

# Ectomycorrhizas and putative ectomycorrhizal fungi of *Afzelia africana* Sm. and *Uapaca guineensis* Müll. Arg. in southern Senegal

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(Received 3 April 1989; accepted 18 August 1989)

## SUMMARY

Ectomycorrhizas and ectomycorrhizal fungi of *Afzelia africana* Sm. and *Uapaca guineensis* Müll. Arg. are reported in forests of southern Senegal. Ectomycorrhizas occurred in dry and wet conditions, at different soil contents of available phosphorus (0-17.5  $\mu\text{g g}^{-1}$ ). *U. guineensis* was confined to groundwater forests. Individual trees had both ecto- and endomycorrhizas, *A. africana* grew scattered in semi-evergreen and riverside forests, whereas in the woodland it formed larger patches and could dominate the canopy. Eighteen putative ectomycorrhizal fungi grew under *U. guineensis* and thirty-one under *A. africana*. Only six species were common to both trees, indicating an ecological and/or taxonomical selection. The fungi belonged to the following Orders: *Russulales* (16), *Boletales* (11), *Agaricales* (9), *Cantharellales* (2), *Sclerodermatales* (2), *Hymenogastrales* (1), *Gautieriales* (1), *Aphylophorales* (1). Some of them had a wide Sudano-Zambezian or Guineo-Congolian distribution and reached their northern limit in Senegal.

Key words: Ectomycorrhizal fungi, tropical trees, dual symbiosis, ectomycorrhizas, W. Africa.

## INTRODUCTION

During the last decade there has been renewed interest in tropical mycorrhizas. Field observations have increased the number of tropical tree genera known to form ectomycorrhizas (ECM) (Newbery *et al.*, 1988). In tropical Africa, ECM were reported among the following families (or subfamilies) and genera: Caesalpinioideae (*Afzelia*, *Aphanocalyx*, *Anthothis*, *Berlinia*, *Brachystegia*, *Didelotia*, *Gilbertiodendron*, *Isoberlinia*, *Julbernardia*, *Microberlinia*, *Monopetalanthus*, *Paramacrolobium*, *Tetraberlinia*), Dipterocarpaceae (*Marquesia*, *Monotes*), Euphorbiaceae (*Uapaca*), Papilionoideae (*Pericopsis*), Proteaceae (*Faurea*) (Peyronel & Fassi, 1957, 1960; Fassi & Fontana, 1961, 1962; Jenik & Mensah, 1967; Redhead, 1968a, 1968b, 1980, 1982; Högborg & Nylund, 1981; Högborg, 1982; Högborg & Pearce, 1986; Alexander & Högborg, 1986; Alexander, 1985, 1987; Newbery *et al.*, 1988). However, only a few putative ectomycorrhizal fungi were identified and their host specificity is poorly documented. An *Inocybe* sp. was observed associated with

*Afzelia bella* in Nigeria (Redhead, 1968b). A *Russula* and an unknown member of the Hygrophoraceae were recorded under *A. bella* in Ghana (Alexander, 1985). In the Zambian miombo woodland the main putative ectomycorrhizal fungi belonged to the genera *Amanita*, *Cantharellus*, *Lactarius* and *Russula* (Högborg & Pearce, 1986).

In this paper we present observations on the ectomycorrhizal fungi and the ECM of *Afzelia africana* Sm. and *Uapaca guineensis* Müll. Arg. The ectomycorrhizal status of *A. africana* in Ghana (Jenik & Mensah, 1967) and in Nigeria (Redhead, 1968a) has already been reported. The mycorrhizal status of *U. guineensis* is reported now for the first time.

## MATERIALS AND METHODS

### Sites

The forests range from the Guinean to the Sudano-Guinean type (Fig. 1 and Table 1). Annual rainfall varies from an average of 1200 mm to more than 1700 mm (period 1931-60). In recent years, these

