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Ectomycorrhizal fungi and their leguminous hosts in the Pakaraima Mountains of Guyana

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Ecologically important ectomycorrhizal (EM) associations are poorly known from equatorial rain forests of South America. Recent field studies in the Pakaraima Mountains of western Guyana revealed previously undocumented forests dominated by EM leguminous trees, with a rich assemblage of EM mycobionts. Along transects, basidiomes from 75 species or morphospecies of putatively EM fungi were spatially associated with leguminous host trees. These fungi belonged to the basidiomycete families *Boletaceae*, *Amanitaceae*, *Russulaceae*, *Cortinariaceae*, *Cantharellaceae*, *Clavulinaceae*, and *Entolomataceae*, all of which are poorly documented from the lowland neotropics. Ectomycorrhizas were confirmed on *D. corymbosa*, *D. altsonii*, and *D. jenmanii* (*Caesalpiniaceae*, tribe *Amherstieae*), and a fourth species, *Aldina insignis* (*Papilionaceae*). The tribe *Amherstieae* contains most of the EM leguminous species forming monodominant forests in Guineo-Congolian Africa. *Dicymbe* species constituted the first record of EM *Amherstieae* in the New World. A variety of other co-occurring caesalpiniaceous trees failed to exhibit ectomycorrhizas. Transect surveys indicated that *D. corymbosa* and *D. altsonii* were: (1) highly clumped and dominant at specific sites; (2) occurred on soils with widely varying chemical and textural characteristics; and (3) the most important hosts for EM fungi in the local landscape. *Dicymbe* species have life history attributes, including the ectomycorrhizal habit, which enhance their competitive abilities irrespective of soil conditions. The spatial restriction of EM fungal basidiomes indicated that discrete groves of EM trees harbour an important component of regional macromycete diversity.

INTRODUCTION

Much observational and experimental evidence demonstrates that mycorrhizal symbioses are ubiquitous features of terrestrial plant communities and are ecologically important (Boucher 1985, Allen 1991). The primary benefit of these symbioses to host plants is that the extraradical hyphae of mycorrhizas promote uptake of poorly mobile nutrient ions which are transferred to the host (Smith & Read 1997). Of the two most common mycorrhiza types, arbuscular mycorrhiza, formed by fungi in the order *Glomales*, are widespread in temperate and tropical ecosystems and occur in a broad range of vascular plant families (Newman & Reddell 1987). Ectomycorrhizas, on the other hand, are formed with larger basidiomycete and ascomycete fungi, and are mostly known from temperate and boreal regions, where they associate with a narrow range of host plant families, primarily the *Pinaceae*, *Fagaceae*, *Betulaceae*, and *Salicaceae*, as well as *Myrtaceae* subfamily *Leptospermoideae* in Australia (Smith & Read 1997). Ectomycorrhizal fungi are concentrated in specific basidiomycete (e.g. *Russulaceae*, *Boletaceae*) and ascomycete (e.g. *Elaphomycetaceae*) families and account for at least 30% of the known diversity of fleshy fungi worldwide, numbering at least 5000 species (Miller 1983, Molina, Massicotte & Trappe 1992, Hawksworth *et al*. 1995). A growing body of evidence suggests that ectomycorrhizas have different abilities for exploration and exploitation of soil compared to arbuscular mycorrhizas which may enhance the competitive abilities of ectomycorrhizal (EM) host plants (Finlay, Frostegard & Sonnerfeldt 1992, Bending & Read 1995, Chen, Brundrett & Dell 2000). Despite the relatively small number of EM vascular plant species (approximately 3% worldwide; Meyer 1973), EM tree species disproportionately occupy extensive areas of forest at higher latitudes (Barbour & Billings 2000).

In contrast to EM-rich temperate forests, tropical rainforest had long been thought to be impoverished in EM associations (Dennis 1970, Pirozynski 1981, Hedger 1985). This impression was based on surveys indicating

a prevalence of arbuscular mycorrhizal (AM) trees in lowland rainforests, and the concomitant lack of typically EM fungal groups (Janse 1896, Redhead 1968, Thomazini 1974, St John 1980, Bereau, Gazel & Garbaye 1997). Hypotheses proposed for the prevalence of arbuscular mycorrhizae in lowland tropical forests centered around the lack of host specificity in AM fungi and the resulting competitive equivalence of host trees, which are acted upon by a variety of factors which foster high tree diversity, such as density-dependent mortality, disturbance and stochastic recruitment, and niche diversification (Connell, Tracey & Webb 1984, Janos 1987, Connell & Lowman 1989).

This paradigm has shifted in recent years. Mycological studies in the paleotropics have indicated a wide diversity of EM fungi in association with caesalpinioid legumes in Africa, and with *Dipterocarpaceae* and *Fagaceae* in Asia (Beeli 1935, Heim 1955, Heinemann 1954, Corner & Bas 1962, Corner 1972, Watling & Lee 1995, Buyck, Thoen & Watling 1996). A few studies have unequivocally confirmed, via root excavations, the presence of ectomycorrhizas on a limited array of tropical trees, including members of the *Dipterocarpaceae* (Singh 1966, Becker 1983, Alexander & Hogberg 1986); *Caesalpiniaceae*, tribes *Amherstieae* and *Detarieae* (Alexander & Hogberg 1986, Newberry *et al*. 1988, Bakarr & Janos 1997); *Nyctaginaceae* (Ashford & Allaway 1982); and *Euphorbiaceae* (Thoen & Ba 1987). In certain areas of the paleotropics, EM trees are not rare but indeed abundant. Examples include *Gilbertiodendron dewevrei* (*Caesalpiniaceae*) which dominates large areas of forest in the Upper Congo Basin of Africa (Richards 1996a). In Southeast Asia, the dipterocarps *Dryobalanops aromatica* and *Shorea albida* heavily dominate areas of a few to hundreds of hectares in the Malay peninsula, Sumatra, and northwest Borneo (Whitmore 1984). Dominance of rainforests by multiple species of *Dipterocarpaceae* is the norm throughout much of Southeast Asia (Richards 1996a). In the paleotropics, the majority of monospecifically dominated forests are formed by EM trees (Alexander 1989, Connell & Lowman 1989) and a number of studies have addressed the role of ectomycorrhizas in structuring these communities (Newbery *et al*. 1988, Torti & Coley 1999, Torti, Coley & Kursar 2001).

Little is known, however, concerning ectomycorrhizas in the vast neotropical rain forests. Evidence from the mainland, low elevation neotropics is limited to collections of EM fungi in association with *Quercus oleoides* in Costa Rica and with the leguminous hosts *Aldina heterophylla* in Central Amazonia (Singer, Araujo & Ivory 1983, Singer, Garcia & Gomez 1991) and *A. kunhardtiana* and *A. latifolia* in southern Venezuela (Moyersoen 1993). In addition, Singer & Araujo (1979) confirmed ectomycorrhizas on *Glycoxylon inophyllum* (*Sapotaceae*) and an unidentified species of the gymnosperm liana *Gnetum* from the Central Amazon of Brazil. Scattered records exist for ectomycorrhizas on species of *Neea* and *Pisonia* (*Nyctaginaceae*) and *Coccoloba* (*Polygonaceae*) in Venezuela and the Caribbean (Moyersoen 1993, Lodge 1996, Miller, Lodge & Baroni 2000, Henkel & Terborgh, unpubl.). While Singer speculated on the implications of the ectomycorrhizal condition for Amazonian forest trees in terms of plant competition and macrofungal diversity, little ecological or mycofloristic followup work on Singer's pioneering discovery in the South American rain forest has taken place (Singer 1984, Moyersoen 1993).

The recent discovery of putatively EM fungi and EM trees in the Pakaraima Mountains of Guyana has opened important avenues for study of neotropical ectomycorrhizas (Henkel 1999, 2001, Henkel, Aime & Miller 2000, Miller *et al*. 2001, Simmons, Henkel & Bas 2002). Initial field observations suggested that, unlike in temperate zones where EM tree species are widely distributed and often dominant, in the Guyanese rainforests EM associations may be restricted to sharply demarcated stands where leguminous host trees dominate, and absent from adjacent, non-ectomycorrhizal (NEM) mixed forests. This perceived pattern has important implications for role that ectomycorrhizas may serve in structuring rain forest communities. This study characterizes the EM fungi and their host trees in the Upper Ireng Basin of Guyana. Specific objectives were to: (1) unequivocally identify EM host trees; (2) assess the degree of clumping and dominance in EM trees; (3) assess the distribution of EM and saprotrophic macrofungal guilds in various forest types; and (4) assess the relationship between edaphic factors and woody plant community composition along transects.

