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Arbuscular mycorrhizal relations of mangrove plant community at the Ganges river estuary in India

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Abstract Mangroves are climax formation of hydrohalophytes inhabiting estuarine or marine salt marshes in the tropics and subtropics. As a terrestrial plant community inhabiting tidally inundated estuarine or marine sediments, mangroves show considerable adaptation to salinity, water-logging and nutrient stress. Thirty-one species of mangrove and mangrove associates and 23 species of transported flora, belonging to 25 families at four physiographic stages of succession of the mangrove plant community at the terminal part of the Ganges river estuary in India were examined for arbuscular mycorrhizal (AM) root association. Dominant members of the mangrove plant community were all AM, mostly with ‘Paris’ type structures. Many of the known non-mycotrophic plant families, except the Cyperaceae, also showed AM association, with intracellular hyphae and vesicles as the most discernible endophyte structures. Intensity of AM colonization varied both with the species and situations of their occurrence, being more intense and also more extensive in less saline dry ridge mangroves than in more saline formative and developed swamp mangroves. Introduced exotic trees on the ridges and embankments were infected by AM, but less than the declining mangroves in the same location. Seven species of AM fungi in common with those of the upstream mesophytic plants were isolated from root-free rhizosphere soils of the mangroves, three of which predominated in root association. These species, individually and as mixtures, infected roots of salinity tolerant herbs and trees in both locational silt and upstream alluvial soil with obvious improvements in their biomass yield and phosphorus nutrition. AM infective potential of root-free rhizosphere soils of the dominant members of the mangrove community were negatively related to salinity level of the sediment soil of the successional stages. The evidences of AM asso-

ciation of mangroves and other salt marsh plants obtained here and those reported elsewhere are discussed.

Keywords Mangroves · (V) A mycorrhiza · Ecology · Salt marsh plants · Estuary

Introduction

Mangroves, the climax formation of hydrohalophytes belonging to several plant families, inhabit tropical and sub-tropical estuarine or marine salt marshes. Mangrove forests are considered as open ‘interface’ ecosystems connecting upland terrestrial and coastal estuarine ecosystems (Lugo and Snedaker 1974). Contributors to the geo-aquatic food chain, mangrove forests are important for biomass production and coastline protection. In the context of our studies on microbiological aspects of ecosystemic adaptation of mangroves to salinity, inundation and nutrient stress, we have examined arbuscular mycorrhizal (AM) relations of four eco-successional stages of the mangrove plant community at the terminal part of the Ganges river estuary in India. We have previously reported the occurrence of AM in four species of pioneer salt marsh plants (Sengupta and Chaudhuri 1990), heterotrophic dinitrogen fixation in mangrove root association (Sengupta and Chaudhuri 1991), and the presence of seemingly mycorrhizal, dark septate mycelial endophytes in mangrove roots (Sengupta and Chaudhuri 1994), from the same location. The recognition that dominant plants of each biome – large, easily defined terrestrial plant community units (Odum 1971) – engage in mutualistic root associations with soil fungi to form mycorrhiza (Read 1993), prompted us to see whether the tropical hydrohalophytic mangrove biome inhabiting estuarine, semi-aquatic, saline sediments belongs to the above generalization.

Materials and methods

Study location and sample collection

The terminal part of the deltaic drainage basin of the river Ganges in India, known as ‘Sundarban’ (21°30′ – 22°30′N, 88°10′ – 89°51′E)

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Table 1 Physical and chemical properties of soils of the successional stages of mangrove plant community of the Ganges river estuary in India^a

Successional stage	pH	Salinity index (EC) (dSm ⁻¹)	Organic matter (g/kg)	Total N (g/kg)	NO ₃ -N (mg/kg)	NH ₄ -N (mg/kg)	Phosphorus (mg/kg)		Exchangeable K (meq/100 g)
							Total	Available	
I. Formative mangrove swamp	8.0	16.0	4.60	0.9	108	21	240.8	11.24	1.74
II. Developed mangrove swamp	7.8	14.5	14.27	1.0	324	28	278.3	22.11	1.98
III. Declining ridge mangrove	7.4	4.5	8.77	1.5	509	36	336.8	10.87	1.45
IV. Protected agricultural land	7.2	2.5	12.93	1.7	606	43	402.7	8.34	0.92

