

LRH: Brearley

RRH: Diptero­carpaceae Mycorrhizas

## **Ectomycorrhizal Associations of the Diptero­carpaceae**

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**ABSTRACT**

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Dipterocarps are one of the most important tree families in the lowland forests of Southeast Asia and are somewhat unusual among tropical trees in that they form ectomycorrhizal (EcM) symbiotic root-inhabiting fungal associations. It has been hypothesised that dipterocarps have been partnered in this mutualistic association prior to the separation of Gondwana. Under many conditions EcMs form rapidly on dipterocarp seedlings through inocula present in the soil, although few studies have been conducted to provide evidence that they improve seedling establishment and performance. There are hundreds of EcM species associated with dipterocarps. Fungal fruit body surveys suggest the most important families are Amanitaceae, Boletaceae and Russulaceae, although Thelephoraceae also become numerically important when root tips are examined. EcM communities are affected by various biotic and abiotic factors, as well as anthropogenic perturbations, and I examine the importance of these in structuring EcM communities.

*Key words:* fungi; mycorrhiza; molecular identification; mutualism; seedling performance; soils; symbiosis.

22    LOWLAND EVERGREEN RAIN FORESTS OF SOUTHEAST ASIA ARE HIGHLY SPECIES RICH.  
23    Their tree communities are dominated by members of the Dipterocarpaceae (Proctor *et*  
24    *al.* 1983, Newman *et al.* 1996, 1998; Brearley *et al.* 2004, Slik *et al.* 2009). In addition  
25    to their ecological dominance, dipterocarps also provide significant economic resources,  
26    producing not only valuable timber, but also a number of non-timber forest products  
27    such as oils, nuts and resins (Shiva & Jantan 1998). With continued degradation of  
28    forests in the Southeast Asian region, there is an increased interest in establishing  
29    plantations of forest trees and promoting restoration strategies (Kettle 2010). Due to  
30    their important ecological and economic roles, understanding the growth and  
31    regeneration of dipterocarps is an important research priority. The role of light and  
32    nutrients in seedling growth and performance has received much attention in this regard;  
33    that of mycorrhizas has often been invoked but much less studied.

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35    Mycorrhizas are an intimate symbiotic association between specialised root-inhabiting  
36    fungi and the roots of living plants; they are generally considered mutualistic as benefits  
37    are accrued by both partners. The plant provides the fungus with carbon derived from its  
38    photosynthetic activity and, in return, the fungus can improve nutrient uptake, growth,  
39    water relations, pathogen and heavy metal resistance of the plant (van der Heijden &  
40    Sanders 2002, Smith & Read 2008, and references therein). Mycorrhizas are important  
41    as they extend roots' nutrient depletion zones, especially for poorly mobile inorganic  
42    nutrients such as phosphorus (P) that are found at especially low concentrations in many  
43    tropical soils (Proctor *et al.* 1983, Brearley 2003, Brearley *et al.* 2004, Paoli *et al.* 2006).  
44    Early work on mycorrhizas focused on this nutrient uptake capability of the symbiosis  
45    but we are now aware of the multifunctional role played by mycorrhizas in enhancing  
46    protection against a number of environmental stresses, and it is clear that this role acts

47 independently of improved plant nutrition (Read 1986, Newsham *et al.* 1995). This led  
48 Read (1998) to propose a definition of mycorrhizas as ‘structures in which a symbiotic  
49 union between fungi and plant roots leads to increases in fitness of one or both  
50 partners’. An estimated 95 percent of plant species are in characteristically mycorrhizal  
51 families (Read 1999) and they are found in almost every terrestrial ecosystem. The  
52 arbuscular mycorrhizal (AM) symbiosis, formed by members of the Glomeromycota, is  
53 the most abundant type of mycorrhiza, and most tropical trees form AMs (de Alwis &  
54 Abeynayake 1980, St. John 1980, Chalermpongse 1987, Newbery *et al.* 1988,  
55 Moyersoer 1993, Béreau *et al.* 1997, McGuire *et al.* 2008). An important, and often  
56 dominant, minority of tropical tree families, including the Dipterocarpaceae, form EcMs  
57 (Figure 1) that are mostly members of the Basidiomycota or Ascomycota. EcM trees in  
58 the tropics often form monodominant stands (Connell & Lowman 1989, Henkel 2003,  
59 Peh *et al.* 2011) but the dipterocarps rarely do so.

60

61 In this review, I outline the current state of knowledge of dipterocarp EcM fungi and  
62 their role in tropical ecosystems. The vast majority of current work is from the Asian  
63 dipterocarps and studies on these species, therefore, form most of the body of this  
64 review. I focus on the role of EcMs in improving seedling growth and performance (see  
65 also Brearley 2011), and on EcM species diversity and factors affecting patterns of  
66 diversity. I start with a brief history of dipterocarp mycorrhizal research and the  
67 biogeographical insights it has provided. I then examine the role of EcMs in the growth  
68 and performance of dipterocarp seedlings under both nursery and field conditions. The  
69 range of fungal species that form EcMs on dipterocarps is then explored, and I outline  
70 the how new molecular techniques have improved our knowledge of dipterocarp EcMs.  
71 Key determinants of EcM community dynamics, including various biotic and abiotic

72 factors and perturbations, are then evaluated. Colonization by other symbiotic fungi is  
73 briefly assessed. The review concludes with some thoughts on future research priorities.

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## 75 **BRIEF HISTORY OF DIPTEROCARP MYCORRHIZAL RESEARCH**

76 Van Rosendael and Thorenaar (1924) and de Voogd (1933) both noted the presence of  
77 ‘mycorrhizas’ on the roots of dipterocarp seedlings although it is not clear exactly what  
78 they saw as they did not publish pictures or record further observations. Although John  
79 Corner (1972, among others) noted EcM fungal fruiting bodies in dipterocarp forests, he  
80 attributed this to the presence of the Fagaceae (long known to be EcM in temperate  
81 regions), and it was not until 1966 that Singh recorded that dipterocarps, in common  
82 with a few other tropical angiosperms (Peyronel & Fassi 1957), formed EcMs. Early  
83 work (1960s to 1980s) simply noted various dipterocarp species as forming EcM  
84 associations (Singh 1966, de Alwis & Abeyneyake 1980, Alexander & Högberg 1986)  
85 and made cursory attempts to ascertain which fungal species were putative EcM formers  
86 (Hong 1979). The first attempts at *in vitro* synthesis of EcMs were not reported until the  
87 late 1980s (Louis & Scott 1987, de Alwis & Abeyneyake 1988) along with early reports  
88 of increased growth of inoculated seedlings also around this time (Hadi & Santoso  
89 1988, Santoso 1988). In the late 1980s and early 1990s, Lee Su See’s work advanced  
90 EcM research by examining functional aspects of the symbiosis *e.g.*, interactions of  
91 EcMs with nutrients to determine seedling growth (Lee & Alexander 1994), and the  
92 succession of EcM fungi on seedlings (Lee & Alexander 1996) and her collaborations  
93 with Frédéric Lapeyrie advanced inoculation techniques with a range of fungal species  
94 (Yazid *et al.* 1994, 1996; Lee *et al.* 1995b, 2008). Throughout the 1990s to mid 2000s  
95 the IUFRO-SPDC funded BIO-REFOR conferences led to more work being published  
96 in the region; although some of these papers were valuable, many had limited value due

97 to inappropriate design or lack of detail in reporting (Brearley 2011). The involvement  
98 of Roy Watling in the 1990s started to build knowledge of the fungal flora of Peninsular  
99 Malaysia from the strong foundations laid by Corner (Watling & Lee 1995, 1998, 2007;  
100 Watling *et al.* 1995a, 1998, 2002, 2006; Lee *et al.* 2002a, 2003; Lee 2005).  
101 Subsequent eco-physiological work examined how EcM communities were affected by  
102 biotic and abiotic perturbations (Brearley 2006, Brearley *et al.* 2003, 2007) and  
103 examined the role of EcMs in organic nitrogen acquisition (Brearley *et al.* 2003). The  
104 first molecular study of dipterocarp EcM communities appeared in 2003  
105 (Sirikantaramas *et al.* 2003), and since then there have been a few more (Moyerseon  
106 2006, Yuwa-Amornpitak *et al.* 2006, Tedersoo *et al.* 2007a, Peay *et al.* 2010) although  
107 until the comprehensive study by Peay *et al.* (2010) these had mostly focused on rare or  
108 outlying members of the Dipterocarpaceae. Most recently, advances based on early  
109 nursery-based inoculation studies have been extended to the field performance of  
110 dipterocarp seedlings (Brearley 2003, Turjaman *et al.* 2007, Lee *et al.* 2008, Tata *et al.*  
111 2010).

112

113 **INSIGHTS FROM ECTOMYCORRHIZAS INTO THE ORIGINS AND**  
114 **BIOGEOGRAPHY OF THE DIPTEROCARPACEAE**

115 The biogeography of the Dipterocarpaceae is interesting as the vast majority of the 520  
116 or so species are found in Southeast Asia with around 30 species in Africa and two in  
117 South America (Dayanandan *et al.* 1999). The consistent EcM status of  
118 Dipterocarpaceae in Southeast Asia, the dipterocarp sub-family Monotoideae in Africa  
119 and the Neotropical genus *Pakaraimaea*, suggests a common EcM ancestor and  
120 evolution of the EcM habit before continental separation of Gondwana. Doucouso *et*  
121 *al.* (2004) placed the origin of the EcM habit at least 88 million yr ago, prior to the

122 separation of Madagascar and India, as the closest relative of the Dipterocarpaceae  
123 sharing a common ancestor, the Madagascan Sarcoleanaceae, are also EcM. The more  
124 recent discovery by Moyersoen (2006) that *Pakaraimaea dipterocarpacea*, basal in the  
125 dipterocarp clade, is also EcM suggests an earlier origin of the EcM habit to around 135  
126 million yr ago before the continental separation of South America from Africa. This  
127 predates the earliest EcM fossils, which are around 50 million yr old (LePage *et al.*  
128 1997, Beimforde *et al.* 2011) and sets the evolution of the EcM habit on the same  
129 timescale as the rise and radiation of the angiosperms. The evidence is not conclusive,  
130 however, as Alexander (2006) suggests that the Dipterocarpaceae might not have been  
131 EcM prior to the separation of the continents but became EcM at a later stage.

