous obligatorily ectomycorrhizal mycelia and carpophores, connected with several tree species all through the area and are particularly and specifically present on the dominant trees (Aldina heterophylla Spr. ex Benth. and probably also other Leguminosae such as some Swartzia and Eperua spp. as well as Sapotaceae, specifically Glycoxylon inophyllum (Mart. ex Miq.) Ducke). The ectotrophic element is also represented in test area III (CR) and is abundantly present in other campinarana forests along the road to Caracaraí (km 114-5, km 125) which belong to the same general type of ectotroph forest although they may well be described as different subassociations or associations of the campinarana type because they are floristically and in soil characteristics somewhat different from the area III. A list of the fungus components of ectotrophs observed in all campinarana forests investigated is given below (those with asterisk (*) demonstrably linked with Leguminosae or Sapotaceae; the rest expected to be ectomycorrhizal because of taxonomic position and occurrence restricted to campina, campinarana and black-water inundable forests subject to inundation (igapó) and growing under Leguminosae and Sapotaceae, or because they were demonstrably linked with gymnosperms or Psychotria roots):

GASTEROMYCETES:

Mycelium, ectomycorrhizal with Gnetum cf. paniculatum Spr. (also in TF). Scleroderma sinnamariense Mont..

APHYLLOPHORALES:

Sarcodon atroviridis (Morg.) Banker (widespread).

AGARICALES:

*Amanita campinaranae Bas
Amanita sulcatissima Bas (widespread)

*Amanita xerocybe Bas
Boletellus ananas (Curt.) Murr. var. minor ined. (type variety widespread)
*Cantharellus guyanensis Mont. (widespread)
Cortinarius (subgenus Cortinarius) sp.
Cortinarius (subgenus Telamonia), four species, collections B 11021, B 11026, B 11026a, B 11313.
Craterellus orinocensis Pat. & Gaill. (widespread)
Fistulinella campinaranae Sing.
*Hebelomina amazonensis Sing. ined
Inocybe (subgenus Inocybe) sp.
Lactarius amazoniensis Sing. ined.
Lactarius annulifer Sing. ined.
Lactarius brasiliensis Sing. ined.
*Lactarius reticulatus (Berk.) Sing. (also in igapó).
Lactarius venezuelanus Dennis (widespread)
Phyllobolites miniatus (Rick) Sing. (widespread).
Phylloporus gymnocystis Sing. ined.
Porphyrellus olivaceus Sing. ined.
Russula ? orinocensis Pat. (widespread)
Russula puiggarii (Speg.) Sing. (widespread, also in igapó and secondary forest — only facultatively mycorrhizal)
*Russula nanella Sing.
*Russula pachycystis Sing.
Strobilomyces pauper Sing. ined.
*Tylopilus arenarius Sing. & I. Araujo
Tylopilus potamogeton Sing. & I. Araujo (also in campina and igapó).
*Xerocomus amazonicus Sing. & I. Araujo
Xerocomus aff. brasiliensis (Rick) Sing.
*Xerocomus globulifer Sing. ined.
Xerocomus scrobiculatus Sing. ined.

The seemingly small representation (little over 1% of the carpophores counted and scarcely 3% of the species observed) of the 36 species enumerated above within the test area III is obviously not due to the scarcity of the total biomass since everywhere including test area III ectomycorrhizal shortroots were numerous (although in obligatory as well as cicatrizing mycorrhizae we find the root system of an individual ectotroph of Amazonian primary as well as secondary forest is not consistently shortroot-like). The reason for the scathered fruiting may be attributed to three factors: (1) ectomycorrhizal fungi produce,

especially in the tropical rain forest, much larger carpophores than most litter fungi; in the test area III, one carpophore of *Xerocomus amazonicus equals*, by dry weight as well as by volume, the sum of all other carpophores collected and counted that day; (2) the corresponding volume of substratum reached by the hyphae of the individual mycelium of the carpophore of an ectomycorrhizal fungus carpophore is considerably larger than that of the non-mycorrhizal species (since there is an obvious proportional relation between the mass of the carpophores and the extension of the mycelium); (3) the observations in campina-rana as well as in other ectotroph forests (Lange, 1948; Singer, 1971) show that ecto-mycorrizal fungi do not fruit — as many saprophytes do — continuously or in a succession of "flushes" — but appear solitarily or in small groups at longer intervals all through the rainy season, especially at the beginning and towards the end of the rainy season, because the living root, their carbohydrate source, is continually available during the whole year and independent of the conditions modifying their capacity of producing enzymatic cellulose breakdown.