^a All data are means of five separate determinations of a single bulked sample for each stage.

is the home of the Indian sub-group of “Old World mangroves” (Chapman 1975). Based on physiographic characters and floristic development, the mangrove forest of Sundarban is divided into four distinct eco-successional stages: (I) formative mangrove swamps, (II) developed mangrove swamps, (III) declining ridge mangroves, and (IV) declined mangroves on embankment-protected highlands where crop agriculture and forestry with salinity tolerant plant species have been introduced (Sengupta and Chaudhuri 1991).

Soil and root samples of mangrove and associated plants were collected during Spring (February–April) from the four physiographic stages of mangrove succession over a 10-km² area of the riverine delta. Five representative samples of soil or root for any location, or a plant species from a location, were collected and combined for analysis. As far as practicable, soil and root samples were collected from single stands of the different plant species within a designated physiographic stage. Herbaceous plants and young tree seedlings were removed from mud flats along with a ball of soil adhering to the roots with the help of a core sampler. Roots still attached with the plants were freed of soil, washed and sampled for mycorrhizal analysis. For older trees, juvenile nutritive roots were located by digging, taken out with adhering soil and sampled similarly. Root-adhered soil was air dried, bulked for a plant species from a stage and also irrespective of the plant species for a stage, sieved and then used for analysis of AM fungal spores and infective inoculum density.

Analytical methods

Standard methods of soil analysis (Jackson 1967; Dewis and Freitas 1984) were used to analyze the common physical and chemical properties of root-associated soil samples taken from the surface layer of the estuarine sediment (1–15 cm).

AM root infection intensity was assessed by the slide micro-metric method (Kormanik and McGraw 1984) from roots cleared and stained according to Philips and Hayman (1970), with some modification (Sengupta and Chaudhuri 1990). Three hundred 1 cm root segments taken from composite root samples were examined for each plant species from a location. The presence of any of the endophytic elements – hyphae, coils, vesicles and arbuscules – was taken as evidence of mycorrhization and used for estimating root infection intensity. Designation of the arbuscular endophytic association as either ‘Arum’ type or ‘Paris’ type was made according to the description given by Smith and Smith (1997). The wet sieving and decantation method of Gerdemann and Nicolson (1963) and density gradient centrifugation (Watrud 1984) were used to isolate spores of AM fungi from root-associated soil. Most probable number (MPN) of infective AM propagules was determined by the standard 10-fold serial dilution end-point technique (Powell 1980), taking *Cajanus cajan* (L.) Millsp. as the test plant. Riverine silt soil from the location was used as diluent. Root-based AM inoculum was prepared with surface-sterilized spores of the different AM fungus species isolates (Watrud 1984), singly or in mixtures, taking maize as the host plant, in sterile sand:soil (1:1) mixture in plastic containers. A growth response study of selected herbs and trees with AM inoculation was carried out in a

greenhouse during the Spring – Summer season (March–June) with 5 and 12 kg soil in plastic planters, for 75 and 100 days, respectively. Fresh, air-dried root-based inoculum in 5–8 mm pieces at the rate of 3 g per kg soil was used for soil inoculation. Heat-killed maize root in equivalent amount was added to the control set. The AM fungi were identified from spore morphology by reference to type descriptions of the species (Schenck and Perez 1990). The AM fungal species isolates are maintained in the author’s (S.C.) laboratory for future reference.