132

### 133 **EFFECTS OF ECTOMYCORRHIZAL COLONIZATION ON THE GROWTH** 134 **AND PERFORMANCE OF DIPTEROCARP SEEDLINGS**

135 The importance of EcMs for dipterocarp seedling growth and performance has been  
136 reviewed recently (Brearley 2011) and so this topic is only briefly addressed here.  
137 Numerous nursery experiments show that EcMs improve dipterocarp seedling growth  
138 and nutrient uptake (Hadi & Santoso 1988, 1989; Santoso 1988, 1991; Lee & Alexander  
139 1994; Yazid *et al.* 1994, 1996; Turjaman *et al.* 2005, 2006; Lee *et al.* 2008) and  
140 facilitate access to organic N sources (Brearley *et al.* 2003). These experiments have  
141 often been conducted with exotic EcM isolates, as it has proved difficult to isolate fungi  
142 from fruit bodies found in Southeast Asian forests. Simple observations and  
143 experiments have also correlated seedling biomass (Turner *et al.* 1993), relative growth  
144 rates (Saner *et al.* 2011) and foliar P concentrations (Lee & Lim 1989) with percentage  
145 EcM colonization. It should be reiterated, however, that most of the above experiments

146 have been conducted under controlled nursery conditions, sometimes with only a single  
147 species of EcM inoculated onto the roots of the experimental seedlings.  
148  
149 Experiments under field conditions are rarer and seedlings do not show as clear a  
150 response to the presence of EcMs when planted in natural forest or rubber agroforest  
151 (Brearley 2003, Tata *et al.* 2010). For example, there was no clear biomass response of  
152 *Hopea nervosa* and *Parashorea tomentella* seedlings to a reduction in EcM colonization  
153 by fungicide addition, though foliar nutrient concentrations did show a decline (Brearley  
154 2003). There are significant challenges, however, in conducting field experiments, the  
155 major one being that it is very difficult to create truly non-mycorrhizal controls.  
156 Similarly, for inoculation experiments, such as that of Tata *et al.* (2010), where EcM  
157 inoculum is already present in the soil, the benefits of inoculating seedlings are not  
158 clear, especially if the inoculated EcM species does not remain on the roots of the  
159 seedlings. In contrast, the work of Turjaman *et al.* (2007) in degraded peat swamp forest  
160 did show improved growth of inoculated dipterocarp seedlings when out-planted in a  
161 degraded peat swamp area. This suggests that EcMs are most likely to benefit seedling  
162 performance when seedlings are planted in degraded areas where suitable EcM  
163 inoculum is not available, such as mine tailings (Lee *et al.* 2008), burnt areas (Akema *et*  
164 *al.* 2009), degraded peatlands (Turjaman *et al.* 2007) or areas previously used for  
165 agriculture (Ingleby *et al.* 2000). In many cases, such as in logged forest, EcM  
166 colonization occurs rapidly and naturally (Lee & Alexander 1996, Lee *et al.* 1996b) and  
167 under such conditions inoculation might not be worthwhile (Brearley 2011).  
168 Furthermore, inoculated EcM species do not always remain on the seedling roots, for  
169 example Chang *et al.* (1994, 1995) showed that a species of *Pisolithus* in Malaysian



170 inoculation experiments had mostly disappeared from roots six months after colonised  
171 seedlings were planted into the field.

172

173 Clearly, we need to further evaluate the growth and survival of EcM *versus* non-EcM  
174 seedlings in the field, as positive responses to EcMs in simplified nursery environment  
175 are unlikely to be representative of those found in forest sites. In addition, we need an  
176 effective way to create truly non-mycorrhizal control seedlings for comparisons with  
177 experimental seedlings.

178

### 179 **NURSING ROLE OF PARENT TREES**

180 Early colonization of dipterocarps is dependent upon mycorrhizal connections made  
181 with parent trees (Alexander *et al.* 1992), but the importance of these connections for  
182 carbon transfer between plants *via* hyphal connections of non host-specific fungi, which  
183 has been demonstrated by Simard *et al.* (1997) in boreo-temperate forests, is not clear.  
184 Potentially, movement of compounds through hyphal connections could provide an  
185 important carbon subsidy to maintain dipterocarp seedlings in a light-limited state in the  
186 forest understory. Two experiments conducted in Malaysian Borneo have shown that  
187 inter-individual connections by EcM hyphal networks do not appear to influence  
188 dipterocarp seedling growth (Brearley 2003, Saner 2009). These results contrast with  
189 that of McGuire (2007) who found that incorporation into an EcM hyphal network was  
190 important for seedling growth in a similarly EcM-dominated forest of Guyana.  
191 Differences among these forest systems could be related to the differences in tree  
192 diversity between the sites, with a monodominant stand in Guyana compared with the  
193 high-diversity sites in Southeast Asia. Where there are many EcM parent trees

194 belonging to different species, as in Southeast Asia, supporting heterospecific seedlings  
195 with carbon compounds may well be selected against.

196

## 197 **FUNGAL FLORAS AND NEW FUNGAL SPECIES**

198 The fungal flora of most dipterocarp forests is still very poorly known. Hong (1979)  
199 made the first note of putative EcM fungi including *Amanita*, *Boletus*, *Gyrodon*,  
200 *Lactarius* and *Russula* species from around dipterocarps at the Forest Research Institute  
201 of Malaysia's grounds at Kepong, Peninsular Malaysia. Malaysia is probably one of the  
202 best-documented tropical countries in terms of its fungal flora but, even here, it is  
203 estimated that only 20 percent of the Peninsula's larger fungi have been collected  
204 (Corner, in Lee *et al.* 1995a).

205 The main site where detailed fruit body surveys have been carried out is Pasoh Forest  
206 Reserve in Peninsular Malaysia where Lee Su See, Roy Watling and colleagues have  
207 been working since the early 1990s (Lee *et al.* 2002a, 2003; Watling *et al.* 1998, 2002,  
208 2006). From these surveys, we know that the most common families found as fruiting  
209 bodies are Russulaceae, Boletaceae and Amanitaceae, and 296 species of fruiting body  
210 (in 19 predominantly EcM-forming families) have been recorded over a six-yr period  
211 (Lee *et al.* 2003). Around two-thirds of these were undescribed, and over three-quarters  
212 of the species were only collected once. Good information on fungal communities is  
213 also available from planted dipterocarps at Kepong, Peninsular Malaysia (Lee *et al.*  
214 1996a, Watling & Lee 1995, 1998) and natural forest at Wanariset Samboja,  
215 Kalimantan (Smits 1994, Yasman 1995) and from Corner's early work in Malaysia and  
216 Singapore (Corner 1988).

217 The fruiting bodies in the more seasonal dipterocarp forests of Thailand are broadly  
218 similar at the family level to those in Malaysia and Indonesia, with addition of *Astraeus*

219 (Chalermpongse 1987) that appears to be absent from the more aseasonal forests. There  
220 are also minor fungal inventories from Uppangala in the Western Ghats of India  
221 (Natarajan *et al.* 2005) and Sakaerat in Thailand (Chalermpongse 1987) which show  
222 similar patterns to the more extensive inventories. López-Quintero *et al.* (in press) have  
223 provided the first records of EcM fruiting bodies associated with the Neotropical  
224 dipterocarp *Pseudomonotes tropenbosii* in Colombia.

225

## 226 **DESCRIPTIONS OF DIPTEROCARP-ASSOCIATED ECTOMYCORRHIZAS**

227 There are very few published descriptions of dipterocarp EcMs and this hinders research  
228 for ecologists and mycologists who lack access to molecular sequencing facilities.

229 Becker (1983) and Lee (1988, Lee *et al.* 1997) described over 25 EcM morphotypes  
230 from the roots of *Shorea leprosula*, and this is currently the most comprehensive set of  
231 dipterocarp EcM descriptions that we have. Watling *et al.* (1995a) described the EcM  
232 formed by *Pisolithus aurantioscabrosus*, Tedersoo *et al.* (2007a,b) described the EcMs  
233 formed by Sordariomycete and *Coltriciella* species on *Vateriopsis seychellarum* and  
234 Jülich (1985) described the distinctive EcMs of *Riessia* and *Riessiella* with abundant  
235 cystidia (noted as conidia by Jülich: 1985), with Lee *et al.* (1997) showing how these  
236 particular species differ from many EcMs in lacking a Hartig net. Lee *et al.* (2010) also  
237 described a new Thelephoraceae species (FP160; most probably *Tomentella*) used in  
238 Malaysian inoculation trials.

239

## 240 **MOLECULAR STUDIES ON DIPTEROCARP-ASSOCIATED** 241 **ECTOMYCORRHIZAS**

242 Two of the most comprehensive studies of dipterocarp EcM communities have,  
243 ironically, been conducted on rare or outlying species within monospecific genera.

244 Moyersoen (2006) found nine EcM species on *Pakaraimea dipterocarpacea* in  
245 Venezuela, and Tedersoo *et al.* (2007a) found 18 EcM species on *Vateriopsis*  
246 *sechellarum* in the Seychelles. In Malaysian forests, Sirikantaramas *et al.* (2003) took  
247 root samples from five sites and showed that, belowground, the family producing the  
248 greatest number of sequences was the Thelephoraceae with just over half of the  
249 sequences. Other important families were Boletaceae, Russulaceae and  
250 Sclerodermataceae. Numerically this was similar to the results of Yuwa-Amornpitak *et*  
251 *al.* (2006) who obtained sequences from root tips from eight sites in Thailand and  
252 found, again, Thelephoraceae to provide the greatest number of sequences followed by  
253 Russulaceae and Sclerodermataceae. Sirikantaramas *et al.* (2003) also suggested that  
254 Thelephoraceae were often found associated with *Shorea* species but did not present  
255 further evidence to support their case. Currently, the most comprehensive study we have  
256 is that of Peay *et al.* (2010) who examined EcMs in two soil types at Lambir Hills in  
257 Sarawak and found that members of the Russulales represented around one-third of the  
258 sequences, and the Thelephorales were the fourth most abundant clade (after Boletales  
259 and Agaricales). In a dry dipterocarp forest in Thailand, Phosri *et al.* (in press) found  
260 Russulales and Thelephorales to be the most important taxa. In addition, Roy *et al.*  
261 (2009) determined that EcM fungi were associated with three Thai orchid species (two  
262 from forests with dipterocarps). These orchids are highly likely to be obtaining carbon  
263 subsidies from the associated dipterocarps. Numerically important fungal groups  
264 associated with these orchids were Thelephoraceae, Russulaceae, Clavulinaceae and  
265 Sebaciniales. Tedersoo *et al.* (2011) have also noted the important EcM species in two  
266 African forests containing dipterocarps as non-dominant species. Table 1 summarises  
267 the importance of various fungal groups in the studies above with some additional  
268 studies also reported.

269

270 Tedersoo and Nara (2010) suggest that tropical regions have lower EcM species  
271 diversity than temperate regions due to reduced phylogenetic diversity of host trees, and  
272 a simpler soil profile, among other reasons. It is difficult, however, to reconcile this  
273 suggestion with the very high diversity of fruit bodies collected by Lee *et al.* (2003) as  
274 noted above, especially as belowground diversity has been shown to be higher than  
275 aboveground diversity in tropical forest EcM fungal surveys (Henkel *et al.* in press);  
276 clearly more work is needed to resolve this problem.

277

278 **ECTOMYCORRHIZAL COMMUNITY DIVERSITY, DYNAMICS AND**  
279 **RESPONSES TO PERTURBATIONS**

280 On *Shorea leprosula*, Lee *et al.* (1997) described 24 EcM morphotypes from various  
281 sites in Peninsular Malaysia and 36 at Danum Valley in Borneo (Lee *et al.* 1996b),  
282 Ingleby *et al.* (1998) found a similar number (26) on the roots of *Shorea parvifolia* as  
283 did Moyersoen (2000) on *Shorea pachycarpa* (29). A much higher richness of 56 EcM  
284 morphotypes were found on *Hopea nervosa* at Danum Valley (Lee *et al.* 1996b). The  
285 number of EcM morphotypes found in two nursery studies (14 and 16 species, Brearley  
286 2003 and Saner *et al.* 2011 respectively) appears to be lower than the field studies as  
287 many late-stage fungi (*sensu* Deacon *et al.* 1983) will be absent from nurseries.  
288 Individual seedlings may possess up to five different EcM morphotypes with 2–3 being  
289 the median number (Lee & Alexander 1996, Brearley *et al.* 2003). A succession of EcM  
290 fungi was observed on *Shorea leprosula* seedling root tips during early seedling  
291 establishment, and the number of morphotypes increased over the first seven months of  
292 seedling growth (Lee & Alexander 1996). Comparisons between seedling EcM  
293 communities will therefore be sensitive to seedling age.