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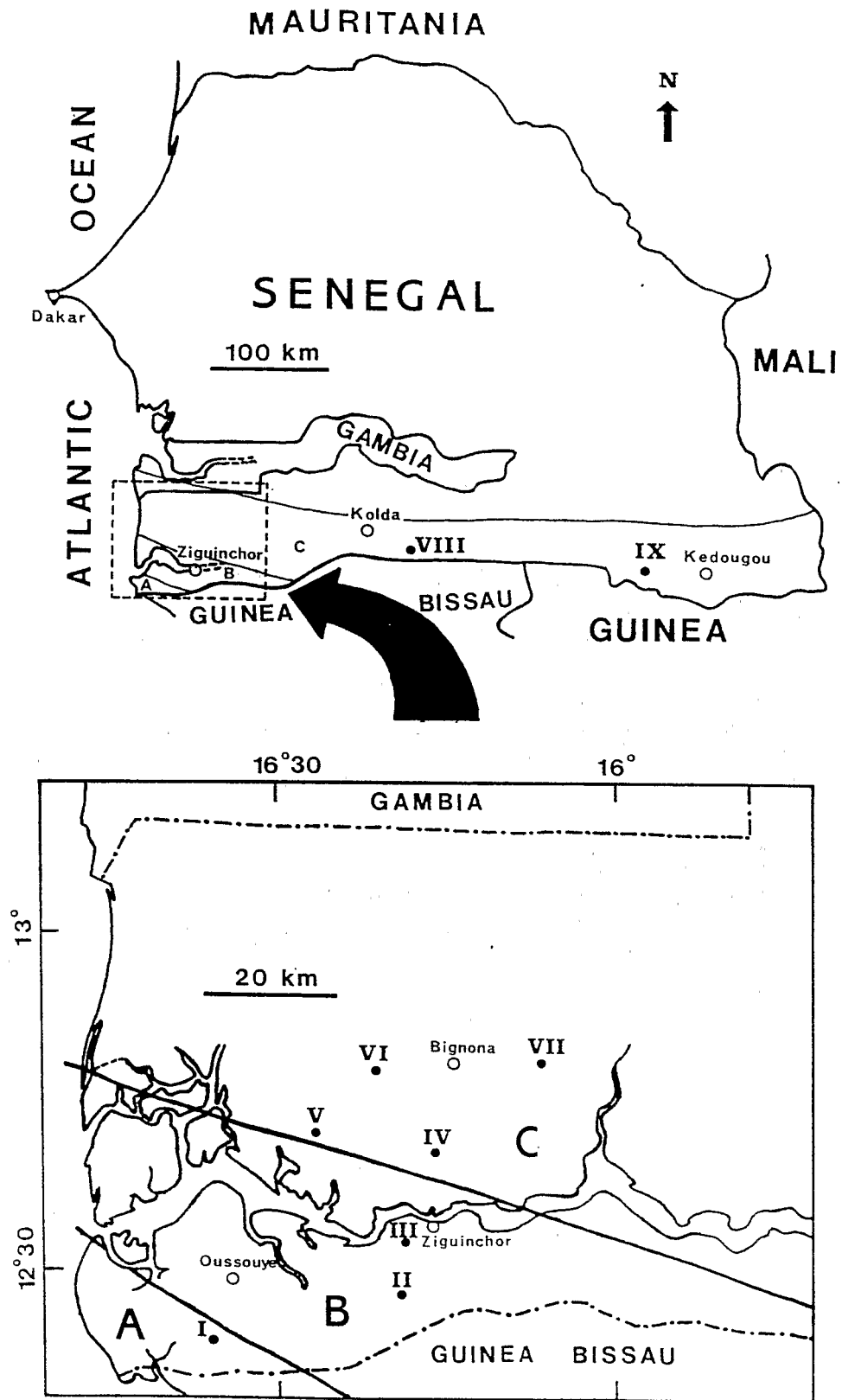


Figure 1. Location of the sampling sites (I-IX) in southern Senegal. Key: A, Guinean region; B, Guineo-Sudanian domain; C, Sudano-Guinean domain (phytogeographical units after Adam *et al.*, 1965).

Table 1. Sampling sites. The numbers I-IX refer to localities given in Fig. 1 and Table 2

Site no.	Locality	Altitude (m)	Mean annual rainfall (mm) (1931-60)	Phytogeographical region or domain	Soil type
I	Santiaba Manjak (12° 24' N, 16° 35' W)	10	1700-1800	Guinean	Hydromorphic soil and latosol
II	Bayottes (12° 29' N, 16° 17' W)	10	1600-1700	Guineo-Sudanian	Latosol
III	Djibelor (12° 34' N, 16° 17' W)	10	1500-1600	Guineo-Sudanian	Latosol
IV	Tobor (12° 43' N, 16° 14' W)	20	1400-1500	Sudano-Guinean	Latosol
V	Tendouk (12° 46' N, 16° 27' W)	20	1400-1500	Sudano-Guinean	Latosol
VI	Diegoun (12° 49' N, 16° 19' W)	25	1400-1500	Sudano-Guinean	Latosol
VII	Kalounayes (12° 50' N, 16° 8' W)	30	1300-1400	Sudano-Guinean	Latosol
VIII	Thiara (12° 44' N, 14° 32' W)	40	1200-1300	Sudano-Guinean	Grey ferruginous soil
IX	Dakateli (12° 27' N, 12° 40' W)	80	1200-1300	Sudano-Guinean	Hydromorphic soil

Table 2. Main physico-chemical characteristics of the upper soil layer (site no. as in Table 1)

Site no.	Ia*	Ib**	II*	III*	IV*	V*	VI*	VII*	VIII*
Clay (%)	4.2	12.6	3.7	6.0	9.8	4.5	5.3	1.6	12.7
Silt (%)	26.5	18.6	31.0	9.4	8.9	32.7	36.8	22.6	23.2
Sand (%)	67.0	65.0	67.9	83.9	79.5	61.0	56.6	74.3	63.1
pH (water)	6.1	4.0	5.8	4.9	5.8	6.2	5.5	6.1	5.1
pH (KCl)	5.6	3.5	5.4	3.8	5.0	5.3	5.0	5.5	4.7
Carbon (%)	11.7	31.9	29.4	4.1	11.7	10.9	19.6	15.1	15.2
Nitrogen (%)	1.0	2.5	2.5	0.3	0.7	1.0	1.7	1.5	1.1
C/N	12	13	12	12	13	11	12	10	14
Total phosphorus ( $\mu\text{g g}^{-1}$ )	83	148	223	19	24	109	122	135	140
Available phosphorus ( $\mu\text{g g}^{-1}$ )	0.0	4.4	13.1	3.9	8.3	4.4	4.4	8.7	17.5
V (%)***	95	9	97	—	85	78	70	83	56

\* Soil samples taken under *Afzelia africana*; \*\*, soil sample taken under *Uapaca guineensis*; \*\*\*, metallic cations percentage saturation of soil.

figures have decreased by an average of approx. 100-200 mm. The rainy season extends from June to October and is followed by a marked dry season.

The Sudano-Guinean tree *Afzelia africana* has a wide range of habitats. In the semi-evergreen forests and in the riverside forests it is scattered (Fig. 2a), whereas in the woodlands it occurs in small or large patches and then dominates the canopy. It is present in all the sample sites. *Uapaca guineensis* is a relict Guinean tree in Senegal, confined to azonal, hydromorphic soils. In the study area, it is abundant on the border of a wet depression (site I) and scattered in a riverside forest (site IX). Stilt roots are an adaptation to waterlogging (Fig. 2b).

