Please cite the Published Version

Brearley, FQ (2012) Ectomycorrhizal Associations of the Dipterocarpaceae. Biotropica, 44 (5). pp. 637-648. ISSN 0006-3606

DOI: https://doi.org/10.1111/j.1744-7429.2012.00862.x

Publisher: Wiley

Version: Accepted Version

Ectomycorrhizal Associations of the Dipterocarpaceae

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Received 16 April 2011; revision accepted 10 October 2011.

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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.

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

Mycorrhizas are an intimate symbiotic association between specialised root-inhabiting fungi and the roots of living plants; they are generally considered mutualistic as benefits are accrued by both partners. The plant provides the fungus with carbon derived from its photosynthetic activity and, in return, the fungus can improve nutrient uptake, growth, water relations, pathogen and heavy metal resistance of the plant (van der Heijden & Sanders 2002, Smith & Read 2008, and references therein). Mycorrhizas are important as they extend roots' nutrient depletion zones, especially for poorly mobile inorganic nutrients such as phosphorus (P) that are found at especially low concentrations in many tropical soils (Proctor *et al*. 1983, Brearley 2003, Brearley *et al*. 2004, Paoli *et al*. 2006). Early work on mycorrhizas focused on this nutrient uptake capability of the symbiosis but we are now aware of the multifunctional role played by mycorrhizas in enhancing protection against a number of environmental stresses, and it is clear that this role acts independently of improved plant nutrition (Read 1986, Newsham *et al*. 1995). This led Read (1998) to propose a definition of mycorrhizas as ‘structures in which a symbiotic union between fungi and plant roots leads to increases in fitness of one or both partners’. An estimated 95 percent of plant species are in characteristically mycorrhizal families (Read 1999) and they are found in almost every terrestrial ecosystem. The arbuscular mycorrhizal (AM) symbiosis, formed by members of the Glomeromycota, is the most abundant type of mycorrhiza, and most tropical trees form AMs (de Alwis & Abeynayake 1980, St. John 1980, Chalermpongse 1987, Newbery *et al*. 1988, Moyersoen 1993, Béreau *et al*. 1997, McGuire *et al*. 2008). An important, and often dominant, minority of tropical tree families, including the Dipterocarpaceae, form EcMs (Figure 1) that are mostly members of the Basidiomycota or Ascomycota. EcM trees in the tropics often form monodominant stands (Connell & Lowman 1989, Henkel 2003, Peh *et al*. 2011) but the dipterocarps rarely do so.

In this review, I outline the current state of knowledge of dipterocarp EcM fungi and their role in tropical ecosystems. The vast majority of current work is from the Asian dipterocarps and studies on these species, therefore, form most of the body of this review. I focus on the role of EcMs in improving seedling growth and performance (see also Brearley 2011), and on EcM species diversity and factors affecting patterns of diversity. I start with a brief history of dipterocarp mycorrhizal research and the biogeographical insights it has provided. I then examine the role of EcMs in the growth and performance of dipterocarp seedlings under both nursery and field conditions. The range of fungal species that form EcMs on dipterocarps is then explored, and I outline the how new molecular techniques have improved our knowledge of dipterocarp EcMs. Key determinants of EcM community dynamics, including various biotic and abiotic factors and perturbations, are then evaluated. Colonization by other symbiotic fungi is briefly assessed. The review concludes with some thoughts on future research priorities.

