9. Ectomycorrhizae in the tropics

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1. Introduction

Ectomycorrhizae are symbiotic associations between fungi and plant roots in which the fungus forms a sheath around all or some of the fine absorbing rootlets. Hyphae penetrate between the root cells and occasionally enter the cells but they never penetrate beyond the cortex and any intracellular hyphae do not cause destruction of the host cell.

The association was first described on tree roots by Frank [19] who realised the association was a naturally occurring, non-pathogenic relationship. Other workers, including the distinguished forester Hartig [31], believed the fungus was a parasite. At that time work was largely descriptive and speculation on the nature of the relationship continued for many years. Gradually experimental evidence accumulated confirming that the ectomycorrhizal association had a beneficial effect and under certain conditions was essential for the growth of both partners [26, 27, 32, 50, 51, 52].

In contrast to the ubiquitous endomycorrhizae, ectomycorrhizae are not common in the tropics. They are, however, very important in the afforestation of poor lands and members of the genus *Pinus* will not grow unless they develop ectomycorrhizae. Their occurrence in the families Caesalpiniaceae and Dipterocarpaceae may help to explain why these families dominate two of the world's most extensive plant formations in the tropics, the miombo woodland of Central Africa and the tropical rain forest of Malaysia and South East Asia.

2. Occurrence

Ectomycorrhizae were not described in the tropics until the early 1960's despite extensive surveys of mycorrhizal associations [35, 37]. The association was first recorded in the West African lowland rain forest on several species of the family Caesalpiniaceae [15, 64].

Records of the ectotrophic association in natural ecosystems are still few: eleven species of Caesalpiniaceae [14, 15, 36, 64, 65, 79], 30 species of Dipterocarpaceae [12, 33, 71], one species of Euphorbiaceae [67], one species of Fagaceae [71] and one species of Myrtaceae [79]. It is also reported that ectomycorrhizae occur in the Sapindaceae [2].

More recently Mr. P. Högberg, of the Swedish University of Agricultural Sciences, has found ectomycorrhizae on several miombo woodland species in Tanzania (Table 1).

Table 1. Some ectomycorrhizal species in the miombo woodland of Tanzania

Caesalpiniaceae	*Brachystegia boehmii*
	B. bussei
	B. longifolia
	B. microphylla
	B. spiciformis
	Julbernardia globiflora
Dipterocarpaceae	*Monotes elegans*
Euphorbiaceae	*Uapaca kirkiana*

Dr. M.H. Ivory of the Commonwealth Forestry Institute, Oxford, has recently made extensive collections in natural stands of *Pinus caribaea* and *P. oocarpa* in Central America and the Bahamas. He confirmed that many of these fungi form ectomycorrhizae on pine under laboratory conditions (Table 2).

Table 2. Fungi forming mycorrhizal associations on pines in the laboratory

Fungus	Source
Gyroporus castaneus	Mixed *P. caribaea* and *P. oocarpa* forests
Pisolithus tinctorius	Both *P. caribaea* and *P. oocarpa* forests
Rhizopogon nigrescens	*P. caribaea* and *P. oocarpa* hosts and from the alkaline soils of the Bahamas
Suillus cothurnatus	*P. caribaea* on alkaline soils
Suillus cf. *Holoeacus*	*P. caribaea* forest
Scleroderma (geaster)?	*P. caribaea* and mixed pine forests
Tylopilus gracilis	*P. caribaea* and *P. oocarpa* forests

Sporocarps of fungi, well known to be mycorrhizal in temperate regions, are regularly found in stands of exotic pines (Table 3).

The identity of fungi-forming ectomycorrhizae on tropical angiosperms is not known. Hong [33] has associated six genera of Basidiomycetes with a range of dipterocarp species and there is circumstantial evidence that a species of *Inocybe* forms ectomycorrhizae on *Afzelia bella* [66]. Attempts to culture fungi from ectomycorrhizae of *Afzelia africana, A. bella, A. bipindensis* and *Brachystegia eurycoma* were unsuccessful. The varied hyphal structure indicated that several different fungi could form associations on these species; some bearing clamp connections were Basidiomycetes. Sterile-raised plants of these species exposed to the open air readily formed ectomycorrhizae with a range of different fungi from air-borne propagules and from mycorrhizal root fragments. These species, however, would not form ectomycorrhizae when inoculated with ectomycorrhizae formed by *Rhizopogon luteolus* on *Pinus caribaea.*

Table 3. Fungal sporocarps commonly found associated with exotic pines in the tropics