F. Identity of the fungi observed and their ecological specialization — A list of all the species occurring, the quantity observed in each survey in test areas I, II, and III has, with the exception of the ectotroph-forming species, thus far not been completed. These data as well as the data available on host specialization are now being collected for the second part of this paper. For the purpose of the present part they are not essential. It may however be mentioned here that the genera observed most commonly in the foliicolous category are:

TF test areas: *Mycena, Marasmius, Hemimycena, Marasmiellus, Gloiocephala, Hydropus.*
CR test area: *Mycena, Marasmius, Hemimycena, Marasmiellus, Hygrotrama, Clavulinopsis.*

Although we have registered in the foliicolous category a wide spectrum of fungus families, it is remarkable that the Agaricales are most strongly represented. Helotiales were poorly and Pezizales very poorly represented. This observation is corroborated by

Dr. K. Dumont who (personal communication) finds a much stronger representation of Discomycetes in general in the tropical-montane forests and in the lowland forests closer to the Andine chains as well as in the subtropical forests. Likewise Gasteromycetes and Aphyllophorales, although often encountered, represent a definite minority among the litter decomposing foliicolous fungi.

Among the terrestrial fungi, the genera *Lepicta, Rhodophyllus, Hygrocybe, Conocybe, Callistodermatium* are prominent. It is remarkable that in Amazonia in general, hypogeous fungi and "secotiaceous" Basidiomycetes are so poorly represented that until now not one specimen has come to our attention. Among the Basidiolichens, only one species, *Multiclavula* sp. is common.

We have not counted and incorporated in our charts the insect-parasites (Clavicipitales and Deuteromycetes) and endotrophically mycorrhizal Basidiomycetes (orchid mycorrhizae) and Zygomycetes (VA-mycorrhiza). All three categories do, however, occur in all test areas, in variable numbers and different host specialization (see Discussion).

In the lignicolous group, the genera most frequently found are aside from, again *Mycena, Marasmius, Hemimycena, Marasmiellus, Hydropus* the following: *Lactocollybia, Gerronema, Collybia, Polyporus, Pyrrhoglossum, Stigmatolemma.* While we did not take into consideration any non-Agaricales in this category, it should be noted that the number of aphyllophoraceous lignicolous species in TF was as a whole lower than that of the Agaricales, with the exception of such prominent species as *Amauroderma* sp. and *Caripia montagnei* (Berk.) O. K., the latter also very common in TF and CR. This is in contrast to the prominence of lignicolous Aphyllophorales in freshly cut or burned primary as well as in secondary forests, on construction wood, lumber piles, fences, etc.

Specialization is generally high as far as habitat categories (foliicolous, lignicolous, etc.) were concerned, and we found no difficulty in classifying the Basidiomycetes in habitat-groups. This is not only interesting but also fortunate insofar as it permits precise

separate counting for each category and reveals a specific pattern of behavior of each category with regard to mycelial development, carpophore production, dependence on precipitation, etc. The relatively high percentage of lignicolous fungi in the tropics has been indicated before (Watling, 1977). It is also obvious in our tables where the lignicolous carpophores comprise one quarter to one half of the total in CR while more or less one eight of the carpophores are lignicolous in the corresponding (i. e. ectotroph) forests of the temperate zone of South America (Singer, 1971; Singer & Moser, 1965). Only very few species are both lignicolous and foliicolous. *Mycena polyadelpha*, occurring predominantly on leaves, grows also occasionally on small pieces of dicotyledonous wood. *Mycena osmundicola* (sensu lato) occurs frequently on both leaves and wood, but may be a heterogeneus taxon since populations vary in minor anatomical and pigment characters, yet only one character combination is found in each, either foliicolous or lignicolous population. This observation was also made by A.H. Smith (1947). In contrast to a statement by Watling (1977) we know of no example where a saprophytic speceis, terricolous in the temperate zones, would be lignicolous in the tropics. An exception to this rule may be seen in the fact that ectotrophically mycorrhizal fungi which are only exceptionally lignicolous in temperate zones very frequently ascend on standing living or dead trunks in the neotropics. However, their established or assumed ectotrophy suggests that the mycelium, at least in its mycorrhizal state, penetrates the soil underneath so that it is in contact with the roots.