Results

Soil analysis data (Table 1) revealed that besides soil salinity, poor availability of major plant nutrients – particularly nitrogen and phosphorus – was a strong stress factor for the plant community of the ecosystem. Except for stage I formative swamp, all other stages had moderate organic matter contents, as is typical of tropical alluvial soil under plant cover. Concentration of total and NO₃ nitrogen, which was lowest in the formative swamps, increased with the stages of physiographic succession of the plant community. Concentrations of exchangeable NH₄ were also very low, particularly in the swampy mangrove sediments. Concentrations of available P in soil sediments of the successional stages were low to moderate, being lowest in the stage IV embankment-protected agricultural land. Concentrations of total phosphorus were relatively high, having an inverse relationship with the stages of succession compared to that of available phosphorus.

Fifty-four plant species from the four successional stages, excluding agricultural crops at stage IV, were examined for the presence of root endophytic fungi. Of these, 31 were mangrove and mangrove-associates and 23 were non-litoral, non-mangrove species, introduced by man or transported by the river to the ecosystem. All the 31 mangrove and associated species belonging to 18 plant families showed the presence of root endophytes, structurally similar to those of AM caused by the Glomalean fungi (Table 2). The non-litoral species, belonging to 13 families, including some commonly reported non-mycotrophic plant families (e.g., Amaranthaceae), but excluding those belonging to the Cyperaceae, also showed the presence of AM endophytes in their roots in their respective physiographic situations. Endophytic colonization of most of the plant species structurally resembled ‘Paris’ type AM (Smith and Smith 1997),

Table 2 List of mangrove, mangrove associate and other plant species (excluding agricultural plants) of the Ganges river estuary in India (Sundarban) examined in the study, their physiographic distribution, plant type designation and arbuscular mycorrhizal (AM) association. *M* Mangrove, *MA* mangrove associate, *NM* non mangrove, *T* tree, *S* shrub, *Se* sedge, *R* reed, *H* herb, *L* liane, *V* vesicle, *A* arbuscule, *I-IV* stages of physiographic succession, *(A)* Arum type, *(P)* Paris type, *(B)* both types