Fungal sporocarp	Country	References	
Amanita muscaria	Malawi		[62]
Boletus spp.	Malawi		[62]
Corticia cinnamomea	West Malaysia		[34]
Hebeloma crustiliniforme	Kenya		[21]
Lycoperdon perlatum	Tanzania	Coll. Maghembe 1980, unpublished	
Pisolithus tinctorius	Ghana	Coll. Ivory 1978, unpublished	
Rhizopogon luteolus	Nigeria		[60]
Rhizopogon sp.	Sri Lanka	Coll. Redhead 1976, unpublished	
	Tanzania	Coll. Maghembe 1979, unpublished	
Scleroderma bovista	Kenya		[21]
Scleroderma sp.	Malawi		[62]
Scleroderma dictyospotum	Tanzania	Coll. Maghembe 1980, unpublished	
Suillus granulatus	Kenya		[63]
	Tanzania		[63]
	West Malaysia		[34]
	Uganda		[8]
	Zaire		[78]
S. luteus (Boletus luteus)	Kenya		[21]
	Tanzania		[63]
S. sibiricus	Tanzania		[63]
Thelephora terrestis	Malawi		[62]
	Tanzania		[38]

3. Development and structure

An ectomycorrhiza develops when a rootlet comes into contact with hyphae spreading from ectomycorrhizae on an adjacent rootlet, from residual ectomycorrhizal root fragments, or from a germinating spore. Growth of the hyphae on the root surface is stimulated by root exudates such as the M-factor [53] and a dense sheath or mantle is formed over the root surface. Other substances produced by the root appear to keep a balance between the parasitic relationship of the host and mycorrhizal fungus [24, 54]. In turn the fungus produces growth regulating substances which cause changes in the rootlet morphology. This is particularly marked in pines and some ectomycorrhizae develop very complex coralloid structures [73]. The morphology is generally changed less in Angiosperms, e.g. in *Brachystegia eurycoma* ectomycorrhizal rootlets are usually shorter and stouter than non-mycorrhizal rootlets due to the thick fungal sheath but in *Afzelia bella* ectomycorrhizae are merely stouter due to the fungal sheath but little affected in length.

In section the mantle may be made up of regularly sized pseudo-parenchymatous

'cells', of compressed hyphae, or have a 2-layered structure. The hyphae penetrating between the rootlet cells are able to dissolve the pectin of the middle lamella [61] and mechanically separate the cells [17, 18]. Hyphae may only penetrate between the cells of the piliferous layer or they may extend between the cortical cells as far as the endodermis to form the so-called Hartig network.

A very high proportion of absorbing rootlets are mycorrhizal in the case of pine [59] and also with *Afzelia* spp. and *Brachystegia eurycoma* [67]. Dissection of beech (*Fagus sylvatica*) mycorrhizae indicated that 40 percent of the total dry weight consisted of mantle. On the assumption that the feeding roots represent 10 percent of the total root mass, Harley [28] concluded that something like 4 percent of this would consist of fungus. Calculations based on ratios of root to shoot dry weights of heavily mycorrhizal and non-mycorrhizal *Brachystegia* seedlings indicated that 23 percent of the seedling root mass consisted of fungus (data from Redhead [68].

Ectomycorrhizal rootlets do not develop root hairs and, although some ectomycorrhizae may appear to be smooth, hyphae radiate out from the mantle surface, often as extensively developed hyphal strands. In *Brachystegia* mycorrhizae were formed by two fungi with distinctly different hyphae which had diameters of 2–3 μm for the hyphae of a white mycorrhizal fungus and 3–4 μm for those of a brown fungus. The extent of mycelium in the soil is difficult to ascertain because it breaks off on examination. In *Brachystegia* mycelial strands were frequently over 3 cm from the mantle, branching frequently to form dense wefts of hyphae. Such hyphae are able to penetrate the fine interstices of the soil whereas rootlets must depend on root hairs for this and, being so short, root hairs can only tap a limited soil volume.

The colour of the mantle, its surface texture, hyphal thickness, and the presence or absence of clamp connections vary with the fungal species and are features which may be used to characterize ectomycorrhizae. All these features may be used in the construction of keys [13, 84]. Unfortunately the morphology also varies with the age of the association and to a lesser extent with the nature of the soil environment. This makes the use of keys to identify mycorrhizal fungi rather difficult and they must be used with caution.