COMPARISON BETWEEN TF AND CR

A. Habitat — It is well known (Prance et al., 1976; Singer, 1978) that the litter in the white-sand stands of forest accumulates to form a deep, soft layer not exposing the mineral soil whereas in the clay soils of terra firme forests no such accumulations of litter and raw humus occur and the mineral soil is exposed over large areas or merely covered by freshly fallen leaves; an accumulation of leaves and wood occurs only in some depressions or other restricted places for purely mechanical reasons. In the fungi this situation is expressed by the fact that terricolous fungi are, if not abundantly or consistently, but undoubtedly present as a definite category in the TF while what may come closest to this habitat group in CR may be termed humicolous. Humicolous mycelia are found in the lower stratum where sand particles are mixed with alread deformed or small fragments of rotting leaves or pieces of wood, recognizable as such but not further identifiable. We registered such fungi as foliicolous respectively lignicolous. The lack of exposed earth in CR also explains the absence or scarcity of basidiolichens.

It is also well established (Anderson, 1978) that the number of species of phanerogams is smaller in the white sand stands than in the terra firme forests which also finds its expression in the enumeration (see Results) of host species in the test lots in TF and in CR. In TF it is impossible to find any single species or even genus that may qualify as dominant and only a group of tree species treated as a unit may be termed leading since their combined individual representations are most numerous and produce the largest biomass, root extension, and litter in a given stand of primary forest. In CR, on the other hand, dominant species may be determined (Prance et. al., 1976). The average height of the trees is greater in TF than in CR, and partly as a consequence of this but also because of a different pattern of leaf shedding, the number of leaves shed during one year is apparently smaller in CR than in TF. Less leaf shedding per surface unit compared with greater litter accumulation in CR than in TF is remarkable and can only be attributed to a lesser degree of activity of litter decomposing fungi in CR than in TF.

Furthermore, the floristic composition of campinarana-type forest and latosol terra firme forests is different (Prance et al., 1976), as is also shown in the enumerations of species influencing the substartum in the three test plots (see above). While there is a small number of species common to both communities, the majority of the species is specific for one or the other community, and the number of genera common to both is relatively small.

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B. Quantitative differences in the TF and CR litter decomposing fungi (saprophytes) — A comparison between our tables and particularly a glance at table III which reflects our counts under equal meteorological and seasonal conditions in both TF and and CR shows significant diffrerences, whereby the fructification (and therefore the number of active mycelia) is indeed considerably smaller in CR than in TF. Consequently the rate of decomposition observed in CR, can be satisfactorily explained by this observation regardless of the accessory role other decomposers may or may not play (see Discussion).

A further difference, perhaps of lesser significance, is the fact that during transition from rainy to dry season the lignicolous component of the litter decomposers increases in CR while in TF it decreases in percentage except in cases where the carpophore production is too small to be statistically significant (see table I).

C. Comparison of neotropical ectotroph forests and ectotroph forests of the south-temperate zone — A previous study of the macro-fungi of the Patagonian Nothofagetum (Singer, 1971; Singer & Moser, 1965) permits a comparison during the time of maximal fructification of a temperate with a neotropical ectotroph-dominated forest (CR). If the data on the former are adjusted to equal surface (5m²) the figures for total carpophore production and for folicicolous fungi are remarkably close in both communities. A lower percentage of carpophores in the lignicolous category in the *Nothofagus* forest corresponds to the generally lower number of lignicolous fungi in temperate as compared to tropical forests, an the higher number of ectomycorrhizal Basidiomycetes in the Nothofagetum *(N. pumilio)* is easily explained by the (a) shorter fructification period and (b) higher density of the ectotrophically mycorrhizal trees in the *Nothofagus pumilio* forests. ■

D. Ectotroph dominance — As pointed out in Introduction and above, CR differs basically from TF in that the former, according to definition, is a typical ectotroph forest, the latter an anectotrophic forest as had been anticipated

(Singer, 1978a and 1978b). This involves a different type of N and P cycling (Went & Stark, 1968) and to a certain degree also C cycling (Lundeberg, 1970), and will inevitably express itself in the characteristics of litter and soil (Harley, 1975).

E. Distribution patterns of the mycoflora of TF and CR — In previous studies by the senior author it has been stated (Singer, 1971; Singer & Moser, 1965) that in ectotroph forests a smaller percentage of the observed fungi is subcosmopolitan or widespread (in the sense that these species occur also outside their communities and over an extensive area) than in the anectotrophic forests. We cannot compare the percentage figures obtained in the papers quoted and in unpublished surveys in the Andine Alneta and adjacent anectotrophic forests with precise figures resulting from the present study while the identification of many species is still pending (see Results). The dominant species in TF belong no doubt in their majority to the widespread type (and are different from those of CR), and the list of the ectomycorrhizal species of the campinarana shows only 34.3% occurring also outside the Rio Negro campinas, where several of these accompany their host tree (e. gr. *Aldina heterophylla)* no further than into the blackwater igapós or the secondary or destroyed forests of Amazonia. Only two of these species are common to CR and TF. Some of the species are much more closely related to paleotropical species than to either temperate or neotropical species, particularly *Strobilomyces pauper* (the genus *Strobilomyces* is new for South America, but is well represented in Africa). However, even in the TF there are several examples of genera restricted to Amazonia and the paleotropics (e. g. *Podabrella)*.