294

295 Studies on the population structure of dipterocarp EcMs appear to be limited to a single  
296 study. Rivière *et al.* (2006) examined the spatial distribution of a *Russula* species in  
297 dipterocarp forests dominated by *Vateria indica* and *Dipterocarpus indicus* in the  
298 Western Ghats of India. The fruiting bodies were highly aggregated but, using  
299 molecular methods, genet size was shown to be vary variable, ranging from a number of  
300 single fruiting body genets, to the largest genet containing three fruiting bodies with a  
301 maximum distance of 70 m between them. These data suggest that *Russula* species can  
302 form large genets, in contrast to earlier work that has shown *Russula* species to form  
303 relatively small genets (Redecker *et al.* 2001, Liang *et al.* 2004).

304

305 HOST SPECIFICITY.— Smits (1983, 1985) provided anecdotal evidence suggesting that  
306 dipterocarp associated EcMs are highly host specific. Unfortunately, due to the lack of  
307 methodology presented in his papers it makes them difficult to evaluate. Furthermore,  
308 these results do not agree with those found in temperate regions where many fungi have  
309 an intermediate to broad host range, certainly at the host genus taxonomic level or  
310 above (Molina *et al.* 1992). Current evidence suggests that host specificity of  
311 dipterocarp EcMs is not as common as claimed by Smits (1983, 1985) with weak  
312 evidence for host specificity provided by Ingleby *et al.* (2000) who showed that  
313 seedlings of *Dipterocarpus alatus* grown in soil from a *Hopea odorata* plantation in  
314 Vietnam formed only one EcM morphotype, and this was different to the four  
315 morphotypes on *Hopea odorata* seedlings. Becker (1983) described ten EcM  
316 morphotypes from *Shorea leprosula* and *Shorea maxwelliana* at Pasoh of which two  
317 were shared between the two hosts. Similarly, Berriman (1986) showed that three out of  
318 11 morphotypes were shared between three *Shorea* seedling species (*Shorea leprosula*,

319 *Shorea lepidota* and *Shorea macroptera*) and seven were found on only one of the  
320 species. In nursery-grown dipterocarp seedlings, seven of 14 EcM morphotypes found  
321 were present on the roots of at least three of the four host seedling species of  
322 *Dryobalanops lanceolata*, *Hopea nervosa*, *Parashorea tomentella* and *Shorea leprosula*  
323 (Brearley *et al.* 2003, 2007). Lee *et al.* (1996b) recorded 61 EcM morphotypes on the  
324 roots of seedlings of *Hopea nervosa* and *Shorea leprosula* in forests at Danum Valley in  
325 Sabah, of which 31 were found on both species, 25 were found on *Hopea nervosa* only,  
326 and only five were found exclusively on *Shorea leprosula*. Examination of associations  
327 of fruit bodies with planted dipterocarp species suggests that *Russula virescens* is  
328 putatively associated with at least ten dipterocarp species and *Boletus aureomycelinus*  
329 with 21 species (Watling and Lee 1998). All of the above evidence suggests a modest  
330 amount of host specificity although the degree to which this simply represents random  
331 sampling of rare species can only be ascertained with more extensive sampling.  
332 At a higher taxonomic level, two dipterocarp-associated EcM fungi (*Pisolithus*  
333 *aurantioscabrosus* and *Tomentella* FP160) have also been shown to form EcMs on  
334 *Acacia mangium* although it is not yet known if these are functionally important (Lee &  
335 Patahayah 2003). Of the 18 species of EcM fungi on *Vateriopsis seychellarum*, three  
336 were shared with *Intsia bijuga*, and another three were shared with introduced  
337 *Eucalyptus robusta* (Tedersoo *et al.* 2007a). As a long-isolated island endemic  
338 (occurring only on a single island of the Seychelles) and an evolutionary basal lineage,  
339 *V. seychellarum* might not, however, be very representative of the Asian dipterocarps in  
340 this respect.

341

342 REPNSES TO NUTRIENT AVAILABILITY.— Many studies show that mycorrhizal  
343 colonization decreases under conditions of higher soil, and especially P, fertility (Jones

344 *et al.* 1990, Baum & Makeschin 2000, Treseder 2004) but the results from dipterocarps  
345 are variable. Turner *et al.* (1993) found that NPK fertilization increased percentage EcM  
346 colonization on *Shorea macroptera* seedlings, and the correlation between percentage  
347 EcM and seedling biomass was stronger if the unfertilised seedlings were analysed  
348 alone. Similarly, Lee and Lim (1989) found that only seedlings from a less fertile site  
349 had a correlation between percentage EcM colonization and foliar P concentrations.  
350 Irino *et al.* (2004) showed that addition of a NPK fertilizer increased EcM colonization  
351 on pot-grown *Dryobalanops lanceolata*, although colonization was very low (8%) in the  
352 control seedlings. In contrast, addition of P in various studies had no effect on % EcM  
353 on *Shorea leprosula* (Suhardi 2000), two species of *Dryobalanops* in two contrasting  
354 soil types (Palmiotto *et al.* 2004), or on *Hopea nervosa* and *Shorea leprosula* (Brearley  
355 *et al.* 2007). However, the latter study did find species-specific responses to increased  
356 nutrient availability, most notably for *Riessiella* sp. that increased following P  
357 fertilization. This suggests that *Riessiella* might not be a fully mutualistic fungus  
358 (Brearley *et al.* 2007); further evidence for this hypothesis is that it also does not  
359 possess a Hartig Net (Lee *et al.* 1997), which is the site of nutrient transfer between the  
360 fungus and the plant. The lack of a consistent response to P fertilization in these studies  
361 suggests that EcMs are important even under conditions of higher nutrient supply as  
362 colonization rarely declines, suggesting they are still involved in assisting in seedling  
363 nutrient uptake.

364

365 When an organic nutrient source of mixed leaf litter was added to the soil medium there  
366 was no change in percentage EcM colonization for three dipterocarp seedling species  
367 (Brearley *et al.* 2003). In contrast, the diversity of EcM species on seedling's roots was  
368 reduced with litter addition; this was partly driven by the reduction in colonization by



369 *Cenococcum geophilum*. Addition of *Imperata cylindrica* (alang-alang) litter reduced  
370 percentage EcM colonization in *Shorea bracteolata* (Suhardi *et al.* 1993), perhaps due  
371 to its allelopathic nature (Brook 1989).

372

373 RESPONSES TO SOIL TYPES .—The EcM community on the roots of nursery-grown  
374 *Dryobalanops lanceolata* is considerably different when seedlings are grown on  
375 ultramafic (with high levels of metals such as Fe, Mg, Ni, Co and Cr) as compared to a  
376 more typical non-ultramafic ultisol soil (Brearley 2006), notably in that *Cenococcum*  
377 *geophilum* and *Inocybe* spp. decreased, and *Boletales* sp. increased in ultramafic soils,  
378 and EcM diversity was also higher. Similarly, Iwamoto and Kitayama (2002) found  
379 eleven EcM morphotypes in ultramafic soil compared to only two in a sedimentary soil  
380 from dipterocarp-dominated forests at around 700 m asl on Mount Kinabalu in Borneo.

381

382 Sandy soils at Lambir Hills, Sarawak, had a greater number of EcM species than clay  
383 soils (65 vs. 41), perhaps due to more differentiated soil horizons of the sandy soils or  
384 the lower nutrient concentrations, allowing coexistence of a greater number of species  
385 (Peay *et al.* 2010). Such results might also, however, be due to different tree  
386 compositions on the different soil types. There was also evidence of more phylogenetic  
387 clustering of EcM species on the clay soil, giving rise to a community more dominated  
388 by Russulales and Thelephorales and lacking Cortinariaceae. Seedlings of  
389 *Dryobalanops lanceolata* (but not *D. aromatica*) at Lambir Hills had more than double  
390 the biomass of EcM when grown on their preferred soil type (clay and sandy soils  
391 respectively; Palmiotto *et al.* 2004)

392

393 REPONSES TO IRRADIANCE.— Studies examining changes in EcM colonization in  
394 response to differing irradiances are somewhat contrasting, most likely this is due to  
395 changes in carbohydrate flow from plant to fungus but will also be due to the differing  
396 environmental conditions associated with higher irradiance, such as higher soil  
397 temperatures. High light conditions (e.g. in forest gaps) appear to increase EcM  
398 colonization (Becker 1983; Ingleby *et al.* 1998). EcM colonization on five Sri Lankan  
399 *Shorea* species was also greatest under higher irradiances, often under full sunlight,  
400 even though this did not correspond to conditions most suited to seedling growth of  
401 these species (Tennakoon *et al.* 2005). In contrast, Yasman (1995) found the greatest  
402 EcM colonization under irradiances where seedling growth was also most rapid, while  
403 other studies have shown no clear difference among different light treatments of EcM  
404 abundance on seedlings of two contrasting species, *Shorea leprosula* and *Hopea*  
405 *nervosa* (Brearley *et al.* 2007). When considering diversity of EcMs under differing  
406 conditions we may also need to examine the size of the root system and the number of  
407 root tips present, as, analogous to a species-area effect, larger root systems with more  
408 root tips may well host more EcM species (see Taylor 2002).

409

410 RESPONSES TO BURNING.— Tata *et al.* (2003) did not find any EcM fruit bodies in  
411 forests burnt in 1998 in East Kalimantan (examined in 2000) and, using two dipterocarp  
412 seedling species as bait plants, she found there was no difference in the proportion of  
413 seedlings with EcM (although values for both species were low at around 5%) among  
414 seedlings grown in the burnt and unburnt forest soils. In contrast, Akema *et al.* (2009)  
415 found that in a severely burnt site (examined in 2002) there were no EcM root tips in the  
416 soil, although there were some fruiting bodies of typically early stage fungi (*Laccaria*  
417 *vinaceoavellana*). In the moderately burnt site, four EcM morphotypes were found, with

418 dominance by one species, compared to a much more even EcM community in  
419 undisturbed forest where eight morphotypes were found. There was also an indication  
420 that EcMs in the unburnt forest were concentrated in the surface soil layer, but were  
421 more evenly distributed in the soil in the moderately fire-affected site. Several reasons  
422 for severe reduction in EcMs in burnt forests include changed microclimate, changes in  
423 the input of leaf litter, volatilization of organically bound nutrients, the death of host  
424 trees, and possible sterilization of upper layers of the soil by the fires (Certini 2005)

425

426 REPOSSES TO LOGGING DISTURBANCE.— Initial fruit body data from Pasoh showed  
427 slightly more EcM species in logged (98) than unlogged (75) forest (largely due to more  
428 *Russula* species), although only around 10 percent of species were shared by both forest  
429 types (Watling *et al.* 1998). Additional data revealed that logged forests contained only  
430 32 percent of the fungal flora of the forest reserve as a whole (Watling *et al.* 2002),  
431 although this number is difficult to put into context given the differences in area and  
432 sampling effort between the logged and unlogged forests. Lee *et al.* (1996b) found no  
433 difference in percentage EcM on *Hopea nervosa* and *Shorea leprosula* in recently  
434 logged (up to three yr previously) and unlogged plots at Danum Valley, Sabah, and the  
435 number of EcM morphotypes on the roots of the seedlings showed no consistent  
436 patterns across the three paired sites studied. Of the 61 EcM morphotypes, 30 were  
437 exclusive to unlogged forest whereas 16 were restricted to logged forest; furthermore, of  
438 29 EcM morphotypes which were found only in one of the sixteen plots, around three-  
439 quarters of these were found in unlogged forest only, suggesting that logging may have  
440 more of a negative impact on uncommon EcM morphotypes. Ingleby *et al.* (1998)  
441 examined EcMs on *Shorea parvifolia* nine months after hand logging and found an  
442 increased diversity of EcM morphotypes under the logged, higher irradiance conditions.