4. Ecological advantage in tropical ecosystems

4.1. Significance for growth

It is common experience that without an appropriate mycorrhizal fungus pines stagnate and eventually die [56]. Briscoe [7] in Puerto Rico found that inoculated seedlings of *Pinus elliottii* var. *elliottii* grew only 12 cm in 4 years after planting out whereas inoculated seedlings grew 149 cm. Few other species have been studied in the tropics but Redhead [68] found that two different mycorrhizal fungi significantly increased the dry weight of *Brachystegia eurycoma* (Tables 4 and 5).

Table 4. Mean stem heights and dry weights of *Brachystegia eurycoma* grown for 13 months at low levels of nutrients after inoculation with two mycorrhizal fungi [68]

Treatment	Stem height (cm)	Mean dry weight (g)			
		Leaves	Stem	Root	Total
Inoculation Sources					
All fertilizer levels combined					
No inoculation	30.5	0.76	1.94	1.60	4.30
B. eurycoma White mycorrhiza	30.5	0.87	2.10^a	2.14^b	5.11^b
B. eurycoma Brown mycorrhiza	32.9	0.86	2.58^a	2.33^b	5.77^b
Fertilizer treatment					
All inocula combined					
No added nutrient	27.3	0.66	1.61	1.58	3.85
6 ppm N + 1 ppm P	31.9	0.79	2.06	1.75	4.60
6 ppm N + 5 ppm P	29.8	0.77	1.94	2.09	4.80
6 ppm N + 25 ppm P	36.0^b	1.07^b	3.05^b	2.55^b	6.67^b

[a] Difference significant at the 5% level
[b] Difference significant at the 1% level

Table 5. Mean stem heights, dry weights and nitrogen content of *Brachystegia eurycoma* grown for 5 months at three levels of nitrogen and two levels of potassium after inoculation with two mycorrhizal fungi [68]

Treatment	Stem height (cm)	Mean dry weight (g)				Nitrogen content dry matter %		
		Leaves	Stem	Roots	Total	Leaves	Stem	Roots
Inoculation sources All fertilizer levels combined								
No inoculation	22.4	0.74	1.07	1.10	2.91	2.2	0.8	0.9
White mycorrhiza	26.3[a]	1.23[b]	1.65[b]	2.05[b]	4.93[b]	2.1	0.8	0.9
Brown mycorrhiza	28.6[a]	1.54[b]	1.94[b]	2.08[b]	5.56[b]	2.2	0.7	0.8
Fertilizer treatments Total daily amount per plant. All fungal inocula combined	b	b	b	b	b	b	b	b
No added nutrient	18.3	0.58	1.00	1.21	2.79	1.7	0.5	0.6
0.0016g N	23.3	0.98	1.24	1.70	3.92	1.9	0.7	0.7
0.0024g N + 0.0011g K	28.2	1.41	2.41	2.74	6.56	2.1	0.7	0.7
0.0040g N + 0.0011g K	30.5	1.46	2.16	2.75	6.37	1.9	0.5	0.8
0.0112g N	23.0	1.01	0.91	0.79	2.71	2.6	1.1	1.2
0.0120 g N + 0.0011g K	31.1	1.57	1.62	1.29	4.48	2.7	1.0	1.3

[a] Difference significant at the 5% level
[b] Difference significant at the 1% level

This beneficial effect on growth is linked to the physiology of the ectomycorrhizal association. The research involved has been carried out in temperate regions but an understanding of the principles is especially relevant for tropical research, especially that related to the afforestation of difficult sites.

In addition to the beneficial effect on growth, ectomycorrhizae also confer disease resistance against some of the most serious nursery pathogens in tropical nurseries.

4.2. Mechanisms of nutrition

The physiology of ectomycorrhizae and the metabolic exchanges between host and fungus have been reviewed by Harley [27] and Marks and Kozlowski [45]. All ectomycorrhizal fungi depend wholly on their host for sugars and the amounts used can be very high [28]. The fungus is an important sink for carbohydrate in the system and there are indications that the fungal share is increased through inhibition of root respiration by the fungus [81]. In turn the root receives water and mineral salts through the fungal component of the system.

With pines a high content of soluble carbohydrate in the rootlet and a low to moderate amount of available nitrogen appear to favour mycorrhizal development. A high light intensity favours a high sugar content [1] and this may partially explain why pines are light-demanding species. The inter-relationships between the sugar content and available nitrogen may be more complicated than Bjorkman suggests and more recent work on this aspect is discussed by Slankis [72].

Hatch [32] found four elements to be important for the development of ectomycorrhizae of pines: nitrogen, phosphorus, potassium and calcium. A certain minimum amount is necessary; if the supply of these elements was in abundance mycorrhizae were few but if there was an inbalance in the availability of one or more of these elements then mycorrhizae were plentiful.