Soils, flora and/or vegetation were described by Doumbia (1966) for sites I-VI, Schneider & Sambou

(1982) for site I, and Vanden Berghen (1984) for site VII. Site VIII has a typical woodland structure with a tree layer and a well developed grass layer. *Afzelia africana* is the dominant tree, accompanied by *Erythrophleum africanum* (Welw.) Harms, *Daniellia oliveri* (R.) Hutch. & Dalz., *Cordyla pinnata* (Lepr.) Mil.-Red., *Pterocarpus erinaceus* Poir., *Burkea africana* Hook., *Prosopis africana* (G. & Perr.) Taub., *Combretum* spp. Site IX is a small riverside forest where individuals of *U. guineensis* and *A. africana* grow together. Surrounding vegetation is a degraded woodland. Under *U. guineensis*, the grass layer is absent and the litter layer is abundant (Fig. 2b), whilst under *A. africana*, the grass layer is well developed and the litter layer is shallow (Fig. 2a).

Table 2 shows the main characteristics of the

upper soil layer (0–20 cm) from sites I to VIII. Under *A. africana* the soils are acid to moderately acid; the metallic cations saturation coefficient (V) ranges between 70% and 97%. Under *U. guineensis*, the soil is very acid (pH 4) and poorly saturated (V = 9%). As the water level fluctuates greatly during the year, leaching occurs causing an important loss of nutrients. The content of available phosphorus in the soil (Olsen method) is very low or moderate. The highest available phosphorus level ( $17.5 \mu\text{g g}^{-1}$ ) is observed in the *Azelia africana* woodland of site VIII.

### Sampling

Sampling was carried out during the rainy season. Superficial roots were excavated, starting from the trunk and working towards the ultimate fine roots. Rootlets (1–5 g) were fixed in formaldehyde-acetic acid (FAA) (Johansen, 1940). For young seedlings the whole root system was fixed.

The fine roots were examined under a dissecting microscope. Rootlets covered by a fungal sheath were gently excised and washed under tap water. Freehand sections were cleared with a 20% sodium hypochlorite solution, rinsed in water, stained with Congo red or toluidine blue and observed with light or phase contrast microscopy. Roots were considered to be ectomycorrhizal when they had a distinctive sheath and a Hartig net. The ratio of the fungal sheath area to the total cross sectional area of root was calculated for the ECM of *A. africana* and of *U. guineensis*. Fine roots were also cleared and stained according to the procedure for VA mycorrhizas of Phillips & Hayman (1970). Roots were considered to be (VA) mycorrhizal when they had intramatrical vesicles, endocellular hyphal coils and arbuscules.

Sporocarps of putative ectomycorrhizal genera were collected, dried at 40–45 °C and identified in the laboratory. Voucher material was deposited in the herbarium of O.R.S.T.O.M. (Bel Air, Dakar) and in the herbarium of the National Botanical Garden of Belgium (BR).

## RESULTS

### Ectomycorrhizal fungi

During the rainy season (from July to October) there was a great diversity of species and a great abundance of sporocarps of putative ectomycorrhizal fungi. Table 3 shows the species found under *A. africana* and *U. guineensis*. Some species fruited after the first significant rainfall, others in the middle or at the end of the rainy season. This suggests the presence of different phenological periods in different species, as has been observed for fungal fruiting in temperate forests (e.g. Thoen, 1971 a, b).

Figures 2 and 3 show some of the main putative ectomycorrhizal fungi of *A. africana* and *U. guine-*

*ensis*. Noteworthy is the great diversity of orders, genera and species in the fungal spectrum of both *A. africana* and *U. guineensis*. The most represented orders are the *Russulales* (16 species), the *Boletales* (11 species) and the *Agaricales* (9 species). Several fungi, such as *Amanita* spp. and *Russula* spp. are still undescribed in Africa and might belong to new species. Noteworthy also is the presence of hypogeous fungi, two under *U. guineensis* and one under *A. africana*. These hypogeous species are so far undescribed. They are the first records of hypogeous fungi in Senegal and perhaps for any tropical forest of West Africa. Only six fungi are common to both *A. africana* and *U. guineensis*. It is, however, untimely to assess any host specificity.

Table 4 shows that some fungi have a wide distribution in tropical Africa. The fungi of *A. africana* and *U. guineensis* are, however, not found in the Sudano-Sahelian region, where endomycorrhizal trees such as *Acacia* spp. are dominant. They reach their northern limit in Senegal in the Sudano-Guinean region.

The dependence of the ectomycorrhizal fungi on host trees is high. Thus, where *A. africana* or *U. guineensis* are absent, the ectomycorrhizal species disappear and are replaced by saprophytic genera, such as *Agaricus*, *Collybia*, *Coprinus*, *Lepiota*, *Leucocoprinus* and *Psathyrella*. On the other hand, ectomycorrhizal fungi are present even when the host tree (*A. africana* or *U. guineensis*) is isolated and surrounded by endomycorrhizal trees. About fifty tree species were examined and shown to be endomycorrhizal.

*Scleroderma verrucosum*, *S. dictyosporum* and *Inocybe* sp. are especially abundant near seedlings of regenerating *A. africana*. These fungi are observed also under seedlings of *A. africana* grown in the state nursery of Djibelor close to site III. Such seedlings show abundant ECM suggesting that *Scleroderma verrucosum*, *S. dictyosporum* and *Inocybe* sp. might be 'early stage' mycorrhizal fungi.