MATERIALS AND METHODS

Site description

The research site was located along the Upper Ireng River which forms the border between Guyana and Brazil in the central Pakaraima Mountains (general area: 5° 05′ N; 59° 58′ W; Fig. 1). Elevations range from 700 m at riverside to 1800 m along the highest ridgelines. Geology of the area is dominated by sandstone and related sedimentary rocks of the Roraima Formation, which forms the eastern extension of the Guayana Highlands (Gibbs & Barron 1993). The Roraima Formation is of great antiquity, with a minimum age of 1.6 Byr, with subsequent periods of step-faulting and uplift (Gibbs & Barron 1993). The resulting terrain of this greatly eroded landscape is of high relief and characterized by deeply cut creek and river valleys amidst remnant plateaus and pinnacled ridgelines.

Annual rainfall for this remote area was inferred from records spanning the years 1935–47 at a Potaro River site located approximately 100 km to the northeast, at the eastern edge of the Pakaraima escarpment (Fanshawe 1952a). Mean precipitation was 3866 mm a^{-1} with a pronounced peak in May and June, a lesser

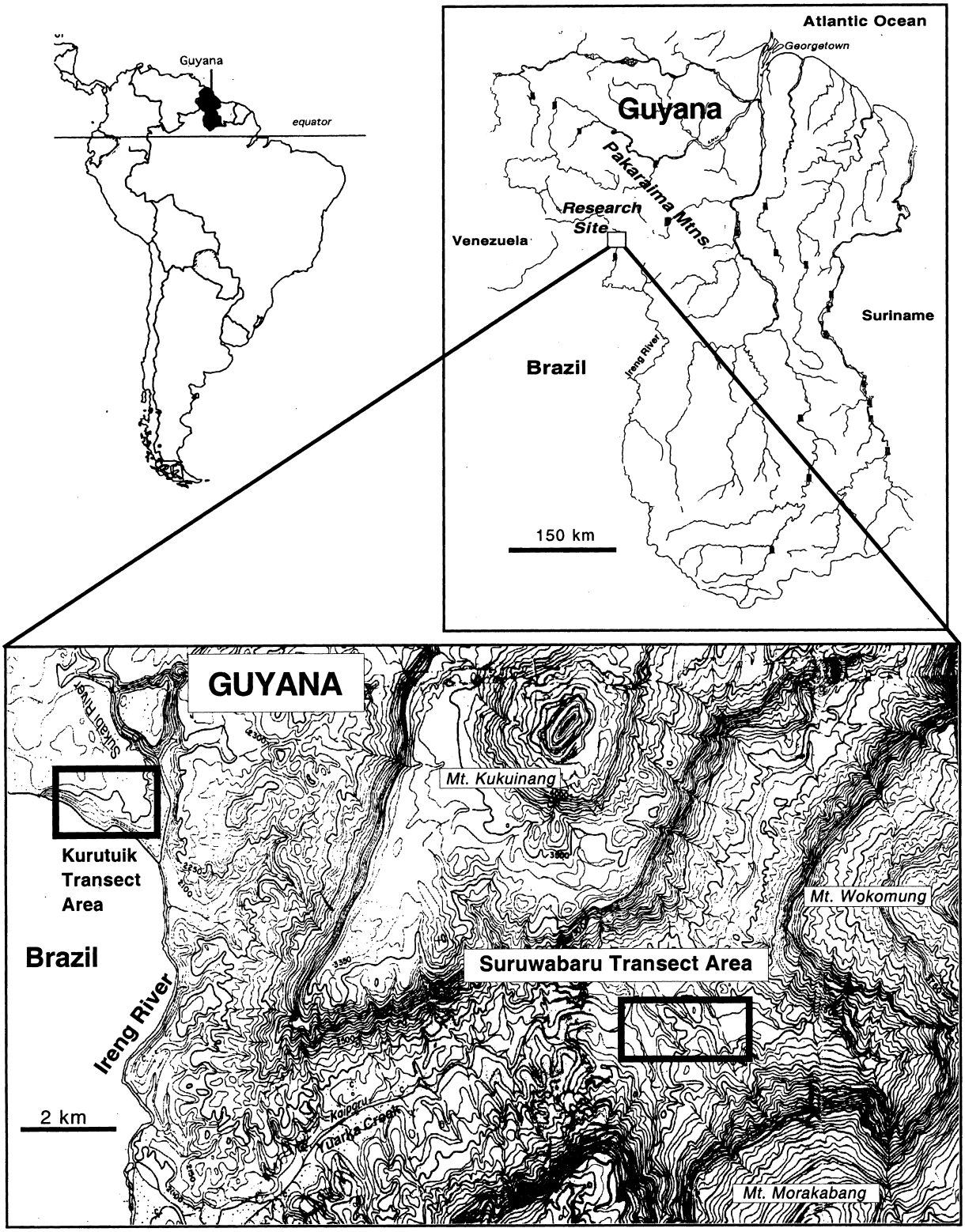

Fig. 1. Map showing Guyana, location of research site in the Pakaraima Mountains, and transect areas in the Upper Ireng River Basin.

peak in December and January, and relatively drier periods between (Fig. 2a). At the Ireng site rainfall peaks during May–June occurred every 2–3 d during 1998 and 1999 (Fig. 2b), and were sufficient to stimulate continual fruiting of macrofungi. Regional temperature records were unavailable, but during the equivalent periods of 1998 and 1999 temperatures were remarkably constant at the Ireng site (daily max.: 25–29 °C; min.: 19–21 °). In general, these data correspond to a classification of Submesothermic Ombrophilous Climate as indicated by Berry, Holst & Yatskievich (1995).

Vegetation of the region corresponds to the Dry Evergreen Forest Formation of the Pakaraima Montane Region (Fanshawe 1952a). Fanshawe considered

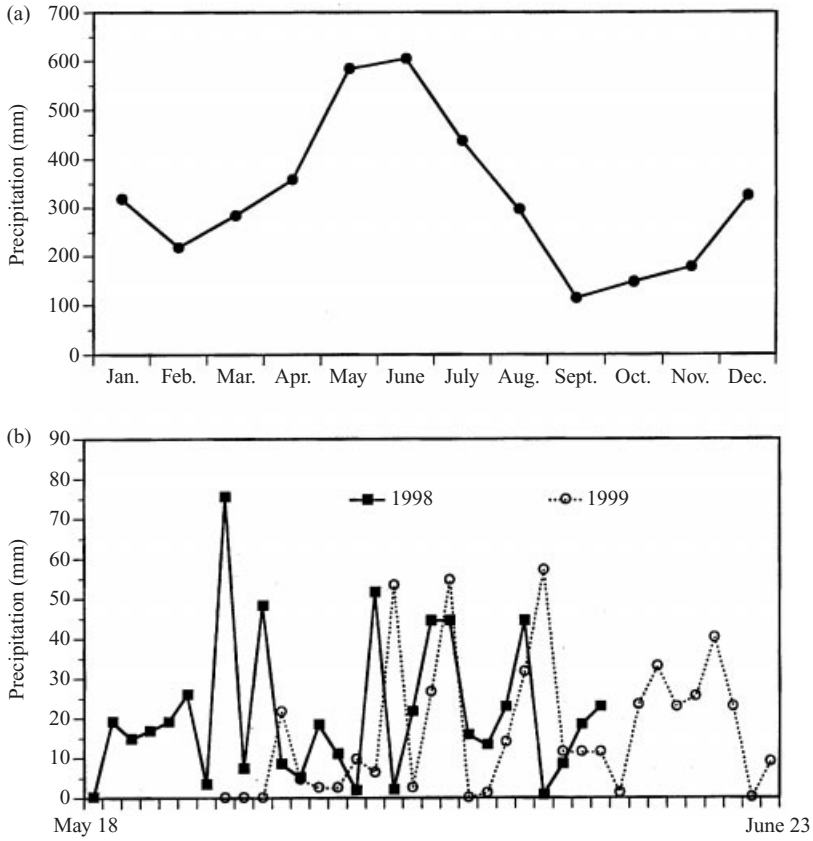

Fig. 2. (a) Mean monthly precipitation at the Potaro River Station, Pakaraima Mountains, British Guiana, 1935–1947 (annual mean = 3866 mm). (b) Daily precipitation at the Upper Ireng River site over a 37 d period during successive rainy seasons, 1998 and 1999.

this formation to predominate throughout the entire sandstone belt composing the Pakaraima Mountains, being subdivided into various associations and facia-tions with attendant dominant tree species according to degree of soil drainage, the series running from sclerophyllous savanna on the most poorly drained sites to well-drained, high canopy forest dominated by species of *Eperua* and *Dicymbe* (*Caesalpiniaceae*) and associated trees.

Soils are generally poor due to the sandstone nature of the parent materials. White and brown sand soils predominate throughout the Pakaraima region. Soils with higher clay content occur in areas where igneous intrusive materials have been exposed and eroded at the surface (Fanshawe 1952a). Soil impoverishment is further evidenced by the abundance of tannin-rich 'blackwater' streams throughout the region (Janzen 1974).