443 However, in this study it is difficult to disentangle the effects of logging from increased  
444 light levels created by logging disturbance. The immediate impacts of logging on the  
445 diversity and functioning of the EcM communities has not yet been assessed.

446

#### 447 **COLONIZATION BY OTHER (SYMBIOTIC) FUNGAL STRUCTURES**

448 There are reports of some dipterocarps also forming arbuscular mycorrhiza (AM)  
449 associations (Shamsudin 1979, Chalermpongse 1987, Ibrahim *et al.* 1995, Dhungana *et*  
450 *al.* 1996, Shi *et al.* 2002, 2007; Tawaraya *et al.* 2003) and an important question is how  
451 common is dual colonization, and are interactions among colonisers beneficial to the  
452 host plants, as seen by Chen *et al.* (2000) for eucalypts? The only data on dual  
453 colonization did not find a difference in the relative growth rate of *Hopea odorata*  
454 seedlings with EcM alone (38 out of 54 seedlings) or dual EcM/AM colonization (16  
455 out of 54 seedlings) (Ibrahim *et al.* 1995). Ectendomycorrhizal colonization has also  
456 been reported in *Shorea parvifolia* (Louis 1988) and other dipterocarps (Chalermpongse  
457 1987, Tupas and Sajise 1976). All of the above information suggests that there could be  
458 a considerable diversity of mycorrhizal morphologies in the Dipterocarpaceae, and  
459 additional morphological information on mycorrhizal symbioses is needed.

460

#### 461 **FUTURE WORK**

462 Increased knowledge of dipterocarp-associated EcM fungal community structure is  
463 being facilitated by extensive and long-term fruiting body surveys as well as molecular  
464 analyses of belowground EcM communities. Nursery and field based studies are  
465 improving understanding of growth and nutrition relations of EcM dipterocarp seedlings  
466 (Brearley 2011). The following areas for future research on dipterocarp-associated EcM  
467 fungi and plant-fungal ecosystem interactions are suggested:

468

469 (1) Bring more EcM fungi into culture and test them for functional symbiotic  
470 capabilities. Fungi that appear to promote plant performance should be further  
471 investigated in field studies where the ecological importance of EcM for dipterocarp  
472 growth and survival is most important although currently equivocal.

473

474 (2) It is important to determine the roles that fungi might be playing in ecosystem  
475 nutrient cycling processes. How do they influence leaf litter decomposition and the  
476 subsequent release of nutrients? This might be achieved by analyses of extracellular  
477 enzyme activities. Do EcMs influence ecosystem processes? A nitrogen isotopic budget  
478 of ecosystem compartments might shed some light on the importance of EcM fungi in  
479 nitrogen-cycling processes (see Hobbie & Hobbie 2008).

480

481 (3) Community studies on EcM root tips and fruiting bodies are needed, as are studies  
482 of community dynamics in response to land-use change or other current global changes.  
483 Our understanding of EcM responses to logging remains rudimentary, and it is not clear  
484 which species or groups of species are more or less affected by disturbances. Although  
485 some studies have suggested that temperate and tropical EcM communities have similar  
486 diversity, tropical studies are mostly short term and have not examined, for example,  
487 differentiation by depth or seasonal changes. Linking fungal diversity with ecosystem  
488 processes in tropical forests, and how such relationships are affected by disturbances is  
489 another area of considerable research importance..

490

491 (4) Taxonomic capacity for fungal studies in the appropriate geographical regions needs  
492 to be improved, for both traditional taxonomy as well as molecular taxonomy. Herbaria

493 provide a valuable repository of sequence diversity (*e.g.*, Brock *et al.* 2008) and  
494 sequences from identified fungal fruit body specimens would allow us to relate  
495 belowground to aboveground fungal diversity in a more meaningful way.

496

497 (5) We should be determining the ecophysiological requirements of selected  
498 functionally important tropical EcM isolates. Other than those studies on species of  
499 interest for inoculation schemes (Patahayah *et al.* 2003, Brearley *et al.* 2005) there is  
500 minimal knowledge on the ecophysiology of tropical EcM fungi. For example, what are  
501 their temperature and nutrient requirements? Can they access organic nutrients, as has  
502 been shown in temperate regions?

503

504 (6) And finally, what is the morphological diversity of mycorrhizal types? Is dual  
505 mycorrhizal colonization common and functionally important? If so, what are the  
506 developmental, physiological and environmental factors in controlling potential dual  
507 colonization?

508

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515

516

517

518 **LITERATURE CITED**

- 519 AKEMA, T., I. NURHIFTISNI, SUCIATMIH, AND H. SIMBOLON. 2009. The impact of the  
520 1998 forest fire on ectomycorrhizae of dipterocarp trees and their recovery in  
521 tropical forests of East Kalimantan, Indonesia. JARQ 43: 137-143.
- 522 ALBRECHT, C., T. BURGESS, B. DELL, AND F. F. LAPEYRIE. 1994. Chitinase and  
523 peroxidase activities are induced in eucalyptus roots according to aggressiveness  
524 of Australian ectomycorrhizal strains of *Pisolithus* sp. New Phytol. 127: 217-222.
- 525 ALEXANDER, I. J. 2006. Ectomycorrhizas – out of Africa? New Phytol. 172: 589-591.
- 526 ALEXANDER, I. J., AND P. HÖGBERG. 1986. Ectomycorrhizas of tropical angiospermous  
527 trees. New Phytol. 102: 541-549.
- 528 ALEXANDER, I. J., A. NORANI, AND S. S. LEE. 1992. The role of mycorrhizas in the  
529 regeneration of some Malaysian forest trees. *In* A. G. Marshall and M. D. Swaine  
530 (Eds.). Tropical Rain Forest: Disturbance and Recovery, pp. 357-367. The Royal  
531 Society, London, UK.
- 532 BAILLIE, I. C., P. S. ASHTON, S. P. CHIN, S. J. DAVIES, P. A. PALMIOTTO, S. E. RUSSO,  
533 AND S. TAN. 2006. Spatial association of humus, nutrients and soil in mixed  
534 dipterocarp forest at Lambir, Sarawak, Malaysian Borneo. J. Trop. Ecol. 22: 543-  
535 553.
- 536 BAUM, C., AND F. MAKESCHIN. 2000. Effects of nitrogen and phosphorus fertilization on  
537 mycorrhizal formation of two poplar clones (*Populus trichocarpa* and *P. tremula x*  
538 *tremuloides*). J. Plant Nutr. Soil Sci. 163: 491-497.
- 539 BECKER, P. 1983. Ectomycorrhizas on *Shorea* (Dipterocarpaceae) seedlings in a  
540 lowland Malaysian rainforest. Malay. For. 46: 146-170.
- 541 BÉREAU, M., M. GAZEL, AND J. GARBAYE. 1997. Les symbioses mycorrhiziennes des  
542 arbres de la forêt tropicale humide de Guyana française. Can. J. Bot. 75: 711-716.

- 543 BEIMFORDE, C., N. SCHÄFER, H. DÖRFELT, P. C. NASCIBENE, H. SINGH, J. HEINRICH,  
544 J. REITNER, R. S. RANA, AND A. R. SCHMIDT. 2011. Ectomycorrhizas from a Lower  
545 Eocene angiosperm forest. *New Phytol.* 192 : 988-996.
- 546 BERRIMAN, C. P. 1986. Mycorrhizas of *Shorea* (Dipterocarpaceae) in Relation to Host  
547 Specificity and Soil Phosphorus Status. B.Sc. Dissertation, University of Aberdeen,  
548 UK.
- 549 BREARLEY, F. Q. 2003. The Role of Ectomycorrhizas in the Regeneration of  
550 Dipterocarp Seedlings. Ph.D. Dissertation, University of Sheffield, UK.
- 551 BREARLEY, F. Q. 2006. Differences in the growth and ectomycorrhizal community of  
552 *Dryobalanops lanceolata* (Dipterocarpaceae) seedlings grown in ultramafic and  
553 non-ultramafic soils. *Soil Biol. Biochem.* 38: 3407-3410.
- 554 BREARLEY, F. Q. 2011. The importance of ectomycorrhizas for the growth of  
555 dipterocarps and the efficacy of ectomycorrhizal inoculation schemes. *In* M. Rai and  
556 A. Varma (Eds.). *Diversity and Biotechnology of Ectomycorrhizae*, pp. 3-17.  
557 Springer-Verlag, Berlin, Germany.
- 558 BREARLEY, F. Q., M. C. PRESS, AND J. D. SCHOLE. 2003. Nutrients obtained from leaf  
559 litter can improve the growth of dipterocarp seedlings. *New Phytol.* 160: 101-110.
- 560 BREARLEY, F. Q., S. PRAJADINATA, P. S. KIDD, J. PROCTOR, AND SURIANTATA 2004.  
561 Structure and floristics of an old secondary rain forest in Central Kalimantan,  
562 Indonesia, and a comparison with adjacent primary forest. *For. Ecol. Manage.* 195:  
563 385-397.
- 564 BREARLEY, F. Q., J. D. SCHOLE, AND S. S. LEE. 2005. Nitrogen nutrition and isotopic  
565 discrimination in tropical ectomycorrhizal fungi. *Res. Microbiol.* 156: 184-190.



- 566 BREARLEY, F. Q., J. D. SCHOLES, M. C. PRESS, AND G. PALFNER. 2007. How does light  
567 and phosphorus fertilisation affect the growth and ectomycorrhizal community of  
568 two contrasting dipterocarp species? *Plant Ecol.* 192: 237-249.
- 569 BROCK, P. M., H. DÖRING, AND M. I. BIDARTONDO. 2008. How to know unknown fungi:  
570 the role of a herbarium. *New Phytol.* 181: 719-724.
- 571 BROOK, R. M. 1989. Review of literature on *Imperata cylindrica* (L.) Raueschel with  
572 particular reference to south east Asia. *Trop. Pest Manage.* 35: 12-25.
- 573 CERTINI, G. 2005. Effects of fires on properties of forest soils: a review. *Oecologia*, 143:  
574 1-10.
- 575 CHALERMPOONGSE, A. 1987. Mycorrhizal survey of dry-deciduous and semi-evergreen  
576 dipterocarp forest ecosystems in Thailand. *In* A. J. C. H. Kostermans (Ed.).  
577 Proceedings of the Third Round Table Conference on Dipterocarps, pp.81-103.  
578 UNESCO Regional Office for Science and Technology, Jakarta, Indonesia.
- 579 CHANG, Y. S., F. F. LAPEYRIE, AND S. S. LEE. 1994. The survival and competitiveness of  
580 *Pisolithus tinctorius* on outplanted seedlings of *Shorea glauca* in Malaysia. *In* S.  
581 Appanah and K. C. Khoo (Eds.). Proceedings of the Fifth Round Table Conference  
582 on Dipterocarps, pp. 165-169. Forest Research Institute of Malaysia, Kepong,  
583 Malaysia.
- 584 CHANG, Y. S., S. S. LEE, F. F. LAPEYRIE, AND S. M. YAZID. 1995. The competitiveness  
585 of two strains of *Pisolithus tinctorius* on seedlings of three species of dipterocarps  
586 under nursery and field conditions: preliminary results. *In* R. Wickneswari, A. Z.  
587 Yahya, A. H. M. Shariff, D. Haji Ahmad, K. C. Khoo, K. Suzuki, S. Sakurai and K.  
588 Ishii (Eds.). Proceedings of the International Workshop of BIO-REFOR, Kangar,  
589 1994, pp. 208-212. BIO-REFOR, IUFRO-SPDC, Tokyo, Japan & Forest Research  
590 Institute of Malaysia, Kepong, Malaysia.