DISCUSSION

From the results here reported it can be deduced that in test plots I and II (TF) the litter decomposing fungi are much more numerous than in plot III (CR) or in Patagonian ectotroph forests. The proportion of litter decomposers measured by carpophore numbers on equal surface in TF and CR respectively varies between 1 : 3.7 and 1 : 4.2.

These figures explain to a large degree the accumulation of litter in CR and in the Patagonian forest and its rapid turnover in TF, but in order to be generalized our results must be compared with those obtained on the activities of other litter-decomposing organisms of the same or comparable forest communities. Dr. H. Lieth has kindly permitted us to quote his report (1978), still unpublished as this is written, on the data obtained by B. Katz with litter samples collected by H. Lieth in San Carlos, Venezuela at two different localities, one characterized as groundwater podzol and the other as latosol. These may be assumed to correspond respectively to CR and TF. Katz was able to isolate a total of 67 (surface litter), 61 (root zone litter), and 39 (below root zone litter) Deutromycetes isolates in latosol and 12 respectively 8 respectively 8 such isolates in the podzol zone. As for bacteria, yeasts and "Phycomycetes", the corresponding figures are 41, 43, 23 in latosol and 33, 44, 48 in podzol. Since Katz's microorganisms of surface litter + root-zone correspond to the foliicolous fungi counted by us, we find for all microorganisms observed in these zones (ages), (and including the two Basidiomycetes, one Ascomycetes and 5 Mycelia sterilia) a total of 220 isolates in latosol and 111 isolates in podzol. This proportion becomes even more significant when we compare the Fungi Imperfecti alone (132 vs. 26), i.e. there is a ratio of 5 : 1. These rations correspond very favorably to ours on foliicolous Higher Fungi (see table III), and appear to confirm the applicability of our method as well as the general value of the resulting data for not merely one single group of fungi but for the sum of all litter fungi. On the other hand the animal communities, especially insects, playing a positive role in litter decomposition, are according to Janzen (1974) reduced in numbers and variety in the tropical nutrient-poor white sand soils.

Janzen (1974) made many observations in paleotropical white sand forests, particularly . Dipterocarpaceae-dominated ones. Although he quotes Brunig and Stark for the frequence of "mycorrhizae" in tropical podzols, he does not seem to be aware that trees of this family, particularly *Shorea* (Bakshi, 1974; Singer, 1971;

Singer & Singh, 1971) are ectomycorrhizal, with Boletaceae, Russuloceae, Amanitaceae and other ectomycorrhizal fungi present in abundance. Consequently, and Janzen makes of a point of it, these paleotropical communities belong, althrough to different associations, in the group of white-sand or blackwater forest communities and are ecologically comparable with our campinarana, and igapó, having all the main characteristics of these viz. those indicated in the comparison between TF and CR, A. Jazen and some ather observers are particularly impressed by the "scleromorphism" or "sclerophylly" (undoubtedly a useful mechanism of nutrient conservation in the living plant) and abundance of "secondary substances" (polyphenols, alkaloids) in these forest communities, whereas mycologists are impressed by what we consider the most important common denominator, viz the fact that all the nutrient-poor white-sand and black-water forests we know are typical ectotroph forests. Both these observations — scleromorphism with toxic substances in the litter and ectomycorrhiza predominance — have been (Janzen, 1974; Singer, 1978b) considered to be, either one or the other, the main reason for the litter accumulation in CR and similar stands. Prance *et al.* (1976) observed in a 10 x 80 m lot of TF immediately adjacent to our test plot among the 29 tree individuals with 15 cm or more diameter, as many as 15 with latex or phenolic substances, i.e. over 50%. Whatever the corresponding percentage in CR might be, it is hard to imagine that it might be responsible for a reduction of litter decomposing fungi to a quarter of those in TF. There is no proof of a negative influence of these secondary substances in the litter upon the fungi and other microorganisms decomposing it and even less so on fungus growth in general; on the contrary, the regular and abundant development of mycorrhizal fungi shows that at least these — Zygo-and Basidiomycetes — are not affected and that many or most litter-decomposing fungi appear to be perfectly adapted to develop and assimilate normally on freshly fallen CR litter as well as on living and dead woody substrata. On the contrary, a tannin-rich zone underneath the mantle in the