### Ectomycorrhizas

*Localisation of ectomycorrhizas in the soil.* The ECM of *U. guineensis* are located below the litter layer between 1 and 5 cm depth. This might be correlated to the fluctuating water level in hydromorphic soils and the greater oxygen availability in the topsoil. The ECM of *A. africana* occur at a depth of 5–20 cm and are located in the mineral soil under the rooting zone of the grasses. No *Rhizobium* root nodules were found on *A. africana*.

*Morphology of ectomycorrhizas.* Several morphological types of ECM are distinguishable in the field by the sheath colour and texture, pattern of ramification and presence or absence of mycelial strands. Figure 4 shows some distinctive morphological types of

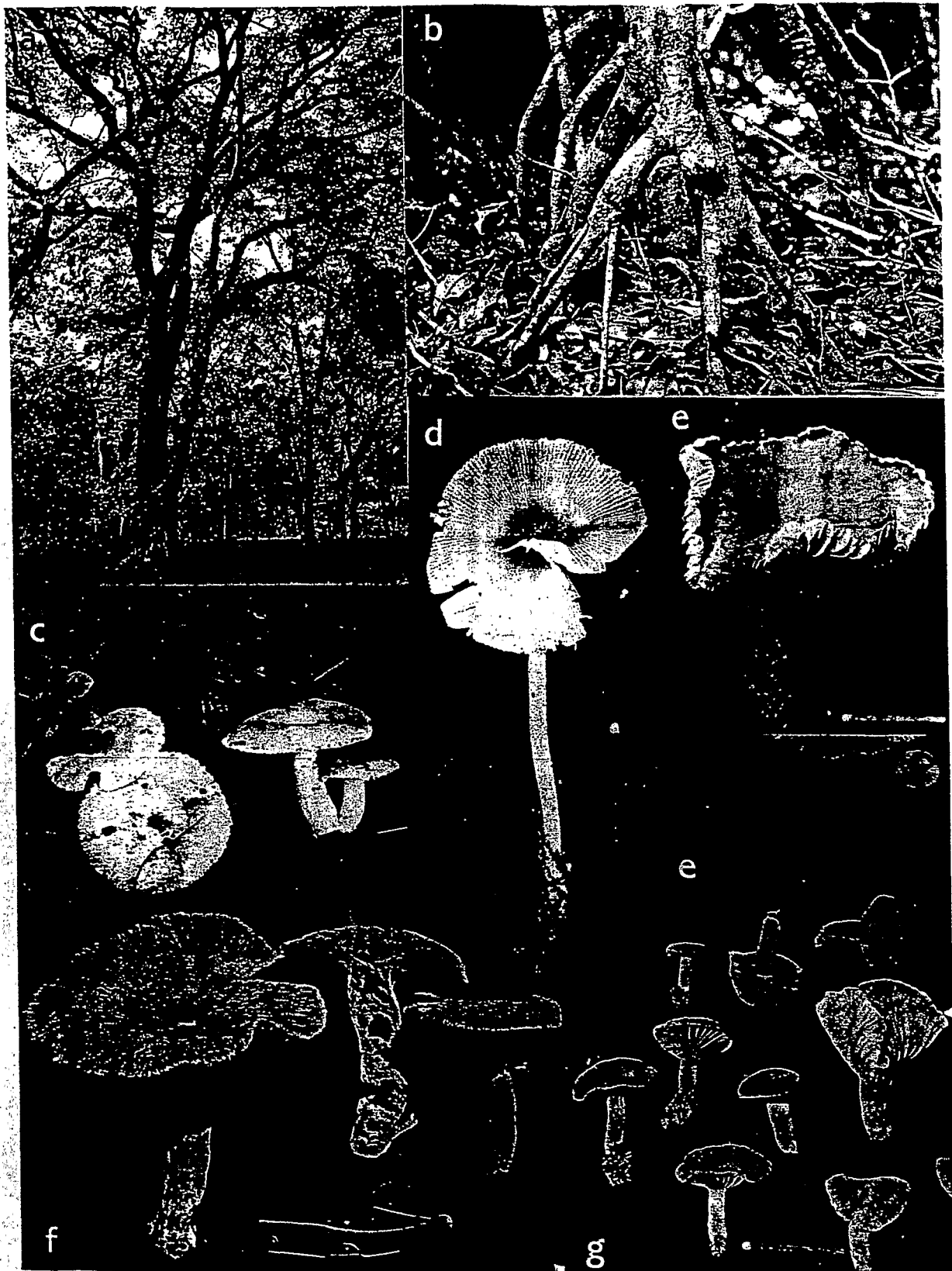


FIGURE 2. Host trees (a, b) and some putative ectomycorrhizal fungi of *Azelia africana* (c, f) and *Uapaca guineensis* (b, d, e, g). (a) *A. africana* in the semi-deciduous forest of Kalounayes, July 1985. (b) Stilt roots of *U. guineensis* and *Tubosaeta brunneosetosa* (N 7462), Santiaba Manjak, July 1985. (c) *Russula* sp. (N 7581), Bayottes, July 1986. (d) *Amanita* sp. (N 7648), Santiaba Manjak, August 1986. (e above) Mature and (e below) young *Lactarius gymnocarpus* (N 7646). Santiaba Manjak, August 1986. (f) *Russula* sp. (N 7669), Thiara, August 1986. (g) *Lactarius* sp. (N 7643), Santiaba Manjak, August 1986.