- 591 CHEN, Y. L., M. C. BRUNDRETT, AND B. DELL. 2000. Effects of ectomycorrhizas and  
592 vesicular-arbuscular mycorrhizas, alone or in competition, on root colonization and  
593 growth of *Eucalyptus globulus* and *E. urophylla*. *New Phytol.* 146: 545-556.
- 594 CONNELL, J. H., AND M. D. LOWMAN. 1989. Low-diversity tropical rain forests: some  
595 possible mechanisms for their existence. *Am. Nat.* 134: 88-119.
- 596 CORNER, E. J. H. 1972. *Boletus* in Malaysia. Government Printing Office, Singapore.
- 597 CORNER, E. J. H. 1988. Higher fungi. *In*: Earl of Cranbrook (Ed.). *Key Environments:*  
598 *Malaysia*, pp. 88-101. Pergamon Press, Oxford, UK.
- 599 DARUSMAN, L. K. 1998. Kinetics of root chitinase during the association process  
600 between *Shorea selanica* and mycorrhiza of *Scleroderma columnare*. *Hayati* 5: 95-  
601 97.
- 602 DAYANANDAN, S., P. S. ASHTON, S. M. WILLIAMS, AND R. B. PRIMACK. 1999.  
603 Phylogeny of the tropical tree family Dipterocarpaceae based on nucleotide  
604 sequences of the chloroplast *rbcL* gene. *Am. J. Bot.* 86: 1182- 1190.
- 605 DE ALWIS, D. P., AND K. ABEYNAYAKE. 1980. A survey of mycorrhiza in some forest  
606 trees in Sri Lanka. *In* P. Mikola (Ed.). *Tropical Mycorrhiza Research*, pp. 146-  
607 153. Clarendon Press, Oxford, UK.
- 608 DE ALWIS, D. P., AND K. ABEYNAYAKE. 1988. Aseptic synthesis of mycorrhizae of  
609 *Dipterocarpus zeylandicus*. *In* F. S. P. Ng (Ed.). *Trees and Mycorrhiza:*  
610 *Proceedings of the Asian Seminar* pp. 215-226. Forest Research Institute of  
611 Malaysia, Kepong, Malaysia.
- 612 DE VOOGD, C. N. A. 1933. Cultuurproeven met *Shorea platyclados* v. Sl. in Redjang en  
613 Lebong. *Tectona* 26: 703-713.
- 614 DEACON, J. W., S. D. DONALDSON, AND F. T. LAST. 1983. Sequences and interactions of  
615 mycorrhizal fungi on birch. *Plant Soil* 71: 257-262.

616 DHUNGANA, H. N., D. DUTTA, G. S. SARMA, AND P. HAZARIKA. 1996. Occurrence of  
617 vesicular-arbuscular mycorrhizae in seedlings of some forest tree species. *J. Trop.*  
618 *For.* 12: 156-158.

619 DUCOUSSO, M., G. BÉNA, C. BOURGEOIS, B. BUYCK, G. EYSSARTIER, M. VINCELETTE, R.  
620 RABEVOHITRA, L. RANDRIHASIPARA, B. DREYFUS, AND Y. PRIN. 2004. The last  
621 common ancestor of Sarcolaenaceae and Asian dipterocarp trees was  
622 ectomycorrhizal before the India-Madagascar separation, about 88 million years  
623 ago. *Mol. Ecol.* 13: 231-236.

624 EYSSARTIER, G., D. STUBBE, R. WALLEYN, AND A. VERBEKEN. 2009. New records of  
625 *Cantharellus* (Basidiomycota, *Cantharellaceae*) from Malaysian dipterocarp  
626 rainforest. *Fungal Div.* 36: 57-67.

627 HADI, S., AND E. SANTOSO. 1988. Effect of *Russula* spp., *Scleroderma* sp. and *Boletus*  
628 sp. on the mycorrhizal development and growth of five dipterocarp species. *In* M.  
629 Mohinder Singh (Ed.). *Agricultural and Biological Research Priorities in Asia*,  
630 *Proceedings of the IFS Symposium of Science Asia* 87, pp. 183-185. International  
631 Foundation for Science & Malaysian Scientific Association, Kuala Lumpur,  
632 Malaysia.

633 HADI, S., AND E. SANTOSO. 1989. Accumulation of macronutrients by five dipterocarp  
634 species inoculated with different species of mycorrhizal fungi. *In* A. Mahadevan, N.  
635 Raman and K. Natarajan (Eds.). *Mycorrhizae for Green Asia: Proceedings of the*  
636 *First Asian Conference on Mycorrhizae*, pp.139-141. Centre for Advanced Studies  
637 on Botany, University of Madras, India.

638 HAWKSWORTH, D. L. 1993. The tropical fungal biota: census, pertinence, prophylaxis,  
639 and prognosis. *In* S. Isaac, J. C. Frankland, R. Watling and A. J. S. Whalley (Eds.).  
640 *Aspects of Tropical Mycology*, pp. 265-293. Cambridge University Press, UK.

- 641 HENKEL, T. W. 2003. Monodominance in the ectomycorrhizal *Dicymbe corymbosa*  
642 (Caesalpiniaceae) from Guyana. *J. Trop. Ecol.* 19: 417-437.
- 643 HENKEL, T. W., M. C. AIME, M. M. L. CHIN, S. L. MILLER, R. VILGALYS AND M. E.  
644 SMITH. In press. Ectomycorrhizal fungal sporocarp diversity and discovery of new  
645 taxa in *Dicymbe* monodominant forests of the Guiana Shield. *Biodivers. Conserv.*
- 646 HOBBIIE, E. A., AND J. E. HOBBIIE. 2008. Natural abundance of  $^{15}\text{N}$  in nitrogen-limited  
647 forests and tundra can estimate nitrogen cycling through mycorrhizal fungi: a  
648 review. *Ecosystems* 11: 815-830.
- 649 HONG, L. T. 1979. A note on dipterocarp mycorrhizal fungi. *Malay. For.* 42: 280-283.
- 650 IBRAHIM, Z., M. N. MAHAT, AND S. S. LEE. 1995. Response of *Hopea odorata* seedlings  
651 to biological soil conditioners. *In* R. Wickneswari, A. Z. Yahya, A. H. M. Shariff,  
652 D. Haji Ahmad, K. C. Khoo, K. Suzuki, S. Sakurai and K. Ishii (Eds.). *Proceedings*  
653 *of the International Workshop of BIO-REFOR, Kangar, 1994*, pp.179-182. BIO-  
654 REFOR, IUFRO-SPDC, Tokyo, Japan & Forest Research Institute of Malaysia,  
655 Kepong, Malaysia.
- 656 INGLEBY, K. 1999. *Inocybe avellana* Horak + *Shorea leprosula* Miq. *In* R. Agerer, R. M.  
657 Danielson, S. Egli, K. Ingleby, D. Luoma and R. Treu (Eds.). *Descriptions of*  
658 *Ectomycorrhizae, Volume 4*, pp. 55-60. Einhorn-Verlag, Schwäbisch Gmünd,  
659 Germany.
- 660 INGLEBY, K., R. C. MUNRO, M. NOOR, P. A. MASON, AND M. J. CLEARWATER. 1998.  
661 Ectomycorrhizal populations and growth of *Shorea parvifolia* (Dipterocarpaceae)  
662 seedlings regenerating under three different forest canopies following logging. *For.*  
663 *Ecol. Manage.* 111: 171-179.

- 664 INGLEBY, K., L. T. T. THUY, N. T. PHONG, AND P. A. MASON. 2000. Ectomycorrhizal  
665 inoculum potential of soils from forest restoration sites in south Vietnam. *J. Trop.*  
666 *For. Sci.* 12: 418-422.
- 667 IRINO, K. O., Y. IBA, S. ISHIZUKA, T. KENZO, S. RIPOT, J. J. KENDAWANG, N. MIYASHITA,  
668 K. NARA, T. HOGETSU, I. NINOMIYA, K. IWASAKI, AND K. SAKURAI. 2004. Effects of  
669 controlled-release fertilizer on growth and ectomycorrhizal colonization of pot-  
670 grown seedlings of the dipterocarp *Dryobalanops lanceolata* in a tropical nursery.  
671 *Soil Sci. Plant Nutr.* 50: 747-753.
- 672 IWAMOTO, K., AND K. KITAYAMA. 2002. Abundances of ectomycorrhizas on the slopes  
673 of Mount Kinabalu, Sabah, Malaysian Borneo. *Sabah Park. Nat. J.* 5: 239-255.
- 674 JONES, M. D., D. M. DURALL, AND P. B. TINKER. 1990. Phosphorus relationships and  
675 production of extramatrical hyphae by two types of willow ectomycorrhizas at  
676 different soil phosphorus levels. *New Phytol.* 115: 259-267
- 677 JÜLICH, W. 1985. Fungi associated with Dipterocarpaceae in Southeast Asia. 1. The  
678 genera *Riessia* and *Riessiella*. *Int. J. Mycol. Lichenol.* 2: 123-140.
- 679 KETTLE, C. J. 2010. Ecological considerations for using dipterocarps for restoration of  
680 lowland rainforest in Southeast Asia. *Biodivers. Conserv.* 19: 1137-1151.
- 681 LEE, S. S. 1998. Root symbiosis and nutrition. *In* S. Appanah and J. M. Turnbull (Eds.),  
682 A Review of Dipterocarps: Taxonomy, Ecology and Silviculture, pp. 99-114.  
683 Centre for International Forestry Research, Bogor, Indonesia.
- 684 LEE, S. S. 2005. Macrofungal diversity in Peninsular Malaysia focusing on the  
685 ectomycorrhizal fungi. *Clusiana* 44: 57-66.
- 686 LEE, S. S., AND I. J. ALEXANDER. 1994. The response of seedlings of two dipterocarp  
687 species to nutrient additions and ectomycorrhizal infection. *Plant Soil* 163: 299-  
688 306.

689 LEE, S. S., AND I. J. ALEXANDER. 1996. The dynamics of ectomycorrhizal infection of  
690 *Shorea leprosula* seedlings in Malaysian rain forests. *New Phytol.* 132: 297-305.

691 LEE, S. S., AND K. L. LIM. 1989. Mycorrhizal infection and foliar phosphorus content of  
692 seedlings of three dipterocarp species grown in selectively logged forest and a  
693 forest plantation. *Plant Soil*, 117: 237-241.

694 LEE, S. S., AND M. PATAHAYAH. 2003. Host specificity of dipterocarp ectomycorrhizal  
695 fungi. *In* H. Aminah, S. Ani, H. C. Sim and B. Krishnapillay (Eds.). Proceedings  
696 of the Seventh Round-Table Conference on Dipterocarps. 7-10 October 2002, pp.  
697 214-217. Asia Pacific Association of Forestry Research Institutions, Kuala  
698 Lumpur, Malaysia.