Plant family	Species	Plant type designation	Distribution	AM structures
Acanthaceae	<i>Acanthus ilicifolius</i> L.	MS	I, II, III	VA (A)
Aizoaceae	<i>Sesuvium portulacastrum</i> L.	MH	II, III	V (P)
Amaranthaceae	<i>Alternanthera polygonoides</i> (L.) R.Br.	NMH	III, IV	V (P)
Apocynaceae	<i>Nerium odorum</i> Soland.	NMS	IV	VA (B)
	<i>Thevetia peruviana</i> (Pers.) Sch.	NMS	III, IV	VA (P)
Arecaceae	<i>Areca catechu</i> L.	NMT	IV	VA (B)
	<i>Borassus flabellifer</i> L.	NMT	IV	VA (B)
	<i>Cocos nucifera</i> L.	NMT	III, IV	VA (A)
	<i>Nipa fruticans</i> Wurm.	MT	II, III	VA (B)
	<i>Phoenix paludosa</i> Roxb.	MS	III	VA (B)
Asclepiadaceae	<i>Calotropis gigantea</i> (L.) R. Br.	NMS	III, IV	VA (P)
	<i>Finlaysonia obovata</i> Wall.	MAC	II	VA (P)
Asteraceae	<i>Parthenium hysterophorus</i> L.	NMH	III, IV	VA (A)
Avicenniaceae	<i>Avicennia alba</i> Bl.	MT	I, II, III	VA (P)
	<i>A. marina</i> (For.) Vierh.	MT	I, II	VA (P)
	<i>A. officinalis</i> L.	MT	I, II, III	VA (P)
Boraginaceae	<i>Heliotropium indicum</i> L.	NMH	III, IV	VA (A)
Casuarinaceae	<i>Casuarina equisetifolia</i> Forst.	NMT	IV	VA (P)
Chenopodiaceae	<i>Arthrocnemum indicum</i> (Willd) Moq.	MH	II, III	VA (P)
	<i>Suaeda maritima</i> (L) Dumort.	MH	II, III	V (P)
Convolvulaceae	<i>Ipomoea pes-caprae</i> (L.) Sw.	MH	III, IV	V (P)
Cyperaceae	<i>Cyperus rotundus</i> L.	NMSe	III, IV	None
	<i>Scirpus</i> sp.	MASe	II, III	None
Euphorbiaceae	<i>Excoecaria agallocha</i> L.	MT	II, III	V (P)
Fabaceae	<i>Derris indica</i> (Lam.) Ben.	MT	II	VA (A)
	<i>D. scandens</i> Benth.	ML	II	VA (A)
	<i>D. trifoliata</i> Lour.	MT	II	VA (A)
Malvaceae	<i>Hibiscus tortuosus</i> Wall.	MT	III, IV	VA (A)
	<i>Thespesia populnea</i> (L.) Sol. ex Corr.	NMT	III, IV	VA (B)
Meliaceae	<i>Xylocarpus</i> Sp.	MT	II, III	VA (B)
Mimosaceae	<i>Acacia auriculaeformis</i> A.Cunn.	NMT	IV	VA (P)
	<i>A. nilotica</i> (L.) ex Del.	NMT	IV	VA (P)
	<i>Prosopis juliflora</i> DC.	NMT	IV	VA (P)
Myrsinaceae	<i>Aegiceras majus</i> Gaertn.	MT	II	VA (P)
Myrtaceae	<i>Eucalyptus globosus</i> Labille.	NMT	IV	VA (P)
Plumbaginaceae	<i>Aegialitis ratundifolia</i> Roxb.	MT	I, II	V (P)
Poaceae	<i>Cynodon dactylon</i> Pers.	NMH	II, III, IV	VA (A)
	<i>Digitaria sanguinalis</i> Scop.	NMH	III, IV	VA (B)
	<i>Echinochloa colona</i> Link.	NMH	III, IV	VA (B)
	<i>Leersia hexandra</i> SW.	NMH	III, IV	VA (B)
	<i>Leptochloa filiformis</i> Roem & Sch.	NMH	III, IV	VA (B)
	<i>Phragmites karka</i> Trin. ex. Steud	NMR	II, III	VA (P)
	<i>Porteresia coarctata</i> (Roxb.) Tak.	MH	I, II	V (P)
Rhizophoraceae	<i>Bruguiera gymnorrhiza</i> (L.) Lam.	MT	I, II	VA (B)
	<i>Bruguiera</i> sp.	MT	I, II	VA (P)
	<i>Ceriops decandra</i> (Griff.) Ding Hou.	MT	I, II	VA (P)
	<i>C. tagal</i> (Pers.) Robins.	MT	I, II	VA (P)
	<i>Rhizophora candelaria</i> DC.	MT	I, II	VA (P)
	<i>R. mucronata</i> Lam.	MT	I, II	VA (P)
Sonneratiaceae	<i>Sonneratia apetala</i> Buch. Ham.	MT	I, II	VA (A)
	<i>S. caseolaris</i> (L.) EngL.	MT	I, II	VA (A)
Sterculiaceae	<i>Heritiera fomes</i> Buch. Ham.	MT	III	VA (B)
Tamaricaceae	<i>Tamarix gallica</i> L.	MAS	III, IV	VA (A)
Verbenaceae	<i>Clerodendrum inerme</i> (L.) Gaertn.	NMS	III, IV	V (P)

with occasional absence of typical arbuscules in some of the plant species (Table 2). Intracellular hyphae, hyphal coils and intracellular vesicles were the most common structures in the majority of the plant roots. Several plant species showed typical 'Arum' type structures with characteristic intercellular hyphae with arbuscules and vesicles. A few species showed both 'Arum' and 'Paris' type structures (Table 2). As reported earlier (Sengupta and Chaudhuri 1990), pioneer salt marsh herbs at the swampy stages of succession, including two species of

the Chenopodiaceae, *Arthrocnemum indicum* (Willd) Moq. and *Suaeda maritima* (L) Dumort., were also seen to be infected by the (V)A endophytic fungi, with intracellular hyphae and vesicles as the most discernible mycorrhizal structures.