Ectomycorrhizal sampling

Ectomycorrhizal status of a variety of leguminous tree species was assessed during the rainy season of May–June, 1998. All trees were sampled within a five kilometre radius of a permanent base camp at the mouth of the Sukabi River, a major tributary of the Upper Ireng watershed (Fig. 1). The following tree species previously suspected of being ectomycorrhizal were sampled: *Dicymbe corymbosa*, *D. altsonii*, *D. jenmanii* (*Caesalpiniaceae*, tribe *Amherstieae*), and *Aldina insignis* (*Papilionaceae*). Other caesalpiniaceous canopy tree species occurring in the area were sampled, including: *Tachigali* sp., *Mora gonggrijpii*, *Eperua falcata*, *Dimorphandra macrostachya*, and two un-identified species of *Macrolobium*. Superficial roots were excavated, starting from the trunk and working towards the ultimate fine roots. Rootlets were examined under magnification in the field for the presence of a fungal mantle. Rootlets (1–5 g) were fixed in form-aldehyde-acetic acid (FAA). Voucher specimens of all root samples were maintained in FAA.

Rootlets were gently excised and washed with tap water. Freehand sections were stained with Congo red and observed with light or phase contrast microscopy. Rootlets were considered to be ectomycorrhizal when they had a distinctive mantle and Hartig net (Agerer 1991).

Vegetation and fungal sampling 1998

Transects – Vegetation

As a preliminary study to characterize forest stands and distribution of ectomycorrhizal fungi, a site was chosen near Kurutuik Falls on the Upper Ireng River, 1 km upstream from the Sukabi base camp (Fig. 1). The area was previously observed to have an array of distinctive

forest stands including those with a preponderance of *Dicymbe corymbosa* (Henkel, Ryan & Chin 1993). All forests were primary with no signs of prior anthropogenic disturbance. The site was situated on upland terrain along the northeastern bank of the Ireng River between 700–800 m elevation. Three belt transects were positioned to pass through stands exhibiting *Dicymbe* dominance and transitions to adjacent mixed forests. Transect 1 ran approximately northwest to southeast, parallel to the Ireng River at a distance of 500 m, for a length of 1000 m; transect 2 ran parallel to transect 1 at a distance of 200 m from the Ireng River, for a length of 1000 m; transect 3 was perpendicular to transects 1 and 2, bissecting them near their midpoint, and terminated at the river's edge for a length of 750 m. Transects were subdivided into 50 m sampling intervals. Within each interval, diameter at breast height (dbh) was measured for all trees > 10 cm dbh within 1 m of the transect tape. Trees were assigned to families and identified to genus and species when possible, or otherwise assigned to morphospecies according to the guidelines of Richards (1996b). Basal area values and number of stems were calculated for each tree species per 50 m interval, and relative dominance (% of total basal area), relative density (% of total number of stems), and frequency (number of intervals occurring in) were calculated for the most prevalent species. To provide an overall idea of tree dominance over the area sampled, data from all three transects were combined and relative dominance, density, and frequency were calculated for the 12 most prevalent species (Greig-Smith 1983). For the purposes of this study, tree species in which ectomycorrhizas were unequivocally confirmed were grouped into an 'EM' category; all other tree species were were considered to be non-ectomycorrhizal and grouped as 'NEM'. Voucher specimens primarily in sterile condition were obtained for all species recorded and deposited at the University of Guyana (BRG) and the US National Herbarium (US).

Transects – EM fungi

An initial assessment of the co-occurrence of EM basidiomes with putative host trees was made on two dates coinciding with the onset of the rainy season in 1998. On 18 May and 7 June the Kurutuik transects were walked and numbers of EM basidiomes within a belt two metres wide on either side of the transect line were recorded for each 50 m segment. Fungi were considered to be putatively ectomycorrhizal if they were members of the basidiomycete families *Boletaceae*, *Amanitaceae*, *Russulaceae*, *Cortinariaceae*, *Cantharellaceae*, or *Entoloma* subgenus *Entoloma* (Miller 1983, Singer 1986). In addition, six undescribed species of *Clavulina* and two undetermined morphospecies of clavarioid fungi that fruited exclusively under *Dicymbe* were included in the EM group (Thacker & Henkel, unpubl.). Fungi were assigned to families and identified to genus and species when possible, and otherwise assigned to morphospecies. Generic designations for *Agaricales* followed Singer (1986) and Dennis (1970); for *Cantharellaceae*, Corner (1966); and for clavarioid fungi, Corner (1950, 1970). Basidiomes of all species were summed over both sampling dates to give the number of EM basidiomes per 50 m interval. Given the brief sampling period, detailed analyses of individual EM fungal species were considered of limited informative value (Bills, Holtzman & Miller 1986, Nantel & Neumann 1992). However, given the strong fruiting response noted for macrofungi during the onset of the tropical rainy season, distribution of EM associations in various forest stands can be assessed by the presence or absence of EM basidiomes, as at least some EM species should be fruiting in any area possessing their below-ground mycelium (Corner 1972, Henkel, unpubl.). Voucher specimens for all species were deposited at the herbarium of the University of Guyana (BRG) and at DUKE.

Vegetation, fungal, and soil sampling – 1999

In May–June of 1999 detailed transect studies were conducted in the vicinity of Suruwabaru Creek, approximately 10 km east of the Kurutuik site (Fig. 1). Two transects were laid out (Suruwabaru 1 and 2): each was 300 m long, 30 m wide, and divided into 30 sampling intervals each 10 m in length. Transects were approximately 500 m apart and situated along N–S uphill clines adjacent to the creek at approximately 700–750 m in elevation. Tree data were obtained for both transects in the manner described for the Kurutuik site. Tree species were grouped into EM and NEM categories as described above.

Basidiomes of EM fungi as well as terrestrial saprotrophic macrofungi were counted every third day along each transect from 22 May to 15 June for a total of eight sampling dates per transect. Terrestrial saprotrophic macrofungi were defined as those in genera normally considered to be saprotrophic whose basidiomes arise from the upper soil horizon or litter layer of the forest floor (*sensu* Miller 1983). Fungi were subsampled from the total transect area by restricting the counts to an area of four meters either side of the center line of the transect (eight metres total width). Data for fungi were compiled for each interval as for the Kurutuik transects.

In order to assess edaphic variability along the transects soil samples were taken at the midpoint of each pair of intervals, for a total of 15 samples/transect. Samples were taken at a 10 cm depth in the mineral soil beneath the leaf litter from a central position in each sampled interval. Samples were air dried to a weight of 100 g, passed through a 2 mm sieve, and stored, upon returning from the field, at 5 °C until analysis. Soil texture was determined using standard particle size analyses (ASTM 1998); extractable P and Al using the Mehlich III extraction (Mehlich 1984), soluble N using a 2N KCL extraction (Dahnke 1990), pH using the

Table 1. Dominance, density, and frequency of woody taxa occurring along the Kurutuik transects (combined transects = 2700 m × 4 m).

Taxon	Family	Relative dominance[b] (%)	Relative density[c] (%)	Frequency[d] (%)
Dicymbe corymbosa[a]	*Caesalpiniaceae*	36.1	20.0	54.5
Micrandra glabra	*Euphorbiaceae*	17.3	14.6	38.2
Dimorphandra macrostachya	*Caesalpiniaceae*	9.9	7.3	41.8
Aldina insignis[a]	*Papilionaceae*	5.4	16.3	32.7
Protium decandrum	*Burseraceae*	3.4	5.8	36.4
Dicymbe jenmanii[a]	*Caesalpiniaceae*	2.8	2.2	7.3
Buchenavia cfr fanshawei	*Combretaceae*	2.4	1.2	5.5
Catostemma altsonii	*Bombacaceae*	2.2	2.2	12.7
Cybianthus sp. 1	*Myrsinaceae*	1.4	1.2	9.1
'Kwaibiek'	indet.	1.1	1.5	9.1
Moronobea cfr coccinea	*Clusiaceae*	0.9	1.7	12.7
Chamaecrista adiantifolia	*Caesalpiniaceae*	1.0	1.7	12.7
	Total = (above 12 taxa)	83.9	75.7	(100)
	Remaining taxa = (~ 40 spp.; 12+ families)	16.1	24.3	72.7

[a] Confirmed ECM hosts.
[b] Percent of total basal area.
[c] Percent of total number of stems > 10 cm dbh.
[d] Percent occurrence in sampling intervals.

methods of McLean (1982), and organic matter using ashing procedures (Storer 1984).