FIGURE 3. Some putative ectomycorrhizal fungi of *Azelia africana* (a, d, e) and of *Uapaca guineensis* (b, c, f). (a) *Xerocomus subspinulosus* (N 7540), Kalounayes forest, July 1986. (b) Close-up view of *Austrogautieria* sp. (N 7873), Santiaba Manjak, September 1987. (c) *Tubosaeta brunneosetosa* (N 7467), Santiaba Manjak, July 1985. (d) *Cantharellus pseudofriesii* (N 7654), Thiara, August 1986. (e) *Amanita hemibapha* (N 7658), Thiara, August 1986. (f) *Amanita aff. rubescens* (N7571), Santiaba Manjak, July 1986.

Table 3. Ectomycorrhizal fungi found under *Uapaca guineensis* and/or *Azelia africana* in sites I-IX

Orders, species	Host trees*		No. of voucher material
	U.g.	A.f.	
<b>Boletales</b>			
<i>Boletellus</i> sp.	+	+	7518, 7569, 7596
<i>Gyrodon cupreus</i> Heinem.	-	+	7460, 7570
<i>Gyrodon intermedius</i> (Pat.) Sing.	-	+	7579, 7729
<i>Gyroporus microsporus</i> (Sing. & Grinl.) Heinem. & Rammeloo var. <i>congolensis</i> (Heinem.) Heinem & Rammeloo	-	+	7613, 7635
<i>Porphyrellus niger</i> Heinem. & Gooss.	-	+	7875
<i>Pulveroboletus</i> aff. <i>trinitensis</i> Heinem.	+	-	7461, 7716
<i>Strobilomyces costatispora</i> (Beeli) Gilb.	-	+	7506
<i>Tubosaeta brunneoseitosa</i> (Sing.) Horak	+	-	7462, 7467, 7573, 7714
<i>Xerocomus</i> aff. <i>hypoxanthus</i> Singer	+	-	7491, 7603, 7645
<i>Xerocomus spinulosus</i> Heinem. & Goos.	-	+	7514
<i>Xerocomus subspinulosus</i> Heinem.	+	+	7489, 7493, 7540
<b>Agaricales</b>			
<i>Amanita</i> cf. <i>crassiconus</i> Bas (nom. prov.)	-	+ <sup>a</sup>	7664, 7882
<i>Amanita hemibapha</i> (Berk. & Br.) Sacc.	-	+ <sup>a</sup>	7658, 7734
<i>Amanita</i> aff. <i>rubescens</i> (Pers.: Fr.) S. F. Gray	+	+	7487, 7566, 7571
<i>Amanita</i> sp. 1 (yellow)	+	-	7644
<i>Amanita</i> sp. 2 (grey brown)	+	-	7648
<i>Amanita</i> sp. 3 (white with blueish gills)	-	+ <sup>a</sup>	7672
<i>Amanita</i> sp. 4 (entirely white)	-	+ <sup>a</sup>	7674
<i>Inocybe</i> sp. 1 (leiosporous)	-	+ <sup>a</sup>	7657
<i>Inocybe</i> sp. 2 (gibbosporous)	-	+	7561, 7624, 7626
<b>Russulales</b>			
<i>Elasmomyces</i> sp. (hypogeous)	+	-	7652
<i>Lactarius gymnocarpus</i> Heim	+	+	7605, 7646, 7881
<i>Lactarius zenkeri</i> P. Henn.	-	+	7702, 7885
<i>Lactarius</i> sp. 1 (pinkish brown)	+	+	7618, 7643
<i>Lactarius</i> sp. 2 (dark brown)	-	+ <sup>a</sup>	7662
<i>Russula annulata</i> Heim	+	-	7606, 7647, 7878
<i>Russula discopus</i> Heim	+	-	7609, 7649, 7872
<i>Russula</i> aff. <i>foetens</i> Pers. ex Fr.	-	+	7617
<i>Russula</i> aff. <i>pectinata</i> Fr.	-	+ <sup>a</sup>	7669, 7886
<i>Russula</i> sp. 1 (vinaceous brown)	+	-	7519
<i>Russula</i> sp. 2 (yellow)	-	+	7581, 7594, 7632
<i>Russula</i> sp. 3 (pinkish red)	-	+	7633
<i>Russula</i> sp. 4 (carmin red)	-	+	7509
<i>Russula</i> sp. 5 (red and ocre)	-	+	7507
<i>Russula</i> sp. 6 (pruinous red)	-	+	7580
<i>Russula</i> sp. 7 (cream)	-	+ <sup>a</sup>	7670
<b>Cantharellales</b>			
<i>Cantharellus congolensis</i> Beeli	+	-	7879
<i>Cantharellus pseudofriesii</i> Heinem.	-	+ <sup>a</sup>	7654
<b>Aphylophorales</b>			
<i>Coltricia cinnamomea</i> (Pers.) Murr.	+	-	7859, 7883
<b>Gautieriales</b>			
<i>Austrogautieria</i> sp. (hypogeous)	+	-	7700, 7873
<b>Hymenogastrales</b>			
<i>Sclerogaster</i> sp. (hypogeous)	-	+ <sup>a</sup>	7660, 7701, 7861
<b>Sclerodermatales</b>			
<i>Scleroderma dictyosporum</i> Pat.	+	+	7510, 7526, 7559
<i>Scleroderma verrucosum</i> Pers.	-	+	7508, 7522, 7560
Number of species (Total = 43)	18	31	

\* U.g., *Uapaca guineensis*; A.f., *Azelia africana*

\* Fungi occurring only in site VIII (Thiara)

Table 4. African distribution and habitat of some putative ectomycorrhizal fungi found under *Azelia africana* and/or *Uapaca guineensis* in Senegal

