

LRH: Brearley

RRH: Dipterocarpaceae Mycorrhizas

Ectomycorrhizal Associations of the Dipterocarpaceae

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ABSTRACT

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.

34

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 Moyersoan 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.

74

75 **BRIEF HISTORY OF DIPTEROCARP MYCORRHIZAL RESEARCH**

76 Van Roosendael 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 Sebacinales. 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 RESPONSES 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

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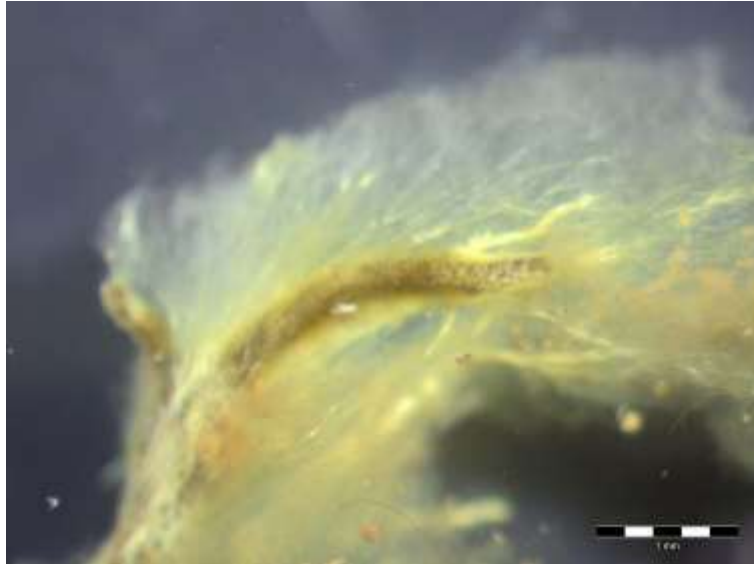
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988 FIGURE 1. Ectomycorrhizas formed by A) *Scleroderma* species, B) *Inocybe* species
989 and C) Thelephorales species on roots of various member of the Dipterocarpaceae
990 (*Photograph C by Götz Palfner*).

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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.
Ascomycota	-	-	-	-	-	-	-	3
Elaphomycetales	-	-	-	-	1	-	4	-
Helotiales	-	-	-	-	1	-	-	-
Pezizales	-	-	-	-	-	-	3	-
Sordariales	-	-	-	11	5	-	6	-
Basidiomycota	-	-	-	-	-	-	-	-
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
Unidentified	-	22	3	-	-	-	-	-