roots of ectomycorrhizal trees seems to be normal and even characteristic for most short-roots (Bakshi, 1974; Bowen, 1973). Capacity to form tannin-rich tissue appears to be a condition rather than a hidrance for the establishment of functioning ectotrophs. Thus the ultimate cause of the reduced activity of litter decomposers in the ectotroph forest is — if secondary substances play any rôle at all — the selective capacity of certain tree species to form ectotrophic mycorrhiza. In order to uphold the toxicity hypothesis one would have to believe (and has believed, cf. Janzen, 1974) that the decomposers can attack the litter only after it has been leached out and its toxicity correspondingly reduced. Our own observations here reported, and those of others (Lieth, 1978) show that the uppermost recently fallen litter is the one richest in observable, active and isolable fungi even when freshly fallen sclerophyll-leaves have anti-leaching shingle-like arrangement (Herrera et al., 1978). Furthermore, if the leaching of the litter by rainfall were responsible for the softening and detoxication of the substratum, and thus the accessibility of the material for fungus attack, the number of mycelia in the upper, freshest, litter layer would be much less drastically reduced during the period of little or no precipitation in the anectotrophic forest (terra firme) than in the ectotroph forest (campinarana). This is not the case as becomes evident on table III.

We do not question the statements (Janzen, 1974) emphasizing the scarcity of assimilable non-toxic nutrition in the black-water and white-sand communities when applied to animals, and particularly arthropods. This seems to be confirmed by recent authors who observed a relatively small (1 - 2%) leaf area consumed by insects (Herrera et al., 1978). It is not quite clear whether the many insects feeding on fungus mycelium and carpophores reduce or increase (by spore dissemination) the overall litter decomposition by fungi, and whether litter reduction by animals (with smaller communities and, it seems, smaller average size of individuals) as a whole is a lesser factor in the ectotroph forests than in the anectotrophic forests of Central Amazonia (cf. Fittkau & Klinge, 1973; Schubart, 1977).

The notion that scleromorphic formations, admittedly abundant in ectotroph forests, may have a decisive influence on the rate of litter decomposition has obviously arisen from the field and laboratory experiments (Cromack Jr. & Monk, 1975; Daubenmire & Prusso, 1963; Melin, 1930; Shanks & Olson, 1961) referring to differences in decomposition rates in various species of trees, components of temperate forests in North America. Aside from still unsolved difficulties related to methods and techniques it must be remembered that in the temperate ectotroph forest different elements may well show different decomposition rates but that these data cannot apply to a comparison of a tropical anectotrophic with a tropical ectotroph-forest, both with a much higher diversity of litter origin and litter characteristics, with a larger number of presumably adapted forms of litter-decomposing microorganisms, much longer yearly periods of activity and a sharply differing extent of ectomycorrhizal development.

An alternative mechanism, which may well be mainly responsible for the reduced litter decomposition in the campinarana stands, has first been suggested by Harley (1975 and 1977). It is the only one that has been experimentally confirmed (Gadgil & Gadgil, 1971) by showing that in the absence of ectomycorrhizal (pine) roots, litter decomposition was significantly higher during a 12 months period than in a plot where the roots were left intact. Harley's hypothesis would attribute this to "short cycling" of nutrients, mineral nutrients in the first place (but possibly also competition for carbon sources by that minority of ectomycorrhizal fungi which are capable of utilizing the polysaccharides of the substratum), thus depriving the entire population of the saprophytic fungi living in soil and litter of an essential part of the available N and P compounds.

In the lower layer of the litter another factor may also to a variable degree be responsible for the smaller number of saprophytes. The exudates originating from ectotrophically mycorrhizal fungi and/or from other fungous elements of the rhizosphere frequently include antibiotics which may selectively influence the populations of soil microorganisms

far beyond the rhizosphere proper although they will hardly affect the microflora of the most recent litter layer above the root level.

Whatever the quantitatively most important mechanism of limiting the activity of saprophytes in the campinarana may be, it is obvious that it is basically the dominance of the ectotroph that is required for its functioning. Consequently, we assume the causal sequence of the phenomenon to be as follows: Oligotrophy, leading to ectotroph dominance, leading to raw humus accumulation.