Data analyses

In order to assess whether ectomycorrhizal trees may have influenced macrofungal community structure, canonical correspondence analysis (CCA) was performed on the Suruwabaru dataset using the statistical package PC–ORD. These transects, unlike those of the Kurutuik site, had counts of both EM and saprotrophic macrofungi. CCA involves ordination of a main data matrix (by reciprocal averaging) while constrained by a multiple regression on variables included on a second matrix (Ter Braak 1994). Thus the ordination of intervals and species is constrained by their relationship to environmental variables. CCA is effective when the objective is to describe how species respond to particular sets of observed environmental variables (McCune 1997). The main data matrix in this analysis contained the basidiome counts of the individual EM and saprotrophic fungal species summed over the entire sampling period. Variables included in the second matrix were: (1) combined basal area of EM trees/interval; and (2) combined basal area of NEM trees/interval. In order to assess the relationship between edaphic factors and tree community composition along the Suruwabaru transects, intervals in tree species space (using number of stems/species) were ordinated with CCA using the soil parameters pH, Mehlich extractable phosphorus, NO_3-N, NH_3-N, percent sand, and percent clay in the second matrix. As one soil sample was taken for each pair of transect intervals, data for each tree species was summed for each interval pair, and these sums were used as the interval values ($n = 15$) in the main matrix. In both the fungal and tree species data matrices, species occurring as only a single individual were excluded, leaving a total of 100 fungal species and 65 tree species in their respective matrices.

RESULTS

Confirmation of ectomycorrhizal host trees

Root excavations confirmed the presence of ectomycorrhizal short roots on *Dicymbe corymbosa*, *D. altsonii*, *D. jenmanii*, and *Aldina insignis*. A variety of morphotypes of ectomycorrhizas were collected from each of the four species. Root excavations failed to confirm ectomycorrhizae on all other caesalpiniaceous tree species examined. In addition, a non-leguminous species, *Micrandra glabra* (*Euphorbiaceae*), was noted to be dominant in certain stands and checked in the field for the presence of an ectomycorrhizal fungal mantle, and was found to have none.

Kurutuik Site

Transects – Vegetation

Combined transect data indicated a prevalence of certain tree species at the Kurutuik site (Table 1). Among the prevailing species, the ectotrophic *Dicymbe corymbosa* was most dominant, dense, and frequent, accounting for 36% of the total basal area, 20% of the stem density, and occurring in nearly 55% of the 50 m segments (Table 1). The ectotrophic trees *D. jenmanii* and *Aldina insignis*, while less prevalent than *D. corymbosa*, contributed substantially to total basal area and stem density, as did the non-ectotrophic euphorb *Micrandra glabra*. Twelve species combined accounted for nearly 84% of the total basal area and 76% of the

Table 2. Woody taxa ⩾ 10 cm dbh occurring on the Kurutuik and Suruwabaru transects, Pakaraima Mountains, Guyana.

Family	Taxon	Transects	Collection number[a]
Anacardiaceae	*Tapirira marchandii*	S2	7761
	Tapirira guianensis	S2, K2	6877
Annonaceae	*Duguetia cfr cuspidata*	S2	7774
	Guaterria atra	S1	7744
	Guatteria sp. 1	S2	7727
	Oxandra asbeckii	S2	6777
Apocynaceae	*Aspidosperma oblongum*	S1	7803
	Aspidosperma excelsum	S1	6671
Araliaceae	*Schefflera morototoni*	K1, K3	6839
Arecaceae	*Socratea exorrhiza*	S2	7805
	Iriartea exorrhiza	S1, K3	7148
Bignoniaceae	*Tabebuia* sp. 1	S1	7185
Bombacaceae	*Catostemma commune*	S1, S2	6830
	Catostemma altsonii	K1, K3	6830
	Catostemma cfr fragrans	S1, K3	7823
Burseraceae	*Dacryodes* sp. 1	S2, K2	7157
	Dacryodes sp. 2	S2	7154
	Protium decandrum	S1, S2, K1, K2, K3	7821
	Tetragastris altissima	S2	7178
Caesalpiniaceae	*Chamaecrista adiantifolia* var. *pteridophylla*	K1, K2, K3	6831
	Dicymbe altsonii	S1, S2	6799
	Dicymbe corymbosa	S1, S2, K1, K2, K3	6583
	Dicymbe jenmanii	K1, K2	6829
	Dimorphandra macrostachya	K1, K2, K3	6825
	Eperua falcata	S1, K2	7776
	Macrolobium sauveolens var. *sauveolens*	S1, K1	7756
	Macrolobium sp. 1	K2, K3	7764
	Macrolobium sp. 2	S1, K2, K3	7818
	Tachigali sp. 1	S1, K1, K2, K3	7784
Caryocaraceae	*Caryocar nuciferum*	S2	7179
	Caryocar cfr microcarpum	S2	7825
	Caryocar glabrum	S2, K2, K3	7135
Celastraceae	*Goupia glabra*	S2	6776
Chrysobalanaceae	*Couepia eflexa*	S2	7188
	Hirtella sp. 1	S1, K1	7169
	Hirtella sp. 2	S1	7170
	Licania laxiflora	S1, S2	7771
	Licania cfr majuscula	K1	7781
	Licania heteromorpha var. *perplexans*	S1, S2, K3	7748
	Licania sp. 1	S1	7759
Clusiaceae	*Moronobea cfr coccinea*	K1, K3	6826
	Platonia insignis	S1	7183
	Symphonia globulifera	S1, S2, K1	7795
	Tovomita cfr albiflora	S1, S2, K2, K3	7720
	indet.	S1	7184
Combretaceae	*Buchenavia cfr fanshawei*	K1, K2	6775
Dilleniaceae	*Doliocarpus cfr brevipedicellatus*	S2	7171
Ebenaceae	*Diospyros dichroa*	S1	7718
	Diospyros guianensis ssp. *guianensis*	S1, S2	7747
Elaeocarpaceae	*Sloanea cfr bracteosa*	S2	7731
	Sloanea cfr grandiflora	S2	7143
Euphorbiaceae	*Alchorneopsis cfr floribunda*	S2, K2	7790
	Chaetocarpus cfr schomburgkianus	K3	7793
	Micrandra cfr spruceana	S1	6827
	Micrandra glabra	S1, K1, K2, K3	7791
	Pera bicolor	K3	6788
	Sapium cfr jenmanii	S1	7152
	Sapium sp. 1	S1, S2	7758
Flacourtiaceae	*Banara cfr guianensis*	S1, S2	7166
	Homalium sp. 1	S2	7121
Lauraceae	*Ocotea wachenheimii*	S1, K1	7136
	Ocotea cfr caudata	S2	7155
	Nectandra sp. 1	K2	7777
	Ocotea cfr iomentella S	S1	7829
	Ocotea sp. 1	S1, S2	7804

(*continued on* p. 522)

Table 2 (*cont.*)

Family	Taxon	Transects	Collection number[a]
	Ocotea sp. 2	S2, K2	7814
Lecythidaceae	*Couratari multiflora*	S1	7827
	Eschweilera sagotiana	S1, S2, K3	7762
Malphigiaceae	*Byrsonima cfr stipulacea*	S1	7139
Melastomataceae	*Miconia cfr guianensis*	S1, S2, K3	7754
	Miconia sp. 1	S2	7709
Meliaceae	*Carapa guianensis*	S1	7773
Mimosaceae	*Inga alba*	S2	6837
	Inga sp. 1	K3	7792
	Inga sp. 2	K2	7812
	Inga sp. 3	S1, S2	7737
	Inga sp. 4	S2	7124
	Inga sp. 5	S1, S2	7159
	Pentaclethra macroloba	S2	7140
	Pithecellobium cfr pedicellare	S2	7151
	Pithecellobium corymbosum	S2	7142
Moraceae	*Cecropia angulata*	S1, K2	7163
	Pourouma cfr tomentosa	S2	7164
	Brosimum sp. 1	S1	7833
	indet.	S2	7186
Myristicaceae	*Iryanthera* sp. 1	S1, S2, K3	7134
Myrsinaceae	*Cybianthus* sp. 1	S1, K1, K3	6824
Myrtaceae	*Marlierea schomburgkiana*	S2	7750
Ochnaceae	*Ouratea* sp. 1	S2, K1, K2	7703
Papilionaceae	*Aldina insignis*	K1, K2, K3	7714
	Clathrotropis macrocarpa	S1	7161
	Diplotropis purpurea	S2, K1, K2	7181
	Hymenolobium sp. 1	S2, K1, K2	7149
	Ormosia cfr coccinea	S1, S2	7757
	Swartzia cfr jenmanii	S1, K1	7712
Quiinaceae	*Quiina guianensis*	S2	7189
Rubiaceae	*Duroia eriopila* var. *eriopila*	S1, K1	6774
Sapindaceae	*Maytaba oligandra*	S2	7176
	Maytaba sp. 1	S2, K1, K2	7122
Sapotaceae	*Chrysophyllum* sp. 1	S1	7172
	Chrysophyllum sp. 2	S2	7132
	Microphilus cfr venulosa	S1, K1, K2	7156
	Oxythece ambelaniifolia	S1, S2, K2	7743
	Pouteria guianensis	S1	7144
	Pouteria speciosa	S1	7807
	Pradosia schomburgkiana	S2	7785
	indet.	S1	7187
Simarubaceae	*Quassia simaruba*	S2	7150
Theaceae	*Ternstroemia* sp. 1	S2	7153
Vochysiaceae	*Qualea* sp. 1	K1	7165
indetermined	16 indet.		