BRIEF HISTORY OF DIPTEROCARP MYCORRHIZAL RESEARCH

Van Roosendael and Thorenaar (1924) and de Voogd (1933) both noted the presence of ‘mycorrhizas’ on the roots of dipterocarp seedlings although it is not clear exactly what they saw as they did not publish pictures or record further observations. Although John Corner (1972, among others) noted EcM fungal fruiting bodies in dipterocarp forests, he attributed this to the presence of the Fagaceae (long known to be EcM in temperate regions), and it was not until 1966 that Singh recorded that dipterocarps, in common with a few other tropical angiosperms (Peyronel & Fassi 1957), formed EcMs. Early work (1960s to 1980s) simply noted various dipterocarp species as forming EcM associations (Singh 1966, de Alwis & Abeyneyake 1980, Alexander & Högberg 1986) and made cursory attempts to ascertain which fungal species were putative EcM formers (Hong 1979). The first attempts at *in vitro* synthesis of EcMs were not reported until the late 1980s (Louis & Scott 1987, de Alwis & Abeyneyake 1988) along with early reports of increased growth of inoculated seedlings also around this time (Hadi & Santoso 1988, Santoso 1988). In the late 1980s and early 1990s, Lee Su See’s work advanced EcM research by examining functional aspects of the symbiosis *e.g.,* interactions of EcMs with nutrients to determine seedling growth (Lee & Alexander 1994), and the succession of EcM fungi on seedlings (Lee & Alexander 1996) and her collaborations with Frédéric Lapeyrie advanced inoculation techniques with a range of fungal species (Yazid *et al*. 1994, 1996; Lee *et al*. 1995b, 2008). Throughout the 1990s to mid 2000s the IUFRO-SPDC funded BIO-REFOR conferences led to more work being published in the region; although some of these papers were valuable, many had limited value due to inappropriate design or lack of detail in reporting (Brearley 2011). The involvement of Roy Watling in the 1990s started to build knowledge of the fungal flora of Peninsular Malaysia from the strong foundations laid by Corner (Watling & Lee 1995, 1998, 2007; Watling *et al*. 1995a, 1998, 2002, 2006; Lee *et al*. 2002a, 2003; Lee 2005). Subsequent eco-physiological work examined how EcM communities were affected by biotic and abiotic perturbations (Brearley 2006, Brearley *et al*. 2003, 2007) and examined the role of EcMs in organic nitrogen acquisition (Brearley *et al*. 2003). The first molecular study of dipterocarp EcM communities appeared in 2003 (Sirikantaramas *et al*. 2003), and since then there have been a few more (Moyerseon 2006, Yuwa-Amornpitak *et al*. 2006, Tedersoo *et al*. 2007a, Peay *et al*. 2010) although until the comprehensive study by Peay *et al*. (2010) these had mostly focused on rare or outlying members of the Dipterocarpaceae. Most recently, advances based on early nursery-based inoculation studies have been extended to the field performance of dipterocarp seedlings (Brearley 2003, Turjaman *et al*. 2007, Lee *et al*. 2008, Tata *et al*. 2010).

INSIGHTS FROM ECTOMYCORRHIZAS INTO THE ORIGINS AND BIOGEOGRAPHY OF THE DIPTEROCARPACEAE

The biogeography of the Dipterocarpaceae is interesting as the vast majority of the 520 or so species are found in Southeast Asia with around 30 species in Africa and two in South America (Dayanandan *et al*. 1999). The consistent EcM status of Dipterocarpaceae in Southeast Asia, the dipterocarp sub-family Monotoideae in Africa and the Neotropical genus *Pakaraimaea*, suggests a common EcM ancestor and evolution of the EcM habit before continental separation of Gondwana. Doucousso *et al*. (2004) placed the origin of the EcM habit at least 88 million yr ago, prior to the separation of Madagascar and India, as the closest relative of the Dipterocarpaceae sharing a common ancestor, the Madagascan Sarcoleanaceae, are also EcM. The more recent discovery by Moyersoen (2006) that *Pakaraimaea dipterocarpacea*, basal in the dipterocarp clade, is also EcM suggests an earlier origin of the EcM habit to around 135 million yr ago before the continental separation of South America from Africa. This predates the earliest EcM fossils, which are around 50 million yr old (LePage *et al*. 1997, Beimforde *et al*. 2011) and sets the evolution of the EcM habit on the same timescale as the rise and radiation of the angiosperms. The evidence is not conclusive, however, as Alexander (2006) suggests that the Dipterocarpaceae might not have been EcM prior to the separation of the continents but became EcM at a later stage.