A recent study (Herrera et al., 1978) using clippings of fresh leaves superimposed on growing rootlets demonstrates transference of P from the leaves to the rootlets in laboratory conditions. The authors, unfortunately, do not identify the type of the forest community or the fungus but its origin in the Upper Rio Negro region and the dominance of Eperua leucantha, the description of the soil as oligotrophic and the fungus mycelium as septate make it virtually certain that the phenomenon described refers to an ectotrophically mycorrhizal fungus in an ectotroph forest of the igapó or campinarana type. At any rate we have experimental evidence of direct cycling of P. This would be exceptional in the latosol terra firme forest where mineral nutrient absorption by the feeder roots seems to be basically sufficient for nutrient conservation in a virtually closed cycling system, but it is, on the basis of our observations of identified ectomycorrhizal partners, characteristic for the Amazonian ectotroph forests.

We are not in a position to introduce a comparative study on the relative importance of endotrophic mycorrhizae in the forest communities under consideration. Orchid mycorrhizae (Basidiomycetes) do occur in both TF and CR. So do VA mycorrhizae according to data kindly supplied by Dr. T. St-John in both campinarana and terra firme forest although the dominant tree species in the test area TF are either devoid of them or have them only sporadically (personal communication, and communication at the Second North American Mycorrhiza Conference Athens, August 1977). Even assuming that both types of

endomycorrhiza are quantitatively equally represented in campinarana and terra firme forests, their impact, although certainly significant for the physiology of the individual tree associated with it (cf. i.a. Daft & Hacskaylo, 1977), cannot be more than accessory on soil and litter of the ectotroph forest when compared with the impact of ectomycorrhiza. The biomass and enormous extension (cf. Burgess & Nicholas, 1961; Trappe & Fogel, 1977) of the mycelial hyphae ectomycorrhizae cannot be matched by VA mycorrhizae, while orchid mycorrhiza is too habitat-restricted to greatly influence the soil and litter formation. Unfortunately, not only in the tropics, but also in temperate regions, there are few data permitting a quantitative comparison of extension and biomass of these three types of mycorrhizae. Those — perhaps not fully representative — estimates available to us suggest a ratio of over a million to one in terms of ectomycorrhizal sclerotia versus VA-sporocarps in temperate forests (Göbl, 1965; Kessler & Blank, 1972; Trappe & Fogel, 1977).

The influence of nitrogen-fixing bacteria has still to be determined. Considering the importance of leguminosous trees in neotropical forest communities, one would obviously wish to supplement mycorrhiza studies with quantitative, comparative studies on nitrogen fixing systems in campinarana and terra firme vegetation. But nodules are practically absent in TF (Rosemary S. Bradley, personal communication). Neither Singer (1978b) nor Herrera et al. (1978, 1978a) have missed the significance of their respective data with regard to the deterioration of tropical ecosystems and soils when the primary forest is partially or totally destroyed (cf. Schubart, 1977). Once we understand the decisive rôle of ectomycorrhiza in the poor white-sand soils, we cannot but wonder whether introduction of ectotrophs previous to forest removal will not permit the formation of a deep raw humus layer even in the latosol forest and thus lend a higher degree of stability to the soils after cutting by increasing resistence to the development of an unfavorable soil microflora and erosion.

In the hands of specialists, our relatively simple methods produce fairly constant, reliable results, matching other available quantitative data which seem to be consistent with accepted theory. They reveal however no consistent behavior in the phenology of lignicolous Agaricales, terricolous basidiolichens and fungi decomposing monocotyledonous litter and give no clue as to the conditions necessary for their development insofar as it appears different from that of the foliicolous fungi. In the case of the monocot litter, the reason may perhaps be the relatively smaller amount of litter derived from Monocotyledones and a different leaf shedding rhythm of these plants. The behavior of the Basidiolichens on our plots is erratic because we have here a different and largely self-contained association which requires a separate study. What is remarkable in this case is that they appear to be linked with a special habitat — raised or denuded (by vertebrate activity ?) mineral soil — and that they appear in large quantities but erratically during certain periods of the rainy season. While their appearence is most noticeable in one restricted locality, they are totally absent in similar habitats in other localities where they have been observed before. The limited time necessary for their development suggests the possibility that there might be some insufficiently explored phenomenon at hand which we may call micromigration.