Although the number and identity of plant species examined for the different stages were not the same, average root infection intensity, calculated on the basis of the AM-infected plant species of a stage, was roughly the same for the two tidally inundated swampy mangrove

Table 3 VA mycorrhizal root infection intensity of mangrove, mangrove associates and other plants in situ at various successional stages of Sundarban mangrove ecosystem^a

^a Data are mean infection intensity (\pm standard deviation) of only the infected species (numbers in parenthesis) predominating at the respective stages (excluding agricultural crops).

Successional stages	Plant type designation	EC dSm ⁻¹	Amount of AM infection	
			Root segments with AM structures (%)	Root length with AM structures (%)
Stage I	Mangroves (9)	16.0	58.6 \pm 7.50	49.5 \pm 7.31
Stage II	Mangroves (11)	14.5	63.3 \pm 8.20	52.9 \pm 8.40
Stage III	Mangroves (6)	4.5	81.0 \pm 2.16	64.8 \pm 3.52
	Non-mangroves (5)		65.7 \pm 5.16	50.3 \pm 6.20
Stage IV	Mangroves (5)	2.5	77.8 \pm 2.22	76.5 \pm 4.33
	Non-mangroves (5)		70.6 \pm 5.80	68.8 \pm 4.37

stages (stages I and II) (Table 3). Similarly, average root infection intensity of the declining and declined ridge mangrove stages, being higher than that of either of the swampy stages, were also almost the same (Table 3). Increases in root infection intensity of the plants at later stages of succession were related to lowering of soil-water salinity and also drier soil environment.

Irrespective of the stages of succession, root infection intensity of plants also varied among the species, the herbs showing higher infection intensity than the trees at any stage of their common occurrence, especially at the drier ridges and embankments. Plant species present in more than one successional stage (e.g., *Avicennia* spp.) showed situation-dependent differences in root infection intensity, being higher in the drier, less saline, stages than in the swampy, more saline, stages. Common salinity tolerant agricultural plants in embankment-protected saline uplands at stage IV of the physiography, such as *Allium cepa* L., *Arachis hypogea* L., *Cajanas cajan* (L.) Millsp., *Capsicum frutescens* L., *Corchorus capsularis* L., *Helianthus* sp., *Hordeum vulgare* L., *Oryza sativa* L., *Phaseolus radiatus* L., *Trigonella foenum-graceum* L., *Vigna unguiculata* (L.) Walp., *Zea mays* L. and some common grass weeds in marsh fringes [*Cynodon dactylon* (L.) Pers., *Echinochloa colona* (L.) Link., *Leersia hexandra* SW., *Leptocloa filiformis* Roem & Sch. etc.], also showed significant root infection intensity (72.8 \pm 6.4% mean root length colonization for the above 12 crop plant species), comparable to that observed in the same plants in mesic situation. Root infection intensity of natural tree colonizers on the occasionally inundated ridges and embankments (declining mangroves and associates) was higher than that of the introduced non-mangrove, non-litoral trees planted there [*Acacia auriculiformis* A. Cunn., *Acacia nilotica* (L.) Willd. ex Del., *Eucalyptus globosus* Labill., *E. tereticornis* Sm., *Prosopis juliflora* DC., *Sesbania grandiflora* (L.) Poir.] The difference was reduced at stage IV embankment-protected uninundated, less saline high lands where the mangroves declined (Table 3).

Spores of Glomalean fungi, which cause AM in mesic habitats, were present in the rhizosphere soils of the AM endophyte-colonized mangrove plant species at all stages of succession. When added to steamed diluent soil, endophyte-infected roots of mangroves and associate plant species from the successional stages caused typical AM infection in the test plants *Zea mays* L., *Cajanas cajan*

Table 4 VAM fungus spore and infective inoculum density of root-free rhizosphere soils of the physiographic stages of mangrove succession of Sundarban based on composite rhizosphere soil samples of the dominant plants mentioned in Table 3 (\pm SD).