[a] Collection numbers are in T. Henkel's collection series 'TH'.

stems; at least one of these 12 species occurred in each of the 50 m intervals examined (Table 1). A complete list of tree species for both the Kurutuik and Suruwabaru sites is given in Table 2.

A closer look at the individual transects revealed a high degree of clumping and dominance on the part of EM tree species (Fig. 3). Most prominently, a 700 m section transect 2 was heavily dominated by *D. corymbosa*, which accounted for 40–100 % of the basal area for most of the 50 m intervals contained therein (intervals 3–16). Two additional stands containing ectotrophic trees other than *D. corymbosa* were identified; the first 100 m of the transect 2 were dominated by *D. jenmanii* (70–75 % total basal area), and most of the final 250 m contained *A. insignis*. Transitions between these stand types were abrupt, ocurring within one 50 m interval (e.g. *D. jenmanii* → *D. corymbosa* at segment 3; *D. corymbosa* → *A. insignis* at segment 17). Along transect 3, the anectotrophic *M. glabra* was moderately dominant for 200 m beyond which there was an abrupt transition from this stand type to the *D. corymbosa*-dominated stand at interval 5 (Fig. 3).

Transects – EM fungi

Basidiomes of EM fungi were abundant along the Kurutuik transects and tracked the occurrence and dominance of EM host trees (Fig. 3). Along transect 1,

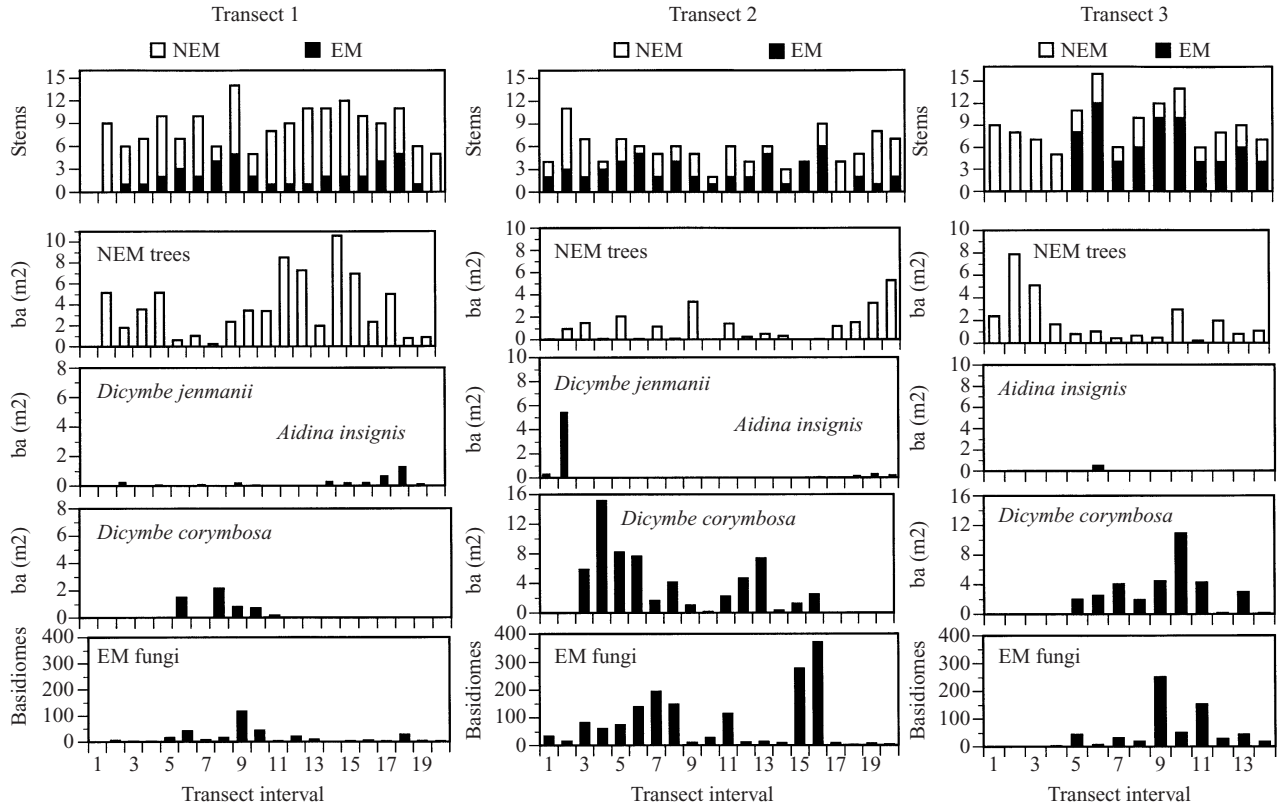

Fig. 3. Kurutuik Transects 1–3. Number of stems $\geqslant$ 10 cm dbh for ectomycorrhizal (EM) and non-ectomycorrhizal (NEM) trees, basal area of combined NEM trees, EM *Dicymbe jenmanii*, *D. corymbosa*, and *Aldina insignis*, and number of EM fungal basidiomes per 50×4 m transect interval (transect 1 = 1000 m, transect 2 = 1050 m, transect 3 = 700 m).

EM basidiomes were reduced as was the combined basal area of EM trees. Along transect 2, EM basidiomes were present throughout. Peaks in basidiome number corresponded roughly to peaks in host tree basal area, though correlations were not statistically significant. In the first 100 m, EM basidiomes were associated with *Dicymbe jenmanii*. Farther along, production of basidiomes was very high (up to 200–375/interval) in areas dominated by *D. corymbosa*. *Dicymbe* trees were completely absent from the final 250 m, though EM basidiomes continued to be present in reduced numbers in association with a low basal area stand of *Aldina insignis*. Along transect 3, EM basidiomes were completely absent from the first 200 m of *Micrandra glabra* forest, appearing abruptly with the transition to *D. corymbosa* (interval 5) and continuing with the host tree to the end of the transect.

Table 3 lists all EM fungal taxa found on the Kurutuik and Suruwabaru transects. Most fungal taxa were rare over the short sampling period, occurring as less than 4% of the total number of basidiomes. Prominent taxa included *Clavulina craterelloides*, *Tylopilus potamogeton* var. *irengensis*, *Amanita calochroa*, and *Clavulina* sp. 2.

Suruwabaru Site

The EM species *Dicymbe corymbosa* and *D. altsonii* exhibited pronounced clumping and dominance at the Suruwabaru site (Fig. 4) . In transect 1, *D. corymbosa* comprised nearly all of the basal area in the first five intervals, with additional peaks in intervals 12–14 (Fig. 4). Basal area of *D. corymbosa* was exceptionally high in several intervals (1–4, 13) due to the presence of very large trees (dbh $>$ 200 cm). While *D. corymbosa* also occurred between the zones of dominance (i.e. 6–11), basal area of the species was reduced, and the species was mixed with *D. altsonii* and NEM trees, in particular *M. glabra*. Beyond interval 15, *D. corymbosa* was absent from the transect. *Dicymbe altsonii* was present in mixed association with *D. corymbosa* in intervals 0–10; in intervals 15–20 *D. altsonii* was dominant, with a majority of the basal area and a roughly equal number of stems with NEM species. Beyond interval 20 both *Dicymbe* species were absent, with a sharp transition to a mixed NEM stand. Prominent tree species from intervals 20–30 included *Carapa guianensis*, *Protium decandrum*, *M. glabra*, *E. falcata*, *Cybianthus* sp. 1, and *Eschweilera sagotiana*.

Along transect 2, EM host trees were confined to a well-defined area between intervals 11–23 (Fig. 4). *Dicymbe altsonii* comprised the majority of the basal area occurring in intervals 11–18, with a transition between *D. altsonii* and *D. corymbosa* occurring in interval 19. *Dicymbe corymbosa* comprised the majority of the basal area in intervals 20–22, with a minor occurrence in interval 23. Mixed forests lacking *Dicymbe* occurred in intervals 1–10, with prominent

Table 3. Putative ectomycorrhizal fungal taxa occurring on the Kurutuik and Suruwabaru transects, Pakaraima Mountains, Guyana.