Species	Habitat and presumed host tree(*)	Country(*)
<i>Cantharellus congolensis</i>	Rainforest, <i>Macrolobium</i>	Zaire
<i>Cantharellus pseudofriesii</i>	Rainforest, <i>Macrolobium</i>	Zaire
<i>Lactarius zenkeri</i>	Rainforest(?)	Cameroon
<i>Porphyrellus niger</i>	Rainforest, <i>Macrolobium</i> , Dry evergreen forest (muhulu)	Zaire
<i>Strobilomyces costatispora</i>	Rainforest, <i>Macrolobium</i>	Zaire
<i>Xerocomus spinulosus</i>	Rainforest, <i>Macrolobium</i>	Zaire
<i>Gyroporus microsporus</i>	Rainforest, <i>Macrolobium</i> Woodland, <i>Brachystegia</i>	Burundi, Zaire, Zambia
<i>Coltricia cinnamomea</i>	Deciduous forest	Burundi, Kenya, Sierra Leone, South Africa, Zambia
<i>Gyrodon cupreus</i>	Woodland(?)	Ethiopia, Kenya, Malawi, Uganda
<i>Lactarius gymnocarpus</i>	Woodland (dry forest)	Cameroon, Ivory Coast, Guinea, Tanzania, Zaire
<i>Russula annulata</i>	Woodland(**)	Tanzania, Zaire(**)
<i>Xerocomus subspinulosus</i>	Woodland	Tanzania, Zaire

\* Source after Heim, 1970; Heinemann, 1954, 1959, 1966; Heinemann & Rammeloo, 1983; Pegler, 1977, 1983; Ryvarden & Johansen (1980).

\*\* Non-published observation, Thoen, 1972.

Table 5. Main characteristics of the ectomycorrhizas of *Azelia africana* and *Uapaca guineensis*

	<i>A. africana</i> (n = 10)	<i>U. guineensis</i> (n = 13)
Range of diameter ( $\mu\text{m}$ )	236–466	390–640
Mean diameter ( $\mu\text{m}$ )	328	488
SEM* ( $\mu\text{m}$ )	88	79
CV** (%)	27	16
Range of sheath thickness ( $\mu\text{m}$ )	14–85	18–80
Mean sheath thickness ( $\mu\text{m}$ )	50	47
SEM* ( $\mu\text{m}$ )	24	16
CV** (%)	48	34
Range of sheath area (%)	20–65	17–54
Mean sheath area (%)	50	35
SEM* (%)	14	9
CV** (%)	28	26
Range of radial depth of the Hartig net ( $\mu\text{m}$ )	18–30	15–68
Range of host tissue diameter ( $\mu\text{m}$ )	166–314	304–550
Mean host tissue diameter ( $\mu\text{m}$ )	226	393
SEM* ( $\mu\text{m}$ )	51	70
CV** (%)	22	18
Number of cortical cells layers	2–3	4–5
Number of protoxylem poles	2	3–4

\* SEM: standard error of the mean; \*\* Coefficient of variability.

ECM. The texture of the sheath varies from entirely smooth to rugose, felty, hairy or bristly, with dull, glossy or waxy aspect. Although the colour of the sheath may change in ageing ECM, we have distinguished white, yellow, pink, beige, brown and maroon ECM on *U. guineensis* and white, yellow, greyish blue, beige, brown and dark brown ECM on *A. africana*. Both trees may bear two or more mycorrhizal types on a single root portion (Fig. 4d). Racemose ECM with a sheath covering the mother

and the lateral roots are common (Fig. 4a). Pinnate (Fig. 4b) and monopodial ectomycorrhizas (Fig. 4c, e) are also observed. Mycelial strands are present on more than 60% of the ECM (Fig. 4a, c, d).

In some cases it is possible to trace mycelial strands and extensive masses of loose hyphae from the base of sporocarps to the most characteristic ECM. In this way, we have established for *Uapaca guineensis* connections between yellow ECM and the hypogeous sporocarps of *Austrogautieria* sp. (Fig. 3b