Another problem, more important for the present study, is that of the lignicolous group of fungi. In test area I, we have counted in the same (lignicolous) category, all Agaricales growing on dead wood, including those appearing on one rotting tree trunk (Eschweilera) crossing part of the test plot (no such trunks were present on test areas II and III). All the high counts of lignicolous fungi in test area I were due to mass fructifications on the Eschweilera trunk. Here, the various mycelia at work are more extensive, apparently compatible with each other within the substratum but with a specific, limited fruiting periodicity which depends on the degree and duration of availability of a water surplus

within the substratum rather than the precipitation even if a six day period previous to the counting date is considered. Furthermore, the respective species were not restricted to the primary latosol terra firme forest but occurred likewise in other communities, i.e. forming part of the characteristic dead-wood mycoflora` which appears after falling and persists in the secondary forest, joining there such characteristic species as *Schizophyllum comune*, *Pycnoporus sanguineus*, *Pleurotus hirtus*, *Panus crinitus*, *P. rudis*, *P. badius*, some species of *Gymnopilus* and *Marasmiellus*. On the other hand, species growing on small fragments of dead woody matter mixed into the litter had fewer carpophores per species at a given time and showed a fruiting pattern similar to that of the other litter fungi. In future assays, it should probably be decided to either exclude the trunk-and log-inhabiting fungi altogether, or, if their particular rôle and fruiting pattern is considered essential for the study, they should be separated into a special category. It is difficult to decide just where the limit of substratum volume should be set; this limit might be at the point where substratum size begins to be little influenced by external humidity, i.e. does not dry out or become wetted thoroughly at the same rate as the rest of the litter.

Resumo

A aplicação de um método micossociológico (adaptação do método de Lange) na Amazônia Central produziu os seguintes resultados: Na campina-

rana, tipo de floresta sobre podzol de areia branca, as árvores dominantes são, obrigatoriamente, ectotroficamente micorrizais; a liteira é acumulada como humus em consequência da dominância de ectótrofos; tanto na estação seca bem como na úmida, o número de folhas habitadas por fungos da liteira é menor do que o número encontrado na floresta úmida de terra firme sobre latossol e os fungos dessa categoria são aqui, mais fortemente representados ("F-dominância") por outras espécies do que nas áreas testadas de terra firme. As árvores ectomicorrizais e fungos são enumerados. Por outro lado, na floresta de terra firme, não ocorreram fungos ectotroficamente micorrizais nas áreas testadas. Na floresta primária de terra firme, quase todas as árvores não são ectomicorrizais; a liteira não é apreciavelmente acumulada como uma camada profunda de humus porque o considerável número de fungos habitantes das folhas da liteira (relação de 4:1 a 4.2:1 em favor da terra firme) e a grande diversidade (um grande número de espécies) permitem que a decomposição seja, potencialmente, maior do que a quantidade de folhas que cai anualmente. Neste estudo, um grupo de fungos que não é representado em experimentos de decomposição da liteira em laboratório, foi principalmente enfocado. Contudo, uma comparação com dados publicados e não publicados mostra que os nossos resultados igualaram satisfatoriamente os dados obtidos com outras classes de microrganismos e observações em outras regiões. No grupo folícola, a quantidade de fungos decompositores da liteira depende, principalmente, da precipitação durante os dias anteriores à contagem. Isto não é válido para todos os fungos lignícolas. As razões para isso, bem como o mecanismo pelo qual os fungos ectomicorrizais podem reduzir a taxa de decomposição da liteira e influenciar os padrões dos ciclos de nutrientes, são discutidos. Os mais importantes gêneros de Basidiomycetes envolvidos na decomposição da liteira nas associações florestais do baixo rio Negro são enumerados. A possível significação econômica de introdução de ectótrofos na floresta de terra firme é indicada.

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TABLE I — Precipitation (in mm) and carpophore count for 37 collecting dates in plot I, TF with respective numbers of carpophores per species (ca/sp.) and F-dominance.