Family	Taxon	Transects	Collection number[a]
Boletaceae	*Tylopilus potamogeton* var. *irengensis*	K1, K2, K3, S1, S2	6425, 6266
	Tylopilus pakaraimensis	K2, K3, S2	6610, 7077
	Tylopilus ballouii	K3, S2	6896
	Tylopilus exiguus	K1, K2, K3, S1, S2	6810
	Tylopilus vinaceipallidus	K3	6284
	Tylopilus sp. 1	S2	7407
	Tylopilus sp. 2	S2	7433
	Tylopilus sp. 3	S1	7885
	Austroboletus festivus	S1	8164
	Boletellus ananas	S1	7400, 7925
	Boletellus sp. 1	K2, K3, S1, S2	7436
	Boletellus sp. 2	K2, K3, S2	7455, 7480
	Xerocomus amazonicus	K3, S2	7438, 7903
	Xerocomus sp. 1	S1, S2	7465
	Xerocomus sp. 2	K2, K3, S2	7416, 7495
	Xerocomus sp. 3	K2, S1	7412
	Xerocomus sp. 4	S1, S2	7512
	Xerocomus sp. 5	K2	7544, 7681
	Xerocomus sp. 6	K2	7437, 7452
	Chalciporus sp. 1	K3	7293, 7511
Amanitaceae	*Amanita lanivolva*	K1, K2, K3, S1, S2	7514
	Amanita xerocybe	K1, K2, K3, S1	7402
	Amanita campinaranae	K1, K2, K3	8006
	Amanita calochroa	K1, K2, K3	7401, 7456
	Amanita aurantiobrunnea	S2	7409, 7444
	Amanita perphaea	K2, S2	7535
	Amanita sp. 1	K2, K3	8034
	Amanita sp. 2	S2	7490
	Amanita sp. 3	K1, K2, K3	7585
	Amanita sp. 4	K3	8057
	Amanita sect. *Vaginatae* sp. 1	K2, S2	7415
	Amanita sect. *Vaginatae* sp. 2	K1, K2	7434
	Amanita sect. *Vaginatae* sp. 3	K2, K3, S1, S2	7477
	Amanita sect. *Vaginatae* sp. 4	K2, K3, S1, S2	7492
	Amanita sect. *Vaginatae* sp. 5	K3, S1, S2	7545
	Amanita sect. *Vaginatae* sp. 6	S1	7643
Russulaceae	*Lactarius panuoides*	K3, S1	6401
	Lactarius sulcatipes	K2, K3, S1, S2	7420, 7677
	Lactarius sp. 1	K1, S1, S2	7453
	Lactarius sp. 2	K1, K3, S2	7578
	Lactarius sp. 3	S2	7447
	Russula campinensis	K2, K3, S1, S2	7023
	Russula cfr metachromatica	K1, K2, K3, S1	7439
	Russula cfr puigarrii	K1, K2, S1, S2	8310
	Russula sp. 1	K2, S1, S2	7525
	Russula sp. 2	K2	8233
	Russula sp. 3	K1	7916
	Russula sp. 4	S1	8339
	Russula sp. 5	K3, S1	7446
	Russula sp. 6	K3	7817
	Russula sp. 7	K3, S1, S2	7879
	Russula sp. 8	K1, K2	7880
	Russula sp. 9	S1, S2	7588
	Russula sp. 10	S1	7555
	Russula sp. 11	S1	7880
	Russula sp. 12	S1, S2	7874
	Russula sp. 13	S1	7909
	Russula sp. 14	S1	7642
	Russula sp. 15	S2	8258
	Russula sp. 16	S1	7534
	Russula sp. 17	S2	8300
Cortinariaceae	*Cortinarius* aff. *violaceous*	K1, K2, K3	8211
	Cortinarius sp. 1	K1, K2, K3, S1, S2	8193
	Cortinarius sp. 2	K2, S1	8005
Entolomataceae	*Entoloma* subgen. *Entoloma* sp. 1	K1, K2, K3	6766

Table 3 (*cont.*)

Family	Taxon	Transects	Collection number[a]
Cantharellaceae	*Cantharellus guyanensis*	K1, K2, K3, S1	7488
	Craterellus sp. 1	K1, K2, K3, S1	7515
Clavulinaceae	*Clavulina craterelloides*	K2, K3, S1, S2	7493
	Clavulina sp. 1	K1, K2, S1	8207
	Clavulina sp. 2	K1, K3, S1, S2	8217
	Clavulina sp. 3	K1, K2, S1	8286
	Clavulina sp. 4	K3	8221
	Clavulina sp. 5	S1, S2	8225
Clavariaceae	indet. sp. 1	S2	7426
	indet. sp. 2	S1, S2	8239

[a] Collection numbers are in T. Henkel's collection series 'TH'.

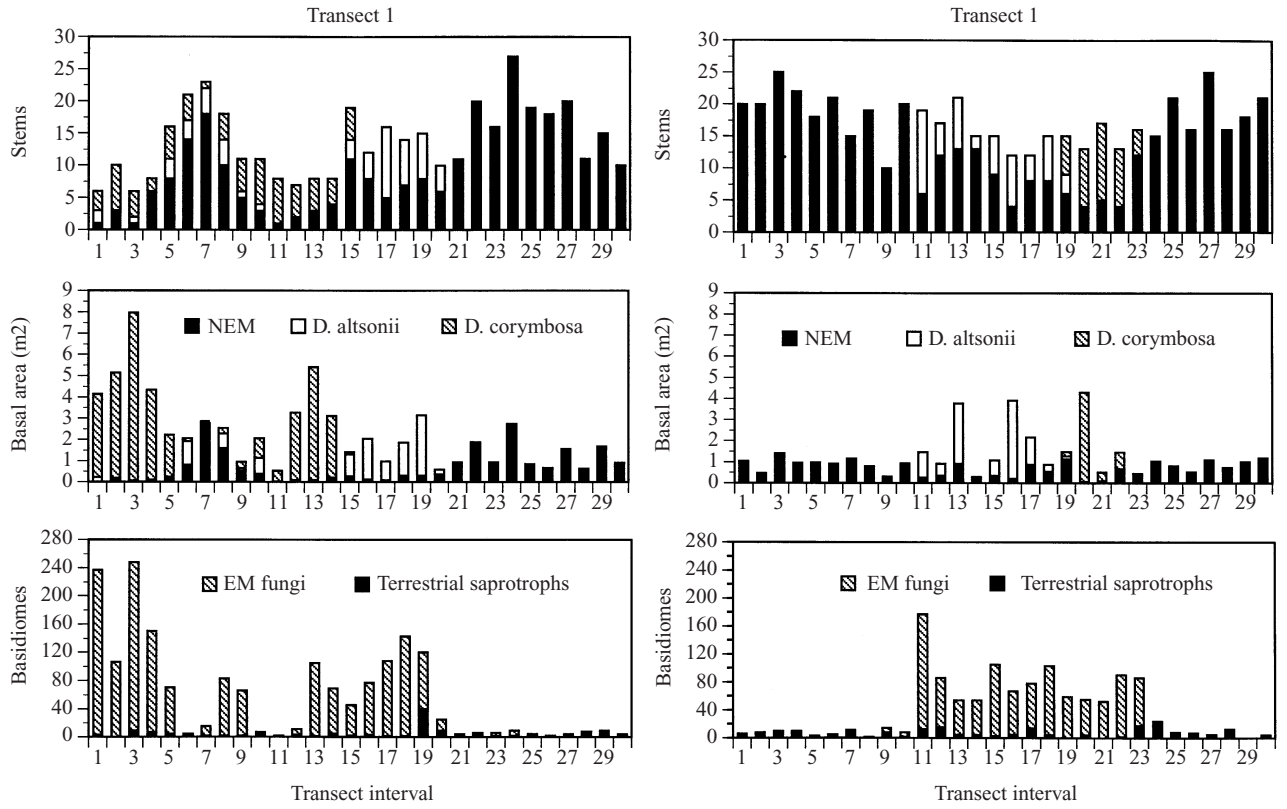

Fig. 4. Suruwabaru Transects 1–3. Number of stems and basal area of trees $\geqslant 10$ cm dbh for combined non-ectomycorrhizal (NEM) trees, ectomycorrhizal (EM) *Dicymbe altsonii* and *D. corymbosa*, and number of basidiomes of EM and terrestrial saprotrophic macrofungi per 10×30 m transect interval (each transect = 300 m).

tree species including *Goupia glabra*, *P. decandrum*, *Pentaclethra macroloba* and *Licania laxiflora*. Mixed forest occurring in intervals 24–30 was well represented in *Banara cfr guianensis*, *Miconia* sp. 1, *Licania heteromorpha*, *Dacryodes* sp. 1, and *Quassia simaruba*.

At Suruwabaru, *Dicymbe corymbosa*- and *D. altsonii*-dominated stands occurred on soils irrespective of sand or clay contents (Fig. 5). Extractable P, soluble N, soil organic matter, cation exchange capacity, and aluminum concentration were also highly variable under *Dicymbe* stands. CCA of transect intervals by tree species (using stem numbers) with soil parameters as environmental variables constraining the ordination indicated a statistically significant species-environment correlation along the first and second axes, suggesting that soil factors have some impact on tree community structure (axis 1: Pearson correlation $r = 0.92$, $P \leqslant 0.01$, percent of variance explained = 12.8; axis 2: Pearson correlation $r = 0.88$, $P \leqslant 0.03$, percent of variance explained = 7.3). Transect intervals containing *D. corymbosa* or *D. altsonii* were not, however, correlated with soil parameters, suggesting that the occurrence and prevalence of these tree species does not respond clearly to edaphic conditions.