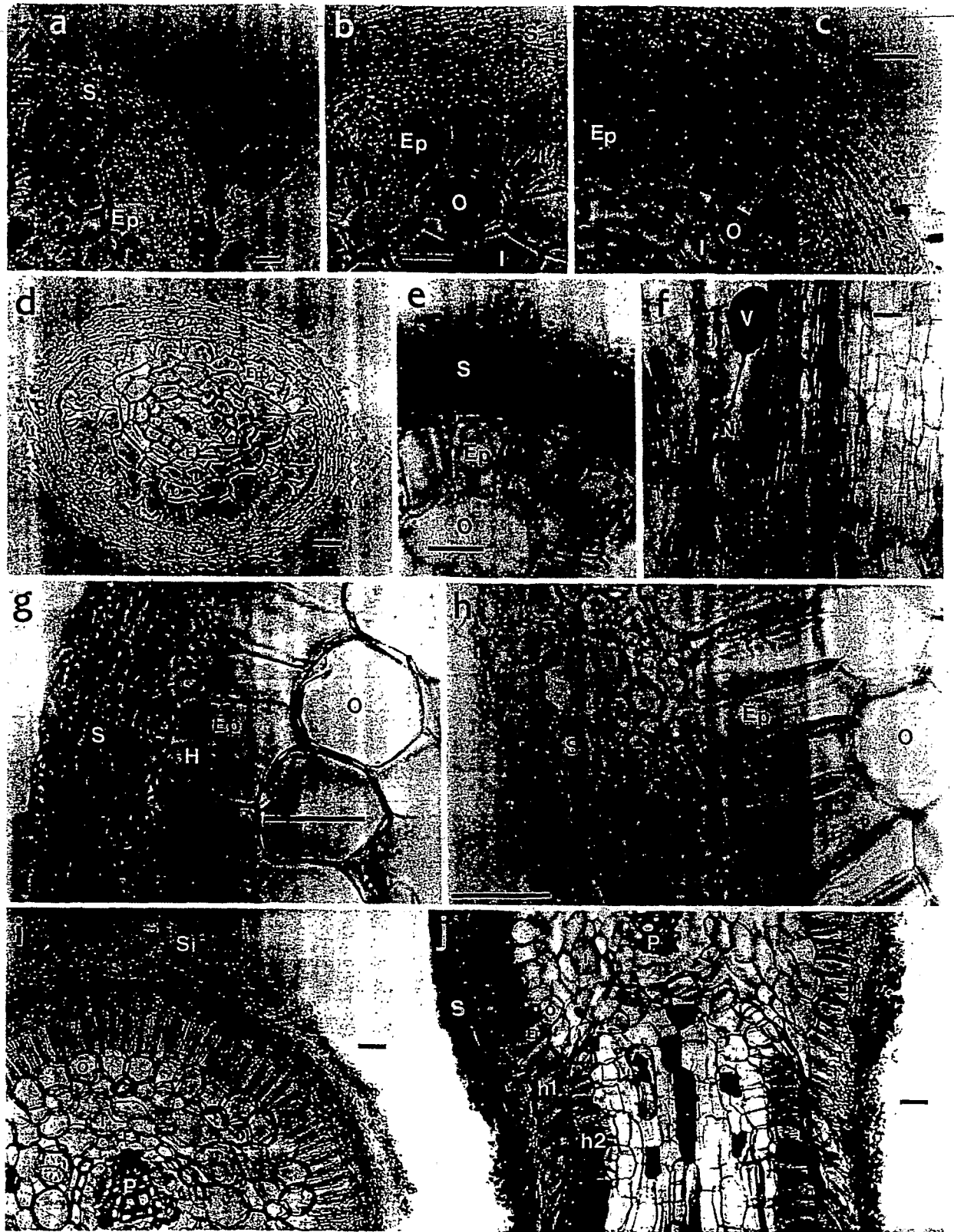


**Figure 4.** Stereomicrographs of ectomycorrhizas of *Uapaca guineensis* (a, b) and *Azelia africana* (c, d, e). (a) Cluster of bright yellow ECM formed by *Austrogautieria* sp., (b) Pinnate, beige ECM formed by *Lactarius gymnocarpus*. (c) White monopodial or poorly branched ECM. (d) White and dark brown ECM on a single root portion. (e) Close-up view of a dark brown ECM showing hairy sheath. Bar = 1 mm.

and Fig. 4a), pinnate, beige ECM and *Lactarius gymnocarpus* (Fig. 4b), pink ECM and *Amanita* aff. *rubescens*, brown, bristly ECM and *Coltricia cinnamomea* (Fig. 4e), and whitish ECM with a sclerodermic smell and *Scleroderma verrucosum*. Connections between sporocarps and the deeper located ECM of *Azelia africana* were more difficult to establish with certainty. However the link between whitish ECM of *A. africana* and *Scleroderma verrucosum* has been proved.

*Anatomy of ectomycorrhizas.* Table 5 shows the main anatomical characteristics of the ECM. The diameter of the ECM of *U. guineensis* is greater than that of *A. africana*. The mean value of the sheath thickness is the same for both species. However, as the host tissue diameter is smaller for *A. africana*, its ratio of sheath to host tissue area is greater than that of *U. guineensis*.

In cross sections, Hartig net penetration is always limited to epidermal cells that are in direct contact



**Figure 5.** Ectomycorrhizas of *Afzelia africana* (a, b, c, d, e), endomycorrhiza (f) and ectomycorrhizas of *Uapaca guineensis* (g, h, i, j). (a) Transverse section through a dark brown ECM. (b) Transverse section through a yellowish ECM. (c) Transverse section through a yellow ECM. (d) Transverse section through a light brown ECM. (e) Transverse section through a white ECM. (f) Endomycorrhizal vesicle and intramatrical hyphae. (g) Transverse section through a maroon brown ECM formed by *Coltricia cinnamomea*. (h) Transverse section through a pink ECM formed by *Amanita aff. rubescens*. (i) Transverse section through a white ECM showing layering and superficial incrustations of the sheath. (j) Transverse section and longitudinal section of an emerging root showing overlapping of Hartig nets H1 and H2; same ECM as (i)

Key: S, fungal sheath; Si, sheath incrustations; H, Hartig net; C, clamp connection on emerging hypha; Ep, epidermis of root; O, outer cortex of root I, inner cortex of root; E, endodermis of root; P, primary xylem of root; V, endomycorrhizal vesicle; N, endomycorrhizal intercellular hypha. Bar = 20  $\mu$ m.

with cortical cells, a pattern described as a 'para-epidermal Hartig net' by Godbout & Fortin (1983). Juxtaposition of Hartig nets occurs when a new lateral root emerges (Fig. 5j). Enlarged hyphae are observed at the transition zone between the sheath and the Hartig net (Fig. 5d, e, g). On *Uapaca* ECM, epidermal cells are strikingly elongated, forming a palisade layer, and are filled with brown phenolics. *Azela* ECM show less epidermal elongation (Fig. 5a, b, c) and phenolics are rare or absent. Layering of the sheath is present in ECM of both tree species (Fig. 5c, i). The outer layer of the sheath is sometimes incrustated with pigments (Fig. 5i, j).

#### Endomycorrhizas

Non-ectomycorrhizal roots of adult *A. africana* and *U. guineensis* were examined for endomycorrhizas (VAM). It was found that *Uapaca guineensis* has VAM whereas *A. africana* has not. Thus, mature trees of *Uapaca guineensis* may have a dual pattern of symbiosis.