Experience with Angiosperms has been different both in temperate and tropical species. Meyer [55] found in beech that adding nitrogen and phosphorus did not preclude formation of mycorrhizae in soils of high fertility. Redhead [68] obtained similar results with *Brachystegia* (Tables 4 and 5). Abundant ectomycorrhizae developed both at very low and very high levels of nitrogen.

It has been suggested that mycorrhizal hyphae are capable of bringing relatively insoluble minerals into solution. This has not been demonstrated experimentally but, there is evidence that mycorrhizal rootlets are several times more efficient than non-mycorrhizal roots at absorbing ions from the soil solution. Harley and McCready [29] showed that excised mycorrhizae of beech had 2.3 to 8.9 times the uptake of phosphorus than did non-mycorrhizal roots. Bowen and Theodorou [4] found similar results with pine. Ions of K, Na, Rb and Zn are also absorbed more rapidly by mycorrhizae [6, 30, 82].

Mycorrhizal hyphae are able to absorb mineral ions from very dilute soil solutions and their place is made up by more ions entering solution from minerals,

e.g. rock phosphate. This is of special significance in the tropics where phosphorus is usually a limiting factor in degraded soils and it enables foresters to use the more cheaply available rock phosphate rather than the more expensive superphosphate fertilizers.

The extensive mycelial phase and the ability for rapid uptake give ectomycorrhizae a competitive advantage in the litter layer. Although the fungi involved cannot break down complex organic molecules such as cellulose [61] in the litter, once this has been done by other organisms the mycorrhizal hyphae can absorb the available solutes more quickly than most other soil microflora, even to the extent of starving such decomposing organisms of nutrients [20]. This rapid absorption is especially important in the tropics where nutrient cycling and leaching takes place so quickly.

4.3. N_2 fixation

Some of the early speculation on the function of ectomycorrhizae include claims that they could fix atmospheric N_2. Some pine plantations have shown evidence of N_2 fixation but there is no experimental evidence that the fungal component of the symbiosis was responsible [69, 70]. It appears that bacteria and blue-green algae, which develop in intimate contact with the fungal mantle, are likely to be responsible for any fixation of atmospheric N_2 by ectomycorrhizae. Foster and Marks [18] published electron micrographs which clearly show bacteria in association with ectomycorrhizae and Katznelson et al. [39] recorded up to ten times the number of bacteria associated with ectomycorrhizae as compared to the rhizosphere of non-mycorrhizal roots.

Recently the N_2-fixing bacterium *Azotobacter* has been successfully incorporated into the hyphae of *Rhizopogon* and used to synthesise mycorrhizae on *Pinus radiata* [22, 23]. This is a development with exciting possibilities for the afforestation of degraded sites in the tropics.

4.4. Water balance

Ectomycorrhizae do not thrive in heavy waterlogged soils but they are efficient at procuring water when it is in short supply. Theodorou and Bowen [76] found that vigorous mycorrhizal *Pinus radiata* seedlings showed fewer deaths from summer drought in the first planting season than did uninoculated seedlings. This is the experience in the tropics and there appear to be two reasons. Firstly the mycelial strands can be so dense and extensive that they help to bind the soil together in a ball when the seedling is lifted and the seedling quickly adjusts to its new site. Secondly some fungal hyphae are able to tolerate much lower water potential than root cells [75] and continue to absorb moisture when root hairs would have collapsed.

This aspect is very important when planting out in the sandy soils of the drier tropical regions as death from drought is the commonest cause of failure. As fungi vary in their ability to grow at low humidities [83] it would be an advantage to ensure that the most suitable mycorrhizal fungus was available.

4.5. Heat tolerance

Fungi vary in their growth at various temperatures and, for most, growth ceases above 35 °C. Lamb and Richards [42] studied the survival of several mycorrhizal fungi and found that the hyphae of six of these fungi were killed by a 48-hour exposure to temperatures between 28° and 38 °C and that of *Pisolithus tinctorius* by 45 °C. This can be a guide to the expected behaviour of ectomycorrhizae in the field although Hacskaylo *et al.* [25] showed that growth of mycorrhizal fungi was greatly influenced by the laboratory medium, and Theodorou and Bowen [77] consider growth in a laboratory medium to be a poor indication of their growth in the rhizosphere.