EFFECTS OF ECTOMYCORRHIZAL COLONIZATION ON THE GROWTH AND PERFORMANCE OF DIPTEROCARP SEEDLINGS

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

Experiments under field conditions are rarer and seedlings do not show as clear a response to the presence of EcMs when planted in natural forest or rubber agroforest (Brearley 2003, Tata *et al*. 2010). For example, there was no clear biomass response of *Hopea nervosa* and *Parashorea tomentella* seedlings to a reduction in EcM colonization by fungicide addition, though foliar nutrient concentrations did show a decline (Brearley 2003). There are significant challenges, however, in conducting field experiments, the major one being that it is very difficult to create truly non-mycorrhizal controls. Similarly, for inoculation experiments, such as that of Tata *et al*. (2010), where EcM inoculum is already present in the soil, the benefits of inoculating seedlings are not clear, especially if the inoculated EcM species does not remain on the roots of the seedlings. In contrast, the work of Turjaman *et al*. (2007) in degraded peat swamp forest did show improved growth of inoculated dipterocarp seedlings when out-planted in a degraded peat swamp area. This suggests that EcMs are most likely to benefit seedling performance when seedlings are planted in degraded areas where suitable EcM inoculum is not available, such as mine tailings (Lee *et al*. 2008), burnt areas (Akema *et al*. 2009), degraded peatlands (Turjaman *et al*. 2007) or areas previously used for agriculture (Ingleby *et al*. 2000). In many cases, such as in logged forest, EcM colonization occurs rapidly and naturally (Lee & Alexander 1996, Lee *et al*. 1996b) and under such conditions inoculation might not be worthwhile (Brearley 2011). Furthermore, inoculated EcM species do not always remain on the seedling roots, for example Chang *et al*. (1994, 1995) showed that a species of *Pisolithus* in Malaysian inoculation experiments had mostly disappeared from roots six months after colonised seedlings were planted into the field.

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

NURSING ROLE OF PARENT TREES

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

FUNGAL FLORAS AND NEW FUNGAL SPECIES

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

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

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

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

DESCRIPTIONS OF DIPTEROCARP-ASSOCIATED ECTOMYCORRHIZAS

There are very few published descriptions of dipterocarp EcMs and this hinders research for ecologists and mycologists who lack access to molecular sequencing facilities. Becker (1983) and Lee (1988, Lee *et al*. 1997) described over 25 EcM morphotypes from the roots of *Shorea leprosula*, and this is currently the most comprehensive set of dipterocarp EcM descriptions that we have. Watling *et al*. (1995a) described the EcM formed by *Pisolithus aurantioscabrosus*, Tedersoo *et al*. (2007a,b) described the EcMs formed by Sordariomycete and *Coltriciella* species on *Vateriopsis seychellarum* and Jülich (1985) described the distinctive EcMs of *Riessia* and *Riessiella* with abundant cystidia (noted as conidia by Jülich: 1985), with Lee *et al*. (1997) showing how these particular species differ from many EcMs in lacking a Hartig net. Lee *et al*. (2010) also described a new Thelephoraceae species (FP160; most probably *Tomentella*) used in Malaysian inoculation trials.