699 LEE, S. S., H. BESL, AND S. UJANG. 1995a. Some fungi of the Sungai Halong and  
700 surrounding areas, Temengor Forest Reserve, Hulu Perak, Malaysia. *Malay. Nat.*  
701 *J.* 48: 147-155.

702 LEE, S. S., F. F. LAPEYRIE AND S. M. YAZID. 1995b. Techniques for controlled  
703 ectomycorrhizal inoculation of dipterocarp seedlings and cuttings. *In* Supriyanto  
704 and J. T. Kartana (Eds.). Proceedings of the Second Symposium on Biology and  
705 Biotechnology of Mycorrhizae and Third Asian Conference on Mycorrhizae  
706 (ACOM III), BIOTROP Special Publication 56, pp.217-221. SEAMEO  
707 BIOTROP, Bogor, Indonesia.

708 LEE, S. S., R. WATLING, AND E. TURNBULL. 1996a. Ectomycorrhizal fungi as possible  
709 bio-indicators in forest management. *In* N. Hussein, P. S. Bacon and K. C. Khoo  
710 (Eds.). *Forestry and Forest Products Research: Proceedings of the Third*  
711 *Conference, Volume 1*, pp. 63-68. Forest Research Institute of Malaysia, Kepong,  
712 Malaysia.

- 713 LEE, S. S., I. J. ALEXANDER, P. H. MOURA-COSTA, AND S. W. YAP. 1996b. Mycorrhizal  
714 infection of dipterocarp seedlings in logged and undisturbed forests. *In* S.  
715 Appanah and K. C. Khoo (Eds.). Proceedings of the Fifth Round Table  
716 Conference on Dipterocarps, pp. 157-164. Forest Research Institute of Malaysia,  
717 Kepong, Malaysia.
- 718 LEE, S. S., I. J. ALEXANDER, AND R. WATLING. 1997. Ectomycorrhizas and putative  
719 ectomycorrhizal fungi of *Shorea leprosula* Miq. (Dipterocarpaceae). *Mycorrhiza*  
720 7: 63-81.
- 721 LEE, S. S., R. WATLING, AND Y. NORAINI SIKIN. 2002a. Ectomycorrhizal basidiomata  
722 fruiting in lowland rain forests of peninsular Malaysia. *Bois Fôr. Trop.* 274(4):  
723 33-43.
- 724 LEE, S. S., M. PATAHAYAH, AND F. F. LAPEYRIE. 2002b. Exotic vs. indigenous  
725 ectomycorrhizal fungi for inoculation of dipterocarps. *In* K. Ishii, M. Matsumori  
726 and K. Suzuki (Eds.). BIO-REFOR: Proceedings of Tokyo-Workshop, pp. 84-87.  
727 BIO-REFOR, IUFRO-SPDC, Tokyo, Japan.
- 728 LEE, S. S., R. WATLING, AND E. TURNBULL. 2003. Diversity of putative ectomycorrhizal  
729 fungi in Pasoh Forest Reserve. *In* T. Okuda, N. Manokaran, Y. Matsumoto, K.  
730 Niiyama, S. C. Thomas and P. S. Ashton (Eds.). Pasoh: Ecology of a Lowland  
731 Rain Forest in Southeast Asia, pp. 149-159. Springer-Verlag, Tokyo, Japan.
- 732 LEE, S. S., M. PATAHAYAH, W. S. CHONG, AND F. F. LAPEYRIE. 2008. Successful  
733 ectomycorrhizal inoculation of two dipterocarp species with a locally isolated  
734 fungus in Peninsular Malaysia. *J. Trop. For. Sci.* 20: 237-247.
- 735 LEE, S. S., B. K. THI, AND M. PATAHAYAH. 2010. An ectomycorrhizal Thelephoroid  
736 fungus of Malaysian dipterocarp seedlings. *J. Trop. For. Sci.* 22: 355-363.

- 737 LEPAGE, B. A., R. S. CURRAH, R. A. STOCKEY, AND G. W. ROTHWELL. 1997. Fossil  
738 ectomycorrhizae from the middle Eocene. *Am. J. Bot.*, 84: 410-412.
- 739 LIANG, Y., L.-D. GUO, AND K.-P. MA. 2004. Genetic structure of a population of the  
740 ectomycorrhizal fungus *Russula vinosa* in subtropical woodlands in southwest  
741 China. *Mycorrhiza* 14: 235-240.
- 742 LÓPEZ-QUINTERO, C. A., G. STRAATSMA, A. E. FRANCO-MOLANO, AND T. BOEKHOUT. in  
743 press. Macrofungal diversity in Colombian Amazon forests varies with regimes of  
744 disturbance. *Biodivers. Conserv.*
- 745 LOUIS, I. 1988. Ecto- and ectendomycorrhizae in the tropical dipterocarp, *Shorea*  
746 *parvifolia*. *Mycologia* 80: 845-849.
- 747 LOUIS, I., AND E. SCOTT. 1987. In vitro synthesis of mycorrhiza in root organ cultures of  
748 a tropical dipterocarp species. *Trans. Br. Mycol. Soc.* 88: 565-568.
- 749 MCGUIRE, K. L. 2007. The common ectomycorrhizal net may maintain monodominance  
750 in a tropical rain forest. *Ecology* 88: 567-574.
- 751 MCGUIRE, K. L., T. W. HENKEL, I. GRANZOW DE LA CERDA, G. VILLA, F. EDMUND, AND  
752 C. ANDREW. 2008. Dual mycorrhizal colonization of forest-dominating tropical  
753 trees and the mycorrhizal status of non-dominant tree and liana  
754 species. *Mycorrhiza* 18: 217-222.
- 755 MOLINA, R., H. B. MASSICOTTE, AND J. M. TRAPPE. 1992. Specificity phenomena in  
756 mycorrhizal symbioses: community ecological consequences and practical  
757 applications. In M. F. Allen (Ed.). *Mycorrhizal Functioning: an Integrative Plant-*  
758 *Fungal Process*, pp. 357-423. Chapman & Hall, New York, USA.
- 759 MOYERSOEN, B. 1993. Ectomicorrizas y micorrizas vesiculares-arbusculares en  
760 Caatinga Amazónica. *Scientia Guaianæ* 3, Caracas, Venezuela.



761 MOYERSON, B. 2000. Diversity of ectomycorrhizal fungi associated with four species  
762 and two genera of Dipterocarpaceae in a field and bioessay experiment in Brunei  
763 Darussalam. *In* Anon. (Ed.). Tropical Mycology 2000 Abstracts, p. 25. British  
764 Mycological Society, London, UK.

765 MOYERSON, B. 2006. *Pakaraimaea dipterocarpacea* is ectomycorrhizal, indicating an  
766 ancient Gondwanaland origin for the ectomycorrhizal habit in Dipterocarpaceae.  
767 *New Phytol.* 172: 753-762.

768 NATARAJAN, K., G. SENTHILARASU, V. KUMARESAN, AND T. RIVIÈRE. 2005. Diversity in  
769 ectomycorrhizal fungi of a dipterocarp forest in Western Ghats. *Curr. Sci.* 88:  
770 1893-1895.

771 NEWBERY, D. MCC., I. J. ALEXANDER, D. W. THOMAS, AND J. S. GARTLAN. 1988.  
772 Ectomycorrhizal rainforest legumes and soil phosphorus in Korup National Park,  
773 Cameroon. *New Phytol.* 109: 433-450.

774 NEWMAN, M. F., P. F. BURGESS, AND T. C. WHITMORE. 1996. Manuals of Dipterocarps  
775 for Foresters: Borneo Island Light Hardwoods. Royal Botanic Garden, Edinburgh,  
776 UK.

777 NEWMAN, M. F., P. F. BURGESS, AND T. C. WHITMORE. 1998. Manuals of Dipterocarps  
778 for Foresters: Borneo Island Medium and Heavy Hardwoods. Royal Botanic  
779 Garden, Edinburgh, UK.

780 NEWSHAM, K. K., A. H. FITTER, AND A. R. WATKINSON. 1995. Multi-functionality and  
781 biodiversity in arbuscular mycorrhizas. *TREE* 10: 407-411.

782 PALMIOTTO, P. A., S. J. DAVIES, K. A. VOGT, P. M. S. ASHTON, D. J. VOGT, AND P. S.  
783 ASHTON. 2004. Soil-related habitat specialization in dipterocarp rain forest tree  
784 species in Borneo. *J. Ecol.* 92: 609-623.

- 785 PAOLI, G. D., L. M. CURRAN, AND D. R. ZAK. 2006. Soil nutrients and beta diversity in  
786 the Bornean Dipterocarpaceae: evidence for niche partitioning by tropical rain  
787 forest trees. *J. Ecol.*, 94: 157-170.
- 788 PATAHAYAH, M., P. C. CYNTHIA, AND S. S. LEE. 2003. Optimizing growth conditions for  
789 ectomycorrhizal inoculum production of the Malaysian strain of *Pisolithus*  
790 *tinctorius*. In A. H. Mohamed, I. H. Parlan, S. Ibrahim, S. Y. M. Yussof, H. F.  
791 Lim, M. A. M. Idris, A. R. A. Ghani, S. Ujang and K. A. Hamzah (Eds.). Tropical  
792 Forestry Research in the New Millennium: Meeting Demands and Challenges.  
793 Proceedings of the International Conference on Forestry and Forest Products  
794 Research (CFFPR 2001), pp. 551-552. Asia Pacific Association of Forestry  
795 Research Institutions & Forest Research Institute of Malaysia, Kuala Lumpur,  
796 Malaysia.
- 797 PEAY, K. G., P. G. KENNEDY, S. J. DAVIES, S. TAN, AND T. D. BRUNS. 2010. Potential  
798 link between plant and fungal distributions in a dipterocarp rainforest: community  
799 and phylogenetic structure of tropical ectomycorrhizal fungi across a plant and  
800 soil ecotone. *New Phytol.* 185: 529-542.
- 801 PEGLER, D. N. 1997. The Larger Fungi of Borneo. Natural History Publications, Kota  
802 Kinabalu, Malaysia.
- 803 PEH K. S.-H., S. L. LEWIS, AND J. LLOYD. 2011. Mechanisms of monodominance in  
804 diverse tropical tree-dominated systems. *J. Ecol.* 99: 891-898.
- 805 PEYRONEL, B., AND B. FASSI. 1957. Micorrize ectotrofiche in una Caesalpinacea del  
806 Congo Belga. *Atti Accad. Sci. Torino* 91: 569-576.
- 807 PHOSRI, C., S. PÖLME, A. F. S. TAYLOR, U. KÖLJALG, N. SUWANNASAI, AND L.  
808 TEDERSOO. in press. Diversity and community composition of ectomycorrhizal  
809 fungi in a dry deciduous dipterocarp forest in Thailand. *Biodivers. Conserv.*