Successional stage	EC (dS m ⁻¹)	Spore number (10g soil ⁻¹)	MPN AM inoculum (g soil ⁻¹)
I	16.0	170 \pm 12	62 \pm 7
II	14.5	238 \pm 18	120 \pm 13
III	4.5	428 \pm 21	204 \pm 17
IV	2.5	793 \pm 26	464 \pm 24

(L.) Millsp., *Echinochloa colona* (L.) Link. and *Sesbania grandiflora* (L.) Poir. The number of Glomalean spores in, and infective inoculum density of, the root-free rhizosphere soils of the predominant plant species of the mangrove stages increased with stages of succession and showed an inverse relationship with levels of soil-water salinity (Table 4).

Seven different Glomalean spore types were obtained from the rhizosphere soils of mangroves and associate plants, taking all the stages of succession into consideration. Six of these were identified as belonging to *Glomus mosseae* (Nicol. & Gerd.) Gerdemann & Trappe, *G. fasciculatum* (Thaxter) Gerdemann & Trappe *emend.* Walker & Koske, *G. macrocarpum* Tul. & Tul., *G. multi-caulis* Gerdemann & Bakshi, *Gigaspora margarita* Baker & Hall and *Acaulospora mellea* Spain & Schenck. One species of *Enterophospora* remained unidentified. Among these, *G. mosseae*, *G. fasciculatum* and *Gigaspora margarita* appeared to be the predominating species as these were present in all successional stages and in rhizospheres of all mycorrhizal plants. The latter three species isolates, when introduced as root-based mixed species inoculum, formed typical AM with *Casuarina equisetifolia* Forst. and *Sesbania grandiflora* (L.) Poir. seedling plants in sterile saline silt of the location. There was a 34 and 53% increase in shoot dry matter yield of these plant species, respectively, at 100 days after inoculation of 10-week-old seedlings over no inoculation. Corresponding increases in shoot phosphorus content due to mycorrhization by inoculation were 36 and 58%, respectively. When used singly as inoculants, the isolates gave similar growth stimulation of, and mycorrhiza formation in, the roots of common mycorrhiza-responsive herbaceous plants (e.g., onion, *Cajanas*, *Paspalum*, maize, etc.) in non-saline upstream alluvial sandy loam soil,

similar in nutrient content to stage IV mangrove sediment soil (Table 1).

Discussion

There is an increased recognition today that mycorrhizas and other miscellaneous endophytic root fungus association(s) may substantially contribute to the life of not only individual plants but of whole communities, the nutrient balances of which, in all but fertile environments, are dependent on and integrated by the mycorrhizal fungi (Read 1993). Mycorrhizas are also functionally implicated in plant tolerance to various types of physical and chemical stresses in soil (Marschner 1995), including soil-water salinity (Juniper and Abbott 1993; Ruiz-Lozano et al. 1996). Whether AM, the dominant form of mycorrhizas of the natural climax communities of nitrogen mineralizing, phosphorus deficient, low organic soils in tropical climates, plays any role in community development and stress tolerance of mangroves, the climax formation of hydrohalophytes in saline, semi-aquatic, estuarine sediments of the tropics, is worth knowing from an ecological standpoint.

Evidence presented here shows that AM endophytes are widespread in the roots of mangrove and associate plants of the estuarine habitat under study. Although the functional role of these fungi as AM for mangroves could not be proved experimentally owing to the difficulties in their artificial culture, the structural and circumstantial evidence obtained would justify assigning them a mycorrhizal role, in the ecological sense, for the community of mangroves and other halophytic plants of the ecosystem. All plant functions, independent or otherwise, have a structural basis and the structural basis of functional AM association – intra- and intercellular hyphae, hyphal coils, arbuscules and vesicles – was well apparent in the roots of dominant plants of the mangrove community.