Along the Suruwabaru transects basidiomes of EM fungi were largely restricted to intervals with *Dicymbe* (Fig. 4). Fifty three EM fungal taxa occurred along Suruwabaru transect 1, and 60 along transect 2 (Table 3). As at the Kurutuik site, most EM taxa were rare. Prominent species included *Russula campinensis*,

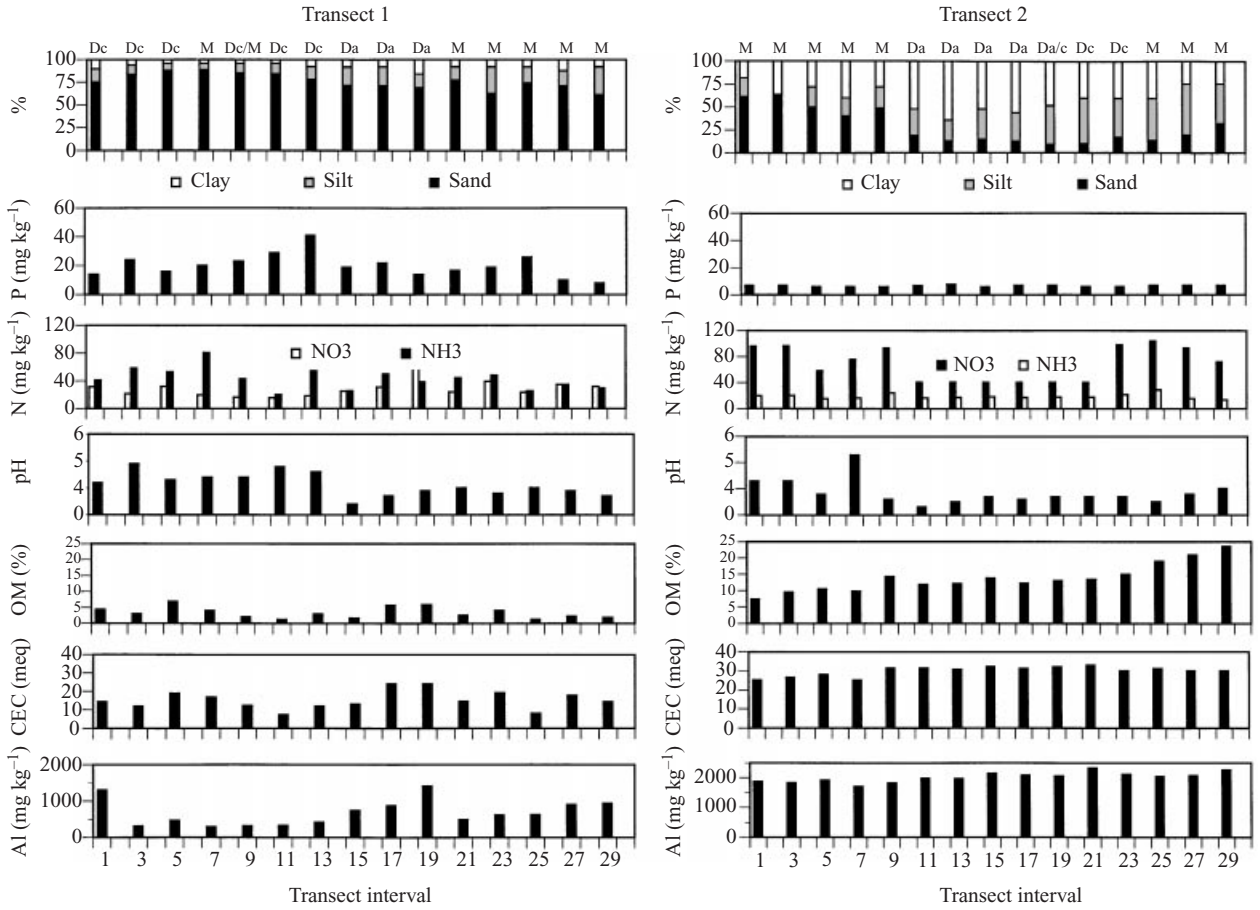

Fig. 5. Suruwabaru Transects 1–2. Selected soils data for samples taken from the upper 10 cm of mineral soils of alternate transect intervals. Letters above intervals on top graphs indicate forest type. Dc = *Dicymbe corymbosa*-dominated; Da = *D. altsonii*-dominated; M = mixed forest; or combinations thereof.

Table 4. Axis summary statistics for canonical correspondence analysis of Suruwabaru transect intervals in fungal species space, with ectomycorrhizal (EM) and non-ectomycorrhizal (NEM) tree parameters as environmental variables.

EM/NEM basal areas		EM/NEM stem numbers	
	Eigenvalue		Eigenvalue
Axis 1	0.51*	Axis 1	0.55*
Axis 2	0.24*	Axis 2	0.26*
	Percent of variance		Percent of variance
Axis 1	3.4	Axis 1	3.7
Axis 2	1.6	Axis 2	1.7
	Species-environment correlation		Species-environment correllation
Axis 1	0.88*	Axis 1	0.88*
Axis 2	0.65	Axis 2	0.7

Note: An asterisk (*) indicates statistical significance at $P \leqslant 0.05$ based on 100 Monte Carlo randomization tests applied to eigenvalues and species-environment correlations.

Russula cfr metachromatica, *Russula* aff. *puigarrii*, *Lactarius panuoides*, *Cantharellus guyanensis*, *Clavulina* sp. 1, and *Clavulina* sp. 2. The terrestrial saprotrophic macrofungal guild was reduced in number and more equitably distributed among mixed and *Dicymbe* stands (Fig. 4). Prominent genera included *Lepiota*, *Nolanea*, *Leptonia*, and *Hygrocybe*.

Canonical correspondence analysis of Suruwabaru fungal data indicated a statistically significant ($P \leqslant 0.05$) species-environment correlation along the first ordination axis. Though the variance in the fungal data explained by the regression was low, these data suggest that the macrofungal community was responding to the tree parameters (Table 4). Multiple regression of intervals in fungal species space on EM tree basal area indicated a positive correlation ($r = 0.899$) for axis 1. Regression on NEM basal area yielded a negative correlation for both axis 1 and axis 2 ($r = -0.832$; $r = -0.90$). These results suggest that the presence and dominance level of EM trees as reflected by basal area

had a marked impact on fungal basidiome community structure over the limited sampling period of this study.

DISCUSSION

Determination of ectomycorrhizal host trees

The determination of four EM leguminous species reported here substantially increases the number of leguminous hosts known from equatorial South America. Unequivocal confirmation of ectomycorrhizas on other neotropical legumes has been limited to species of the papilionoid genera *Aldina*, also corroborated here for the first time for *A. insignis*, and *Andira* (Lodge 1996). Reports of EM in the legume genera *Mora* (Norris 1969), *Eperua* (St John & Uhl 1983) and *Swartzia* (Singer & Araujo 1979) are now considered doubtful (Alexander 1989, Moyersoen 1993) and, at least for *Mora* and *Eperua*, have not been substantiated by recent mycorrhizal assessments of the genera (Bereau *et al.* 1997) and this study.

Alexander (1989) predicted that *Dicymbe* would be ectomycorrhizal based on its position within the caesalpinioid tribe *Amherstieae*. *Amherstieae* species are concentrated in Guinea-Congolian forests and the deciduous woodlands of south-central Africa, and constitute the majority of EM leguminous species. Elsewhere in the *Caesalpiniaceae*, unequivocal evidence of ectomycorrhizas exists only for the *Detarieae* genera *Afzelia* (Guinea-Congolian) and *Intsia* (Malaysia and New Guinea) (Hogberg & Nylund 1981, Alexander & Hogberg 1986, Bakarr & Janos 1997). All but one of the fifteen genera of the African *Amherstieae* have been found to form ectomycorrhizas under field conditions (Alexander 1989). The ectomycorrhizal habit, coupled with the distinctive floral synapomorphy of valvate bracteoles which completely enclose the flower bud until anthesis, appears to support the *Amherstieae* as a natural group (Cowan & Polhill 1981). This point is argued against by some, however, based on other morphological grounds (Breteler 1995); ongoing molecular phylogenetic studies are addressing the monophyly of the *Amherstieae* (P. Herendeen, pers. comm.). The inclusion of the neotropical *Amherstieae* genus *Dicymbe* with the African EM-formers of the tribe emphasizes the systematic relevance of EM-formation in the *Amherstieae*. These findings support the notion that the ectomycorrhizal habit in legumes is primarily restricted to, and concentrated in, a narrow taxonomic range of genera, namely those of the *Amherstieae*, the genus *Aldina*, and selected members of the *Detarieae*, a tribe phylogenetically allied with the *Amherstieae* (Alexander 1989, Kass & Wink 1996). This study failed to confirm ectomycorrhizas on four other common, non-*Amherstieae* caesalpinaceous tree species at the Guyana site. Similarly, of 25 leguminous tree species examined in Sierra Leone, 19 were AM, while of the six that were EM, five were *Amherstieae* and one *Detarieae* (Bakkar & Janos 1997). In French Guiana, Bereau *et al.* (1997) found arbuscular mycorrhizas in each of 22 leguminous species examined, including 13 species in the *Caesalpiniaceae*.