- 810 PROCTOR, J., J. M. ANDERSON, P. CHAI, AND H. W. VALLACK. 1983. Ecological studies  
811 in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak.  
812 I. Forest environment, structure and floristics. *J. Ecol.* 71: 237-260.
- 813 READ, D. J. 1986. Non-nutritional effects of mycorrhizal infection. *In* V. Gianinazzi-  
814 Pearson and S. Gianinazzi (Eds.) *Physiological and Genetical Aspects of*  
815 *Mycorrhizae*, pp. 169-176. INRA, Paris, France.
- 816 READ, D. J. 1998. Mycorrhiza - the state of the art. *In* A. Varma and B. Hock (Eds.).  
817 *Mycorrhiza Structure, Function, Molecular Biology and Biotechnology*, 2<sup>nd</sup>  
818 Edition, pp. 3-34. Springer-Verlag, Berlin, Germany.
- 819 READ, D. J. 1999. The ecophysiology of mycorrhizal symbioses with special reference  
820 to impacts upon plant fitness. *In* M. C. Press, J. D. Scholes and M. G. Barker  
821 (Eds.). *Physiological Plant Ecology*, pp. 133-151. Blackwell Scientific, Oxford,  
822 UK.
- 823 REDECKER, D., T. M. SZARO, R. J. BOWMAN, AND T. D. BRUNS 2001. Small genets of  
824 *Lactarius xanthogalactus*, *Russula cremoricolor* and *Amanita francheti* in late-  
825 stage ectomycorrhizal successions. *Mol. Ecol.* 10: 1025-1034.
- 826 RIVIÈRE, T., K. NATARAJAN, AND B. DREYFUS. 2006. Spatial distribution of  
827 ectomycorrhizal Basidiomycete *Russula* subsect. *Foetentinae* populations in a  
828 primary dipterocarp rainforest. *Mycorrhiza* 16: 143-148.
- 829 ROY, M., S. WATTANA, A. STIER, F. RICHARD, S. VESSABUTR, AND M.-A. SELOSSE 2009.  
830 Two mycoheterotrophic orchids from Thailand tropical dipterocarpacean forests  
831 associate with a broad diversity of ectomycorrhizal fungi. *BMC Biol.* 7: 51.
- 832 SANER, P. G. 2009. Ecosystem Carbon Dynamics in Logged Forests of Malaysian  
833 Borneo. Ph.D. Dissertation, University of Zurich, Switzerland.

- 834 SANER, P. G., C. PHILIPSON, R. C. ONG, N. MAJALAP, S. EGLI, AND A. HECTOR. 2011.  
835 Positive effects of ectomycorrhizal colonization on growth of seedlings of a  
836 tropical tree across a range of forest floor light conditions. *Plant Soil*, 338: 411-  
837 421.
- 838 SANTOSO, E. 1988. Pengaruh mikoriza terhadap diameter batang dan bobot kering  
839 anakan Dipterocarpaceae. *Bul. Penelit. Hutan* (504): 11-21.
- 840 SANTOSO, E. 1991. Pengaruh beberapa fungi mikoriza terhadap penyerapan unsur hara  
841 pada lima jenis Dipterocarpaceae. *Bul. Penelit. Hutan* (532): 11-18.
- 842 SHAMSUDDIN, M. N. 1979. Mycorrhizas of tropical forest trees. *In* J. I. Furtado (Ed.).  
843 Abstracts: Fifth International Symposium of Tropical Ecology, p. 173. University  
844 of Malaya, Kuala Lumpur, Malaysia.
- 845 SHI, Z. Y., Y. L. CHEN, AND R. J. LIU. 2002. Preliminary survey on arbuscular  
846 mycorrhizas of Dipterocarpaceae. *Mycosystemia*, 22: 82-87.
- 847 SHI, Z. Y., F. Y. WANG, Y. L. WEI, AND Y. L. CHEN. 2007. Observations on arbuscular  
848 mycorrhizas on Dipterocarpaceae grown in tropical rainforest in China. *Am.-*  
849 *Eurasian J. Agric. Environ. Sci.* 2: 247-254.
- 850 SHIVA, M. P., AND I. JANTAN. 1998. Non-timber forest products from dipterocarps. *In* S.  
851 Appanah and J. M. Turnbull (Eds.). *A Review of Dipterocarps: Taxonomy,*  
852 *Ecology and Silviculture*, pp. 187-197. Centre for International Forestry Research,  
853 Bogor, Indonesia.
- 854 SIMARD, S. W., D. A. PERRY, M. D. JONES, D. D. MYROLD, D. M. DURALL, AND R.  
855 MOLINA. 1997. Net transfer of carbon between ectomycorrhizal tree species in the  
856 field. *Nature* 388: 579-582.
- 857 SIMS, K. P., R. WATLING, AND P. JEFFRIES. 1995. A revised key to the genus  
858 *Scleroderma*. *Mycotaxon*, 56: 403-420.

- 859 SINGH, K. G. 1966. Ectotrophic mycorrhiza in equatorial rain forests. Malay. For. 29:  
860 13-18.
- 861 SIRIKANTARAMAS, S., N. SUGIOKA, S. S. LEE, L. A. MOHAMED, H. S. LEE, A. E. SZMIDT,  
862 AND T. YAMAZAKI. 2003. Molecular identification of ectomycorrhizal fungi  
863 associated with Dipterocarpaceae. Tropics 13: 69-77.
- 864 SLIK, J. W. F., N. RAES, S.-I. AIBA, F. Q. BREARLEY, C. H. CANNON, E. MEIJAARD, H.  
865 NAGAMASU, R. NILUS, G. D. PAOLI, A. D. POULSEN, D. SHEIL, E. SUZUKI, J. L. C.  
866 H. VAN VALKENBURG, C. O. WEBB, P. WILKIE, AND S. WULFFRAAT. 2009.  
867 Environmental correlates for tropical tree diversity and distribution patterns in  
868 Borneo. Divers. Distrib. 15: 523-532.
- 869 SMITH, S. E., AND D. J. READ. 2008. Mycorrhizal Symbiosis, 3<sup>rd</sup> Edition. Academic  
870 Press, San Diego, USA.
- 871 SMITS, W. T. M. 1983. Dipterocarps and mycorrhiza - an ecological adaptation and a  
872 factor in forest regeneration. Flora Males. Bull. 36: 3926-3937.
- 873 SMITS, W. T. M. 1985. Specificity of dipterocarp mycorrhiza. *In* R. Molina (Ed.).  
874 Proceedings of the 6<sup>th</sup> North American Conference on Mycorrhizae, p. 364. Forest  
875 Research Laboratory, Corvallis, Oregon, USA.
- 876 SMITS, W. T. M. 1994. Dipterocarpaceae: Mycorrhizae and Regeneration. The  
877 Tropenbos Foundation, Wageningen, The Netherlands.
- 878 ST. JOHN, T. V. 1980. A survey of mycorrhizal infection in an Amazonian rain forest.  
879 Acta Amazon. 10: 527-533.
- 880 SUHARDI. 2000. Treatment to development mycorrhizal formation on dipterocarp  
881 seedlings. *In* E. Guhardja, M. Fatawi, M. Sutisna, T. Mori and S. Ohta (Eds.)  
882 Rainforest Ecosystems of East Kalimantan: El Niño, Drought, Fire and Human  
883 Impacts, Ecological Studies 140. pp. 245-250. Springer-Verlag, Tokyo, Japan.

- 884 SUHARDI, A. DARMAWAN, AND E. FARIDAH. 1993. Effect of shading, fertilizer and  
885 mulching with alang-alang to the early growth and mycorrhiza formation of  
886 *Shorea bracteolata* in Bukit Suharto. In Anon. (Ed.). BIO-REFOR: Proceedings  
887 of Tsukuba-Workshop, pp. 161-173. BIO-REFOR, IUFRO-SPDC, Tsukuba  
888 Science City, Japan.
- 889 TATA, M. H. L., S. HADI, C. KUSMANA, AND ACHMAD (2003) Effect of forest fire on the  
890 survival of ectomycorrhizal fungi on dipterocarps. In H. Aminah, S. Ani, H. C.  
891 Sim and B. Krishnapillay (Eds.). Proceedings of the Seventh Round-Table  
892 Conference on Dipterocarps. 7-10 October 2002, pp. 173-178. Asia Pacific  
893 Association of Forestry Research Institutions. Kuala Lumpur, Malaysia.
- 894 TATA M. H. L., M. VAN NOORDWIJK, R. SUMMERBELL, AND M. J. A. WERGER. 2010.  
895 Limited response to nursery-stage mycorrhiza inoculation of *Shorea* seedlings  
896 planted in rubber agroforest in Jambi, Indonesia. *New For.* 39: 51-74.
- 897 TAYLOR, A. F. S. 2002. Fungal diversity in ectomycorrhizal communities: sampling  
898 effort and species detection. *Plant Soil* 244: 19-28.
- 899 TAWARAYA, K., Z. TAKAYA, M. TURJAMAN, S. J. TUAH, S. H. LIMIN, Y. TAMAI, J. Y.  
900 CHA, T. WAGATSUMA, AND M. OSAKI. 2003. Arbuscular mycorrhizal colonization of  
901 tree species grown in peat swamp forests of Central Kalimantan, Indonesia. *For.*  
902 *Ecol. Manage.* 182: 381-386.
- 903 TEDERSOO, L., AND K. NARA. 2010. General latitudinal gradient of biodiversity is  
904 reversed in ectomycorrhizal fungi. *New Phytol.* 185: 351-354.
- 905 TEDERSOO, L., T. SUVI, K. BEAVER, AND U. KÖLJALG. 2007a. Ectomycorrhizal fungi on  
906 the Seychelles: diversity patterns and host shifts from the native *Vateriopsis*  
907 *seychellarum* (Dipterocarpaceae) and *Intsia bijuga* (Caesalpinaceae) to the

908 introduced *Eucalyptus robusta* (Myrtaceae) but not *Pinus caribaea* (Pinaceae).  
909 New Phytol. 175: 321-333.

910 TEDERSOO, L., T. SUVI, K. BEAVER, AND I. SAAR. 2007b. Ectomycorrhizas of *Coltricia*  
911 and *Coltriciella* (Hymenochaetales, Basidiomycota) on Caesalpiniaceae,  
912 Dipterocarpaceae and Myrtaceae in Seychelles. Mycol. Prog. 6: 101-107.

913 TEDERSOO, L., T. W. MAY, AND M. E. SMITH. 2010. Ectomycorrhizal lifestyle in fungi:  
914 global diversity, distribution, and evolution of phylogenetic lineages. Mycorrhiza  
915 20: 217-263.

916 TEDERSOO, L., M. BAHRAM, T. JAIRUS, E. BECHEM, S. CHINOYA, R. MPUMBA, M. LEAL,  
917 E. RANDRIANJOHANY, S. RAZAFIMANDIMBISON, A. SADAM, T. NAADEL, AND U.  
918 KÖLJALG. 2011. Spatial structure and the effects of host and soil environments on  
919 communities of ectomycorrhizal fungi in wooded savannas and rain forests of  
920 Continental Africa and Madagascar. Mol. Ecol. 20: 3071-3080.

921 TENNAKOON, M. M. D., I. A. U. N. GUNATILLEKE, K. M. HAFEEL, G. SENEVIRATNE, C.  
922 V. S. GUNATILLEKE, AND P. M. S. ASHTON. 2005. Ectomycorrhizal colonization  
923 and seedling growth of *Shorea* (Dipterocarpaceae) species in simulated shade  
924 environments of a Sri Lankan rain forest. For. Ecol. Manage. 208: 399-405.

925 TRESEDER, K. K. 2004. A meta-analysis of mycorrhizal responses to nitrogen,  
926 phosphorus and atmospheric CO<sub>2</sub> in field studies. New Phytol. 164: 347-355.

927 TUPAS, G. L., AND P. E. SAJISE. 1976. Mycorrhizal associations in some savanna and  
928 reforestation trees. Kalikasan 5: 235-240.