Marx and Bryan [48] compared the growth of mycorrhizal and non-mycorrhizal *Pinus taeda* at 40 °C and found that 55 percent of the non-mycorrhizal plants died and were generally smaller than the mycorrhizal pines. Marx [47] found that pines with *Pisolithus tinctorius* as the mycorrhizal partner survived on adverse sites, such as exposed coal spoils, better than pines which were mycorrhizal with other fungi. He considers that *Pisolithus* has special merit as a mycorrhizal partner for tropical pines.

Adaptation of a mycorrhiza to heat stress is likely to vary with the fungal partner and most of the known mycorrhizal fungi of pine in tropical plantations (Table 3) are temperate species. This may present little problem for highland areas above 1,000 m. Lowland areas planted with species such as *Pinus caribaea* and *P. oocarpa* present more of a problem. In lowland nurseries in Nigeria using black polypots, and planting out in bare land, it is not uncommon for the surface soil to reach 50 °C for considerable periods of the day. The mycorrhizae formed with *Rhizopogon luteolus* often died and nursery beds had to be sheltered with low walls of straw and planting carried out quickly in order to overcome this problem. During the long, hot, dry season most of the mycorrhizae in the surface layers died but grew again during the following rainy season. It is likely that a more heat tolerant fungus would be a more suitable mycorrhizal partner for these lowland sites. There is the danger that otherwise suitable introductions of species and provenances could be discarded through lack of an appropriate mycorrhizal partner.

4.6. Disease resistance

The developing feeder root attacts or stimulates certain pathogenic fungi in the group commonly known as 'damping-off' fungi, *Fusarium, Phytophthora, Pythium*

and *Rhizoctonia*. These fungi are stimulated by root exudates in a similar way to that in which a mycorrhizal hypha is stimulated.

The cell's reaction to penetration by the hypha of a mycorrhizal fungus is in several ways similar to its reaction to invasion by a pathogen. However, the mycorrhizal fungus is kept in balance and does not cause breakdown of the root cells. The cell nucleus and cytoplasm grow in volume, respiration increases and starch reserves are mobilized [43]. The mycorrhizal fungus also develops to form a symbiotic mycorrhizal association. In contrast the pathogenic fungus invades the succulent tissues of the primary cortex and destroys the rootlet. It depends which fungus reaches the rootlet first, for if a mantle forms before the pathogen arrives the pathogen has to possess the physical and chemical ability to penetrate the fungal mantle and the Hartig net tissues before it can attack the root cells [46].

In addition to the physical barrier afforded by the mantle, at least some mycorrhizal fungi also secrete antibiotics inhibitory to pathogens. This has been demonstrated in the case of the mycorrhizal fungi *Cenococcum graniforme* [40] and *Leucopaxillus cerealis* var. *piceina* and *Suillus luteus* [49].

Damping-off diseases caused by the above pathogens are the most serious diseases in tropical forest nurseries. Soil drenches using Zineb or partial sterilization using methyl bromide are the normal methods of control but the use of an appropriate ectomycorrhizal fungus may offer a potential alternative.

5. Special problems of afforestation

5.1. Afforestation of new lands

An indigenous species will have evolved a relationship with a mycorrhial fungus either endo- or ectomycorrhizal but an exotic species, introduced for the first time, has either to form an association with an indigenous fungus or to be inoculated with an introduced fungus.

There is more information on exotic pines than any other tropical ectomycorrhizal species. If inoculum is present in the soil pines normally take it up readily and become mycorrhizal [80] which perhaps explains why many pines in their native habitats are excellent pioneers and are rapid, aggressive colonizers of open base-poor soils. Introduction into tropical Africa, and other areas where pines were not previously grown, consistently failed until it was realized that it was necessary to inoculate with a suitable mycorrhizal fungus. Mikola [58] gives the following examples: Kenya [21], Malawi [11], Nigeria [44], Puerto Rico [7], Trinidad [41, 56]. It is believed that settlers unwittingly introduced mycorrhizal fungi into Australia, New Zealand, South Africa and South America on the roots of living plants carried from Europe. These have been the origins of most mycorrhizal inoculum in the tropics and for this reason most of the fungi so far identified are themselves exotics (Table 3). In some instances in tropical Africa pines have appeared to have become spontaneously mycorrhizal. The transport of pine soil or

living plants as an inoculum is often prohibited by quarantine regulations and there have been cases where foresters have smuggled inoculum. As Mikola [58] comments, 'such cases, of course, have not been well documented'.