Universality of ectomycorrhizal habit in the *Amherstieae* cannot, however, be fully assumed. Records for dual EM/AM infections exist for several *Amherstieae* species in Africa (e.g. *Gilbertiodendron dewevrei*, Torti & Coley 1999; see also Moyersoen & Fitter 1999). In addition, *Tamarindus*, a relict Afro-Asiatic *Amherstieae* genus, has consistently been shown to possess only arbuscular mycorrhizas (Hogberg 1982, Norani 1983). Recent examinations of *Macrolobium*, the other neotropical genus of *Amherstieae*, have failed to reveal ectomycorrhizas. *M. bifolium* was found to be arbuscular mycorrhizal in French Guiana (Bereau *et al.* 1997), and, in the present study, two undetermined species of *Macrolobium* were not EM. Further investigations of the mycorrhizal status of *Macrolobium* are needed, as this neotropical genus contributes nearly 60 species to the *Amherstieae* (Cowan & Polhill 1981).

Ectomycorrhizal fungi

The restriction of EM fungi to well-demarcated stands of EM host trees at Kurutuik and Suruwabaru contrasts with vegetation patterns in higher latitudes where ectotrophic trees (e.g. *Pinaceae* and *Fagaceae*) and their fungal symbionts are found in most forests. Along the Kurutuik and Suruwabaru transects, transitions from non-EM stands to those containing *Dicymbe* or *Aldina* trees were accompanied by a marked onset of EM basidiome occurrence, and sharp decline with transitions back to mixed forest. In addition, CCA ordination of Suruwabaru transects indicated that fungal community structure was influenced by basal area of EM trees. During the height of the rainy season at least some EM fungi should have fruited in the mixed forests lacking *Dicymbe* or *Aldina* if they were present there as belowground mycelium (Vogt *et al.* 1992). This was not the case for the majority of forest sampled.

Similar patterns characterize other tropical EM forests. EM basidiomes were clustered into discrete groves of EM legumes in the Korup region of southwest Cameroon (Buyck *et al.* 1996, Watling, pers. comm.). Along the Korup transects, saprotrophic macrofungi were more equitably distributed within and without the ectotroph-dominated stands (Læssøe *et al.* 1996), a pattern also exhibited along the Suruwabaru transects reported here. Singer & Araujo (1979) found a similar truncation of EM basidiomes into Brazilian ectotrophic campinarana forests as opposed to anectotrophic terra firme, although no data were given as to prevalence of EM trees in the campinarana. In southern Venezuela, EM basidiomes were found only in forests containing *Aldina* and other EM tree species, and absent from adjacent, endotrophic caatinga forests (Moyersoen 1993). Such results emphasize the important role that EM-dominated rain forests, which occur in spatially limited, site-specific distributions in an otherwise

arbuscular-mycorrhizal forest matrix, play in harbouring the tropical EM fungal guild.

Forest dominance by ectomycorrhizal trees

This study constitutes the first report of extreme forest dominance by confirmed EM legumes in the neotropics. Neotropical legumes previously recorded as forest dominants include the caesalpinioid *Mora excelsa* in Trinidad and Guyana (Davis & Richards 1934, Beard 1946), species of *Peltogyne* in northern Brazil and eastern Venezuela (Nascimento, Proctor & Villeja 1997, Terborgh, unpubl.), and the mimosoid *Pentaclethra macroloba* in eastern Costa Rica (Hartshorn 1972). All of these species have been found to be arbuscular mycorrhizal (Johnston 1949, Absjornsen & Montagnini 1994, Henkel & Terborgh, unpubl.). At Singer and Araujo's central Brazilian site, ectomycorrhizas were confirmed only for *Aldina heterophylla* and no quantitative data were given on the abundance of this species or other non-leguminous EM hosts reported for the site. In southern Venezuela, ectotrophic stands were largely composed of EM species of *Nyctaginaceae*, with *Aldina* as a minor component (Moyersoen 1993).

The occurrence of *Dicymbe corymbosa*-dominated stands in Guyana's Pakaraima Mountains was discussed previously but no subsequent work has been done on the species (Myers 1936, Fanshawe 1952a, b, Richards 1952). At the Kurutuik and Suruwabaru sites reported here, basal area dominance by *D. corymbosa* reached 80–100 % over substantial portions of transects, qualifying those stands as monodominant (*sensu* Connell & Lowman 1989). *D. altsonii* also dominated stands to a lesser degree, and these stands were usually well-differentiated from those containing *D. corymbosa*. Similar dominance levels by EM legumes have been reported in tropical Africa for *Gilbertiodendron dewevrei* in the Congo (Hart, Hart & Murphy 1989, Torti & Coley 1999), along with *Tetraberlinia moreliana*, *Tetraberlinia bifoliata*, and *Microberlinia bisulcata* in the Korup region of Cameroon (Newbery *et al*. 1988, Newbery, Alexander & Rother 1997). Diversity of woody plant species $\geqslant$ 10 cm dbh in *D. corymbosa* stands ranges between 37–56 species/hectare (Henkel, unpubl.), values that are among the lowest recorded for neotropical moist forest (Gentry 1988, Nascimento *et al*. 1997, Ek & Ter Steege 1998). Significantly, monodominant forests of EM legumes have now been shown to occur in the neotropics, and the most important EM genus, *Dicymbe*, is a member of the largely ectotrophic, Africa-centered *Amherstieae*, many of which form monodominant forests in their respective environments.

Distribution of Dicymbe *stands in relation to soil conditions*

Results from the Suruwabaru transects support the observation by Richards (1952) that *Dicymbe corymbosa*-dominated forests have no clear edaphic requirements, occurring on soils ranging from coarse, leached sands to tropical red clays. Although canonical correspondence analysis suggested that the Suruwabaru tree community does respond in total to the set of soil variables included, there was no response to soil variables by *D. corymbosa* or *D. altsonii*. Along transect 1 both *D. corymbosa* and *D. altsonii* stands occurred on soils that differed markedly from those exhibiting *Dicymbe* dominance along transect 2 for important variables such as percent sand (70–89 % *vs* 10–19 %), percent clay (4–16 % *vs* 18–64 %), extractable phosphorus (14–29 mg kg^{-1} *vs* 6–8 mg kg^{-1}), organic matter content (1–7 % *vs* 12–15 %), and aluminum concentration (286–1416 mg kg^{-1} *vs* 1969–2335 mg kg^{-1}). In addition, edaphic conditions did not co-vary in any meaningful way with shifts between *Dicymbe*-dominated stands and adjacent mixed forests. A similar lack of edaphic pattern has been shown in the segregation of *Gilbertiodenron*-dominated stands and adjacent mixed forests in the Congo (Hart *et al*. 1989, Conway & Alexander 1992), and contrasts with the views of Went & Stark (1968) and Singer & Araujo (1979) that tropical EM forests are restricted to highly oligotrophic white sands.

Both the lack of requirement of *Dicymbe* species for specific soil chemical conditions to achieve dominance as well as their occurrence on soils common to the adjacent mixed forests appear to be rare contradictions of the well-known dualism of tree-soil interactions, with edaphic conditions often determining tree composition as well as vice-versa (Terborgh, Foster & Nunez 1996, Newbery *et al*. 1997). This situation argues for a primary role of biotic interactions in fostering competitive superiority of *Dicymbe*. Plot studies have indicated a high recruitment of *D. corymbosa* seedlings and saplings following years of mast-fruiting (Henkel, unpubl.); similar results have been shown for *D. altsonii* (Isaacs *et al*. 1996, Zagt & Werger-Marinus 1997), suggesting that these monodominant systems are persistent through time (Connell & Lowman 1989). In addition, natural coppicing by *D. corymbosa* may encourage self-recruitment into light gaps (Richards 1996, Henkel, unpubl.). Further studies are necessary to evaluate the contribution of various life history traits, including the ectomycorrhizal habit, to the competitive superiority of *Dicymbe* species.

In summary, in Guyana, the clustering of EM leguminous trees into stands well-demarcated from surrounding NEM forests contrasts sharply with temperate and boreal forests where EM species are more equitably distributed over the landscape. In this forest mosaic, the EM fungal guild is restricted to groves of EM trees, which function as habitat islands for these obligately symbiotic fungi. The most important Guyanese EM tree species, *D. corymbosa* and *D. altsonii*, are members of the caesalpinoid tribe *Amherstieae*, which is concentrated in tropical Africa and contains grove-forming species which dominate Guineo-Congolian forests. Distribution of EM *Dicymbe* species was not related to

soil conditions. Dominance levels achieved by EM trees in Guyana, in particular *D. corymbosa*, were extreme and indicated enhanced competitive abilities, which may result from life history attributes of the species, including the EM habit.

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