929 TURJAMAN, M., Y. TAMAI, H. SEGAH, S. H. LIMIN, J. Y. CHA, M. OSAKI, AND K.  
930 TAWARAYA. 2005. Inoculation with the ectomycorrhizal fungi *Pisolithus arhizus*  
931 and *Scleroderma* sp. improves early growth of *Shorea pinanga* nursery seedlings.  
932 New For. 30: 67-73.

- 933 TURJAMAN, M., Y. TAMAI, H. SEGAH, S. H. LIMIN, M. OSAKI, AND K. TAWARAYA. 2006.  
934 Increase in early growth and nutrient uptake of *Shorea seminis* inoculated with two  
935 ectomycorrhizal fungi. *J. Trop. For. Sci.* 18: 243-249.
- 936 TURJAMAN, M., H. SAITO, E. SANTOSO, A. SUSANTO, S. GAMAN, S. H. LIMIN, M.  
937 SHIBUYA, K. TAKAHASHI, Y. TAMAI, M. OSAKI, AND K. TAWARAYA. 2007. Effect of  
938 ectomycorrhizal fungi inoculated on *Shorea balangeran* under field conditions in  
939 peat-swamp forests. *In* J. O. Rieley, C. J. Banks and B. Radjagukguk (Eds.).  
940 Proceedings of the International Symposium and Workshop on Tropical Peatland,  
941 Yogyakarta, 27-29 August 2007, pp 143-148. CARBOPEAT, University of  
942 Leicester, UK.
- 943 TURNER, I. M., N. D. BROWN, AND A. C. NEWTON. 1993. The effect of fertilizer addition  
944 on dipterocarp seedling growth and mycorrhizal infection. *For. Ecol. Manage.* 57:  
945 329-337.
- 946 VAN DER HEIJDEN, M. G. A., AND I. R. SANDERS, I. R. 2002. Mycorrhizal Ecology,  
947 Ecological Studies 157. Springer-Verlag, Berlin, Germany.
- 948 VAN GARDINGEN, P. R., M. J. CLEARWATER, T. NIFINLURI, R. EFFENDI, W.  
949 RUSMANTORO, M. NOOR, P. A. MASON, K. INGLEBY, AND R. C. MUNRO. 1998.  
950 Impacts of logging on the regeneration of lowland dipterocarp forest in Indonesia.  
951 *Commonw. For. Rev.* 77: 71-82.
- 952 VAN ROOSENDAEL, J., AND A. THORENAAR. 1924. De natuurlijke verjonging van  
953 Ngerawan (*Hopea mengarawan* Miq.) in zuid Sumatra. *Tectona*, 16: 519-567.
- 954 WATLING, R., AND S. S. LEE. 1995. Ectomycorrhizal fungi associated with members of  
955 the Dipterocarpaceae in Peninsular Malaysia - I. *J. Trop. For. Sci.* 7: 657-669.
- 956 WATLING, R., AND S. S. LEE. 1998. Ectomycorrhizal fungi associated with members of  
957 the Dipterocarpaceae in Peninsular Malaysia - II. *J. Trop. For. Sci.* 10: 421-430.

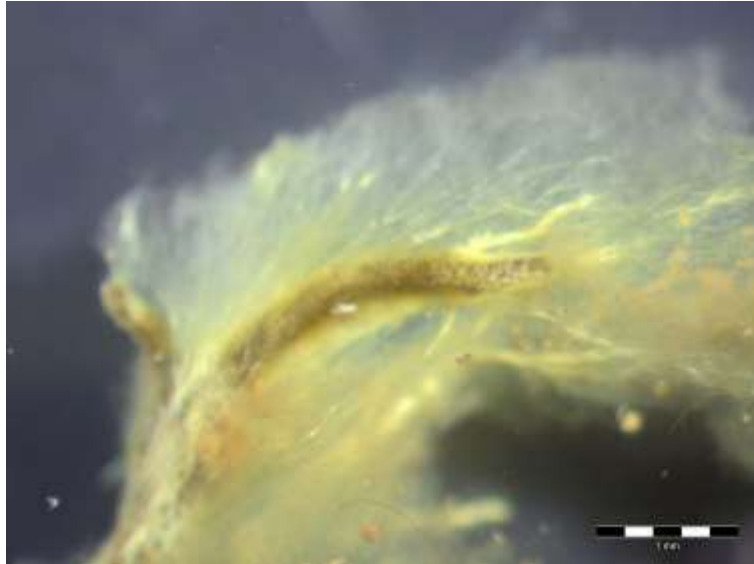


- 958 WATLING, R., AND S. S. LEE. 2007. Mycorrhizal mycodiversity in Malaysia. *In* E. B. G.  
959 Jones, K. D. Hyde and S. Vikineswary (Eds.). Malaysian Fungal Diversity, pp. 201-  
960 219. Mushroom Research Centre, University of Malaya & Ministry of Natural  
961 Resources and Environment, Kuala Lumpur, Malaysia,
- 962 WATLING, R., A. F. S. TAYLOR, S. S. LEE, K. SIMS, AND I. J. ALEXANDER. 1995a. A  
963 rainforest *Pisolithus*; its taxonomy and ecology. *Nova Hedwig*. 61: 417-429.
- 964 WATLING, R, S. S. LEE, AND E. TURNBULL. 1998. Putative ectomycorrhizal fungi of  
965 Pasoh Forest Reserve, Negri Sembilan, Malaysia. *In* S. S. Lee, Y. M. Dan, I. D.  
966 Gauld and J. Bishop (Eds.). Conservation, Management and Development of Forest  
967 Resources, pp. 96-104. Forest Research Institute of Malaysia, Kepong, Malaysia.
- 968 WATLING, R, S. S. LEE, AND E. TURNBULL. 2002. The occurrence and distribution of  
969 putative ectomycorrhizal basidiomycetes in a regenerating south-east Asian  
970 rainforest. *In* R. Watling, J. C. Frankland, A. M. Ainsworth, S. Isaac and C. H.  
971 Robinson (Eds.). Tropical Mycology: Volume 1 Macromycetes, pp. 25-43. CAB  
972 International, Wallingford, UK.
- 973 WATLING, R., S. S. LEE, AND E. TURNBULL. 2006. Notes taxonomiques et floristiques  
974 sur quelques bolets tropicaux et groupes proches. *Bull. Soc. Mycol. Fr.* 122: 327-  
975 352.
- 976 YASMAN, I. 1995. Dipterocarpaceae Tree-Mycorrhizae-Seedling Connections. Ph.D.  
977 Thesis, Wageningen Agricultural University, The Netherlands.
- 978 YAZID, S. M., S. S. LEE, AND F. F. LAPEYRIE. 1994. Growth stimulation of *Hopea* spp.  
979 (Dipterocarpaceae) seedlings following mycorrhizal inoculation with an exotic  
980 strain of *Pisolithus tinctorius*. *For. Ecol. Manage.* 67: 339-343.
- 981 YAZID, S. M., S. S. LEE, AND F. F. LAPEYRIE. 1996. Mycorrhizal inoculation of *Hopea*  
982 *odorata* (Dipterocarpaceae) in the nursery. *J. Trop. For. Sci.* 9: 276-278.

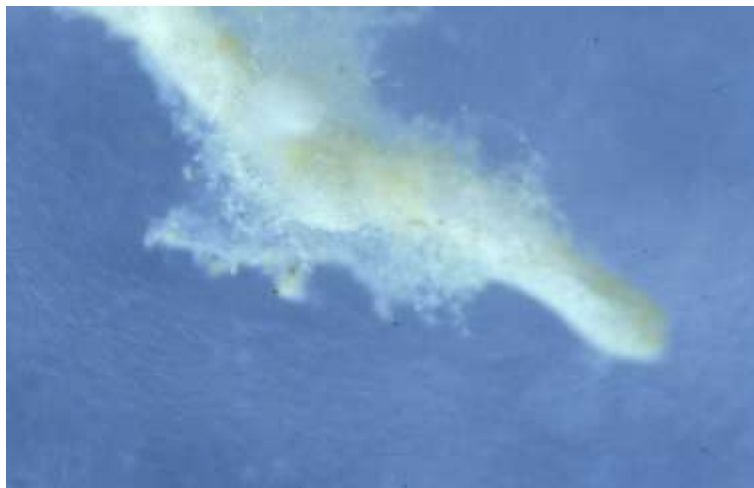
983 YUWA-AMORNPITAK, T., T. VICHITSOONTHONKUL, M. TANTICHAROEN, S.  
984 CHEEVADHANARAK, AND S. RATCHADAWONG. 2006. Diversity of ectomycorrhizal  
985 fungi on Dipterocarpaceae in Thailand. J. Biol. Sci. 6: 1059-1064.  
986  
987

988 FIGURE 1. Ectomycorrhizas formed by A) *Scleroderma* species, B) *Inocybe* species  
989 and C) Thelephorales species on roots of various member of the Dipterocarpaceae  
990 (*Photograph C by Götz Palfner*).

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TABLE 1. Molecular identification of ectomycorrhizas associated with Dipterocarpaceae hosts in a number of studies. All values are the percentage of sequences found within the particular fungal lineage (taxonomic nomenclature follows Tedersoo *et al.* 2010). Note that studies are not strictly comparable due to different primer pairs used to amplify fungal DNA.

	Malaysia (Five sites)	Venezuela ( <i>Pakaraimea dipterocarpacea</i> )	Thailand (Eight sites)	Seychelles ( <i>Vateriopsis seychellarum</i> )	Sarawak (Lambir Hills)	Sumatra (Jambi)	Thailand (Phitsanulok)	Kalimantan (Bukit Bangkirai)
	Sirikantaramas <i>et al.</i> 2003	Moyersoan 2006	Yuwa-Amornpitak <i>et al.</i> 2006	Tedersoo <i>et al.</i> 2007a	Peay <i>et al.</i> 2010	Tata <i>et al.</i> 2010	Phosri <i>et al.</i> in press	Nara pers. comm.
<b>Ascomycota</b>	-	-	-	-	-	-	-	3
Elaphomycetales	-	-	-	-	1	-	4	-
Helotiales	-	-	-	-	1	-	-	-
Pezizales	-	-	-	-	-	-	3	-
Sordariales	-	-	-	11	5	-	6	-
<b>Basidiomycota</b>	-	-	-	-	-	-	-	-
Agaricales	-	-	3	-	3	-	-	-
/amanita	1	11	3	-	3	-	3	6
/cortinarius	1	11	-	11	10	-	-	6
/hygrophorus	1	-	-	-	-	-	-	-
/inocybe	-	22	9	6	-	-	4	2

/laccaria	-	-	-	-	-	-	1	-
Atheliales	-	-	-	-	3	-	1	-
Boletales	-	-	-	-	5	-	-	15
/boletus	17	-	6	6	11	-	1	-
/pisolithus- scleroderma	10	-	21	6	2	25	3	-
Cantharellales	-	-	-	-	3	-	-	11
/cantharellus	2	-	-	6	3	8	4	-
/clavulina	-	22	-	-	6	8	3	-
Hymenochaetales	-	-	-	17	2	-	-	-
Hysterangiales	-	-	-	-	1	-	-	-
Russulales	16	-	18	6	28	-	32	31
Sebacinales	-	11	-	-	2	8	6	2
Thelephorales	51	-	36	33	12	50	25	25
<b>Unidentified</b>	-	22	3	-	-	-	-	-