Considering the physiography of the estuarine location, formed as a deltaic landmass of alluvial deposits of the river at its outfall, AM fungal isolates obtained here were likely to be of upstream origin, brought as spores, root fragments, etc. by riverine sediments from the mesophytic situation and deposited at the saline estuary. These species isolates might have established themselves in the saline marsh situation by associating with mangroves and other plant roots as mycorrhiza. There was nothing unique about the species composition and diversity of the AM fungi of the mangrove ecosystem and only adaptive tolerance to salinity and inundation in the common AM fungi was indicated. Among the observed predominating AM fungal species, *G. margarita* is known for its submergence or high moisture tolerance (Khan 1993). The inundated mangrove swamps are not as anoxic as they are presumed to be, as upwelling and churning of water during high and low tides, twice each in 24 h, introduces enough oxygen to the root region of the mangroves. The estuarine mangrove habitats, as

recent sedimentary alluvial landforms, differ from marine salt marshes in their origin and that may explain why AM has occasionally been reported as absent in marine salt marsh plants (e.g., Mohankumar and Mahadevan 1986). It is interesting to note that salt marsh plants were one of the earliest reported ecological plant groups showing mycorrhiza-like endophytes in roots (Mason 1928). In spite of a small amount of evidence to the contrary (e.g., Peat and Fitter 1993), pioneer salt marsh plants and other obligate hydrohalophytes, belonging to several plant families, have been very often reported as AM in tropical (or sub-tropical) and temperate situations alike (Kim and Weber 1985; Rozema et al. 1986; Van Duin et al. 1989; Sengupta and Chaudhuri 1990; Hoefnagles et al. 1993; Brown and Bledsoe 1996; Hildebrandt et al. 2001). This evidence, together with our present observations, leads us to believe that hydrohalophytes inhabiting inundated estuarine sediments, even those belonging to plant families commonly behaving as non-mycorrhizal in mesic habitats, can also be AM.

The 'nutritive roots' of mangroves, which develop from the vertical tap roots or horizontal cable roots or occasionally from the prop roots are thick, fleshy or spongy, coarsely branched, spread mostly in surface soil and are least extensive among all the kinds of functional root types of mangroves (Waisel 1972). Root hairs are generally absent or are small and poorly developed on these roots. These features of the nutritive roots would make mangroves potentially mycotrophic (Baylis 1975) for acquisition of nutrients from stressed environments. However, salinity, and maybe also inundation, were negatively correlated to mycorrhization of the mangroves, possibly due to stress effects on the mycobionts. There is evidence to show that, at high salt concentrations, mycorrhiza formation of even the mycotrophic plants may be adversely affected (Juniper and Abbott 1993). Introduced trees, exotic to the situation, in the more congenial environment of ridge mangroves were infected by AM, but less than the mangroves and other native flora of the ecosystem, possibly due to lack of host adaptation to the inundated situation. That the dominant members of the mangrove plant community at any stage of physiographic succession were all structurally AM will add credence to the generalization cited earlier (Read 1993) about the role of mycorrhizas in community development of plants.

One important finding of this observational study was the presence of Glomalean endophytes in roots of plants belonging to plant families such as the Chenopodiaceae, Amaranthaceae, Aizoaceae, etc., commonly reported as non-mycorrhizal in mesic habitats. In view of the present observations and some recent claims about the presence of AM endophytes in many non-mycotrophic plant families, particularly in abiotically stressed plant habitats (Neeraj et al. 1991; Meney et al. 1993; Muthukumar et al. 1996; Muthukumar and Udaiyan 2000), including the hydrohalophytes belonging to the Chenopodiaceae (Kim and Weber 1985; Rozema et al. 1986; Van Duin et al. 1989), we consider it fit to suggest that known and

unknown stress factors in an ecosystem may predispose the otherwise independent plants to AM colonization. Can these plant families be described as facultatively mycotrophic?

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