#### Seed germination and seedling infection

Seeds of *U. guineensis* are small (10.5–14 × 7–9 mm), whereas those of *A. africana* are big (20–29.7 × 9.3–14.5 mm) and contain, presumably, larger amounts of food reserves. Seeds of *U. guineensis* germinate in July, at the beginning of the rainy season, as soon as they reach the soil. Seeds of *A. africana* fall in February, in the middle of the dry season, and dormancy occurs until the rainy season. Mycorrhizal infection of both species occurs very soon, even before the emergence of the first leaves. However, *A. africana* is initially infected by ECM, whereas *U. guineensis* is infected by VAM. The stage of development at which *U. guineensis* becomes ectomycorrhizal is unknown.

In one site, which was partially reclaimed and converted to a pluvial rice field after burning, only a few adult trees of *A. africana* remained, yet seeds germinated and sporocarps of *Scleroderma verrucosum* occurred among the rice shoots. Germinants were shown to be early ectomycorrhizal. This demonstrates the ability of fungal propagules to survive in disturbed sites or to spread from the ectomycorrhizal mother trees.

#### DISCUSSION

The diversity of the putative ectomycorrhizal fungi of *Uapaca guineensis* and *Azela africana* is high. It is comparable to the diversity of temperate ectomycorrhizal trees such as *Fagus sylvatica* (Thoen, 1971a, b). Among the Agarics, the mycorrhizal genera belong to the boletes, *Russula*, *Lactarius*, *Amanita* and *Inocybe*. The same genera were recorded in East African forests by Pegler (1977). Some important mycorrhizal genera, namely *Cortin-*

*arius*, *Hebeloma*, *Tricholoma*, which are abundant in temperate forests, are absent in southern Senegal. Several of the ectomycorrhizal fungi found under *A. africana* and *U. guineensis* have a wide range in tropical Africa. These fungi are known from miombo woodlands belonging to the Sudano-Zambezian element or rain forests belonging to the Guineo-Congolian element (White, 1965). These two forest types are known to contain ectomycorrhizal trees (Peyronel & Fassi, 1957, 1960; Fassi & Fontana, 1961, 1962; Högberg & Nylund, 1981; Högberg, 1982; Högberg & Pearce, 1986; Alexander, 1985, 1987; Newbery *et al.*, 1988), namely *Berlinia* spp., *Brachystegia* spp. and *Gilbertiodendron* spp., all trees absent in Senegal. Some fungi of *A. africana* and *U. guineensis* might thus be able to form ECM with other tree genera, showing a low host specificity.

In our plots, *A. africana* is the only Caesalpinioideae to have ECM. Other genera of this subfamily (*Cordyla*, *Daniellia*, *Detarium*, *Erythrophleum*) that we have examined are all endomycorrhizal. *Azela africana* is ectomycorrhizal in all our sites, whatever the available phosphorus level of the soil and the diversity of surrounding endomycorrhizal trees might be. This is consistent with previous observations of Alexander (1975): 'those species [of Caesalpinioideae] which form ectomycorrhizas do so even on soils of higher P status and when they occur as isolated individuals in a matrix of VA [mycorrhizas] forming species'.

Fundamental questions arise as to how the ectomycorrhizal propagules reach isolated individuals of host trees and how they compete with the ubiquitous endomycorrhizal fungi? In *A. africana*, translocation of reserves, such as carbohydrates, from the big and fleshy cotyledons to the roots probably allows early ECM infection. Precocious infection might prevent colonization of the roots by VAM. In *U. guineensis* the seeds and the cotyledons are smaller than those of *Azela*. Endomycorrhizal fungi, requiring a lower carbohydrate level than the ECM (Janos, 1984) colonize the roots first. Ectomycorrhizas (present on adult individuals) must appear later, presumably when enough photosynthetates are transferred to the roots. Primary infection by VAM followed by ECM is reported in the unrelated genera *Helianthemum* (Read, Kianmehr & Malibari, 1977), *Alnus* (Beddiar, 1984) and *Eucalyptus* (Lapeyrie & Chilvers, 1985; Chilvers, Lapeyrie & Horan, 1987). It is noteworthy that these three genera all have small seeds. Adult individuals of *U. guineensis* bear both ECM and VAM, showing that dual symbiosis may be stable. Other dual symbioses are reported for *Uapaca staudtii*, *Azela pachyloba* and *Gilbertiodendron dewevrei* by Newbery *et al.* (1988). Dual symbiosis might be more common than once believed and examination of roots of only young seedlings might lead to erroneous conclusions regarding the mycorrhizal status of a tree species.

*Uapaca guineensis* is the second ectomycorrhizal tree of the genus found to grow in wet conditions; *U. staudtii* being the other (Newbery *et al.*, 1988). Four other ectomycorrhizal *Uapaca* spp. grow in the miombo woodland which has a drier environment (Redhead, 1974; Högborg, 1982; Högborg & Pearce, 1986).

Some fungi such as *Scleroderma verrucosum*, *S. dictyosporum* and *Inocybe* sp. were especially common under regenerating individuals of *A. africana* or under seedlings grown in a nursery. They belong likely to the 'early stage fungi' (Mason *et al.*, 1982) which are of great practical importance for nursery inoculation trials.

Whereas root nodules were once found on *Afzelia quanzensis* (Högborg & Nylund, 1981), they were lacking on *A. africana*. This is consistent with earlier observations on the same species by Jenik & Mensah (1967).

#### ACKNOWLEDGMENTS

We are grateful to Dr P. Heinemann (National Botanical Garden of Belgium, Meise) for help in identifying several fungi and to Samboudian Dedhiou (Ziguinchor, Senegal) for help during field investigations.

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