N.° collect	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
Day	21 AP	4 M	11 M	17 M	25 M	3 JN	14 JN	23 JN	29 JN	6 JL	13 JL	22 JL	29 JL	8 AU	18 AU	29 AU	8 S	20 S	30 S	10 O	20 O	31 O	10 N	25 N	5 D	15 D	26 D	2 JA	10 JA	18 JA	30 JA	9 F	20 F	2 M	13 M	23 M	3 AP
Precipitat previous day	5	0	4	20	3.8	0	0	0	3.2	0.2	7	0	0	0	0	0	0.1	7	45.8	0	6.7	0	0	0	4	0.4	12.3	0	24	7.6	1.7	4.5	5.4	27.3	0	3.7	2.7
Two days	5	0	4	20	6.4	33	2	0	9.2	0.2	7	1.2	4.1	0	0	1.5	3.4	8.4	64	0	18.4	8.9	7.9	0	5.4	9.4	12.3	11.8	50.5	29.7	1.7	4.5	7.3	27.3	0	3.7	2.9
Three days	11	3	9	20	6.4	33	2	4	16	10.2	7.5	1.4	4.1	0	0	1.5	3.4	10.5	71.4	17.9	20.8	30.4	25.2	0	13.4	9.4	29.3	11.8	53	29.7	3.5	4.6	25	27.5	4.4	12	7.1
Six days back	85.8	26	47.1	22.4	8.2	49.2	7.4	10	25.8	25.8	15.7	1.4	26.1	4.9	1.8	3.8	19.3	20.4	108.5	38.5	77.3	33.8	38.3	0	35.8	80.4	71.3	27.5	103.7	29.8	53.9	46	25.8	48	187.8	27.1	41.9
Fol	124	79	114	182	136	69	124	109	131	144	261	0	18	23	6	18	73	70	44	51	165	44	87	1	212	176	321	87	220	103	115	376	155	259	36	258	200
Lign.	176	42	9	104	857	231	130	12	3	3	27	6	3	9	0	0	0	29	410	535.5	359	192	77	3	22	281	512	1038	354	15	24	468	94	103	9	100	134
Monocot.	0	5	0	0	0	1	0	0	0	3	0	0	0	0	0	0	0	0	2	0	0	0	25	0	0	0	0	0	2	0	0	0	0	0	20	0	1
Terricol.	3	3	1	3	2	4	0	0	3	1	9	0	0	0	0	0	0	0	1	0.5	0	4	0	0	0	0	8	7	4	5	1	4	0	9	2	4	8
Bas.-liq.	0	0	0	0	22	21	23	13	0	11	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	2	3	0	0	0	3	0	0	0	0
TOTAL	303	129	124	289	1017	326	277	134	137	162	303	6	21	32	6	18	73	99	457	587	524	240	189	4	234	457	845	1134	582	123	140	848	252	371	67	362	343
Fol. ca/sp.	11.3	7.9	7.6	12.1	12.5	5.8	7.3	6.8	11	9.6	12.4							8.8	5.5	4.5	11	4.4	6.7		10	8.8	10	3.8	7.3	8	5	12.5	6.7	10.4	3.6	8.9	9.5
Lign ca/sp.	25	7	1.8	21	171.4	12	16.3	3	1	1	3.4							9.7	68.3	44.6	32.6	24	25.1		10	35.1	24.4	103.8	1.9		4.8	31.2	6.8	5.2	4.5	7.7	8.9

Dominant fruiting of foliicolous (A) & lignicolous (B) populations. Figure refers to number of carpophores of each

N.° collect	A	B
1	Mycena polyadelpha (53)	Mycena osmundicola (83)
2	Myc. polyadelpha (29)	Marasmius lecythidacearum (29)
3	Myc. polyadelpha (56)	—
4	Myc. polyadelpha (94)	Hydropus hypopolius (190)
5	Myc. polyadelpha (104)	Hydropus omphaliniformis (850)
6	Myc. polyadelpha (48)	Hydr. omphaliniformis (130)
7	Myc. polyadelpha (88)	Hydr. omphaliniformis (88)
8	Myc. polyadelpha (72)	—
9	Myc. polyadelpha (69)	—
10	Myc. polyadelpha (88)	—
11	Myc. polyadelpha (153)	—
12	—	Polyporus leprieurii (5)
13	—	—
14	—	—
15	—	—
16	Marasmius iodactylus (15)	—
17	Mar. iodactylus (26)	—
18	Myc. polyadelpha (26)	Mycena umbilicata (26)
19	Myc. polyadelpha (19)	Lactocollybia aequatorialis (400)
20	Myc. osmundicola (28)	Mar. lecythidacearum (450)
21	Mar. iodactylus (50)	Marasmius B 10208 (185)
22	Myc. polyadelpha (50)	Collybia flavipes (93)
23	Myc. polyadelpha (138)	Lactoc. aequatorialis (75)
24	—	—
25	Myc. polyadelpha (138)	Lactoc. aequatorialis (20)
26	Myc. polyadelpha (75)	Lactoc. aequatorialis (260)
27	Myc. polyadelpha (86)	Marasmius B 10401 (242)
28	Myc. polyadelpha (11)	Hydr. omphaliniformis (900)
29	Myc. polyadelpha (93)	Hydr. omphaliniformis (270)
30	Myc. polyadelpha (60)	—
31	Myc. polyadelpha (41)	Stigmatolemma hyalinum (20)
32	Myc. polyadelpha (87)	Pyrrhoglossum sejunctum (4)
33	Myc. polyadelpha (62)	Hydropus B 10693 (51)
34	Myc. polyadelpha (128)	Marasmius B 10883 (50)
35	Myc. ionocephala (14)	—
36	Myc. polyadelpha (94)	Mar. B 10833 (35)
37	Myc. ionocephala (101)	Mar. B 10833 (50)