Many species of the genus *Eucalyptus* are widely planted as exotics in tropical countries. Several of these are known to be mycorrhizal in their native Australia [9. 10] but their mycorrhizal status has not been studied in the tropics. Eucalypts are key species for the provision of fuel and poles in village afforestation schemes throughout the semi-arid areas of tropical Africa. These are often degraded, overgrazed sites with a long dry season; considerable research is being carried out to select the most suitable species and provenances for planting. There is need to undertake parallel studies of the mycorrhizal associations of the selected species under these exacting conditions.

5.2. Use of soil sterilants

It has become standard practice in several countries to partially sterilize nursery soils with methyl bromide to kill weed seeds and damping-off fungi. In long-established pine nurseries mycorrhizal associations develop both from residual root fragments and air-borne spores [38] and re-inoculation is not essential. Kalaghe demonstrated that if the planting medium is inoculated after sterilization the mycorrhizal association develops much more rapidly and uniformly than if left to nature. It becomes a question of economics as to whether the saving in raising seedlings in six months instead of eight is worth the cost of inoculating the potting medium.

5.3. Provision of inoculum

Marx [47] considers that inoculation of pine with the most appropriate fungus at the nursery stage is very worthwhile. This may be true when it is required to introduce a fungus especially adapted to certain ecological conditions. If the nursery is raising plants for routine planting on favourable sites then purpose-raised inoculum is probably not worthwhile. Unless the new fungus has special survival attributes, it will be replaced on new feeder roots by the fungi already well adapted to the area. The sequences of fungal succession in the formation of ectomycorrhizae is an area requiring further research.

Marx [47] describes the large-scale production of inoculum using a peat moss and vermiculite medium. Prepared inocula have long been used in South America [74] but are still at the experimental stage in tropical Africa. Mikola [57] has reviewed the early work in producing inocula, and Marx [47] discusses present developments which include the incorporation of fungal spores in the coating of pelleted seeds.

6. Research priorities

6.1. Surveys in natural ecosystems

It is not sufficient to find a sporocarp near to a plant and to assume that the plant is mycorrhizal. Careful excavation of the feeder roots is necessary, followed by microscopic examination to be sure that a plant is mycorrhizal. Little has been done in this respect: in tropical Africa less than 5 percent of tree species have been examined.

It is important to carry out this type of survey apart from the ecological interest. Some of the species may prove to be useful afforestation species for special sites and others may be trees of special importance to the village community. For example, Högberg (Table 1) found that *Uapaca kirkiana* is ectomycorrhizal. This tree is a wild fruit tree esteemed throughout large parts of Tanzania and Zambia yet entirely unimproved by selection and breeding. A knowledge of the ectomycorrhizae of such a potentially important tree is obviously important.

6.2. The relationship between ectomycorrhizae and N_2 fixation

The relationship between ectomycorrhizae and associated bacteria, or blue-green algae, requires further study, to ascertain their precise interdependence and the optimum conditions favouring N_2 fixation.

Some members of the Caesalpiniaceae are both ectomycorrhizal and nodulated by N_2 fixing bacteria. Preliminary studies have been carried out on these by Högberg (personal communication) on Tanzanian miombo species and it is hoped this work will continue.

6.3. Identification and culture of ectomycorrhizal fungi

In some cases mycorrhizal fungi, isolated from ectomycorrhizae, can be grown in culture and subsequently matched with cultures from identified sporocarps. Zak [85] discusses the problems involved. Once this has been done it is possible to inoculate plants and to use these plants to select ectomycorrhizal combinations most suited to special sites such as hot, dry lowland areas, areas of unfavourable pH or other poor lands.

Current work in Tanzania indicates that under unfavourable conditions a fungus may grow vegetatively as an ectomycorrhiza but may not fruit. It is therefore difficult to identify except by matching it with cultures from elsewhere. This aspect of mycorrhizal research may eventually help the forester to match his species to site more effectively.

6.4. The ectomycorrhizae of eucalypts

This has already been mentioned as a neglected field. Eucalypts are the most widely planted exotics in the tropics and merit a level of research commensurate with their afforestation importance.

This brief review of some aspects of ectomycorrhizae related to tropical forestry illustrate how important a knowledge of ectomycorrhizae is to efficient use of land in the tropics. The forester has to make a greater impact on the marginal lands which are usually hot and dry, and degraded through neglect and overgrazing.

Most of our present knowledge derives from research in temperate regions. An intelligent application of this experience can extend knowledge to the solution of the many and varied problems of the tropics. These studies have both great ecological interest and the satisfaction that they are essential to meet the material needs for fuel and industrial wood of a rapidly increasing population.

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