MOLECULAR STUDIES ON DIPTEROCARP-ASSOCIATED ECTOMYCORRHIZAS

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

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

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

ECTOMYCORRHIZAL COMMUNITY DIVERSITY, DYNAMICS AND RESPONSES TO PERTURBATIONS

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

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

HOST SPECIFICITY.— Smits (1983, 1985) provided anecdotal evidence suggesting that dipterocarp associated EcMs are highly host specific. Unfortunately, due to the lack of methodology presented in his papers it makes them difficult to evaluate. Furthermore, these results do not agree with those found in temperate regions where many fungi have an intermediate to broad host range, certainly at the host genus taxonomic level or above (Molina *et al*. 1992). Current evidence suggests that host specificity of dipterocarp EcMs is not as common as claimed by Smits (1983, 1985) with weak evidence for host specificity provided by Ingleby *et al*. (2000) who showed that seedlings of *Dipterocarpus alatus* grown in soil from a *Hopea odorata* plantation in Vietnam formed only one EcM morphotype, and this was different to the four morphotypes on *Hopea odorata* seedlings. Becker (1983) described ten EcM morphotypes from *Shorea leprosula* and *Shorea maxwelliana* at Pasoh of which two were shared between the two hosts. Similarly, Berriman (1986) showed that three out of 11 morphotypes were shared between three *Shorea* seedling species (*Shorea leprosula*, *Shorea lepidota* and *Shorea macroptera*) and seven were found on only one of the species. In nursery-grown dipterocarp seedlings, seven of 14 EcM morphotypes found were present on the roots of at least three of the four host seedling species of *Dryobalanops lanceolata*, *Hopea nervosa*, *Parashorea tomentella* and *Shorea leprosula* (Brearley *et al*. 2003, 2007). Lee *et al*. (1996b) recorded 61 EcM morphotypes on the roots of seedlings of *Hopea nervosa* and *Shorea leprosula* in forests at Danum Valley in Sabah, of which 31 were found on both species, 25 were found on *Hopea nervosa* only, and only five were found exclusively on *Shorea leprosula*. Examination of associations of fruit bodies with planted dipterocarp species suggests that *Russula virescens* is putatively associated with at least ten dipterocarp species and *Boletus aureomycelinus* with 21 species (Watling and Lee 1998). All of the above evidence suggests a modest amount of host specificity although the degree to which this simply represents random sampling of rare species can only be ascertained with more extensive sampling.

At a higher taxonomic level, two dipterocarp-associated EcM fungi (*Pisolithus aurantioscabrosus* and *Tomentella* FP160) have also been shown to form EcMs on *Acacia mangium* although it is not yet known if these are functionally important (Lee & Patahayah 2003). Of the 18 species of EcM fungi on *Vateriopsis seychellarum*, three were shared with *Intsia bijuga*, and another three were shared with introduced *Eucalyptus robusta* (Tedersoo *et al*. 2007a). As a long-isolated island endemic (occurring only on a single island of the Seychelles) and an evolutionary basal lineage, *V. seychellarum* might not, however, be very representative of the Asian dipterocarps in this respect.

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

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

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

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

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

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

RESPONSES TO BURNING.— Tata *et al*. (2003) did not find any EcM fruit bodies in forests burnt in 1998 in East Kalimantan (examined in 2000) and, using two dipterocarp seedling species as bait plants, she found there was no difference in the proportion of seedlings with EcM (although values for both species were low at around 5%) among seedlings grown in the burnt and unburnt forest soils. In contrast, Akema *et al*. (2009) found that in a severely burnt site (examined in 2002) there were no EcM root tips in the soil, although there were some fruiting bodies of typically early stage fungi (*Laccaria vinaceoavellana*). In the moderately burnt site, four EcM morphotypes were found, with dominance by one species, compared to a much more even EcM community in undisturbed forest where eight morphotypes were found. There was also an indication that EcMs in the unburnt forest were concentrated in the surface soil layer, but were more evenly distributed in the soil in the moderately fire-affected site. Several reasons for severe reduction in EcMs in burnt forests include changed microclimate, changes in the input of leaf litter, volatilization of organically bound nutrients, the death of host trees, and possible sterilization of upper layers of the soil by the fires (Certini 2005)

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

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

COLONIZATION BY OTHER (SYMBIOTIC) FUNGAL STRUCTURES

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

FUTURE WORK

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

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

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

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

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

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

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

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

ACKNOWLEDGMENTS

I thank the British Ecological Society for funding my Ph.D. research on dipterocarp ectomycorrhizas in Sabah, Malaysia (1999–2003) and Dr. Lee Su See and her staff for collaboration and support of my current research in Peninsular Malaysia (2009 onwards). David Burslem, Jaboury Ghazoul, Bernard Moyersoen and two anonymous reviewers provided helpful comments that improved the manuscript.

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

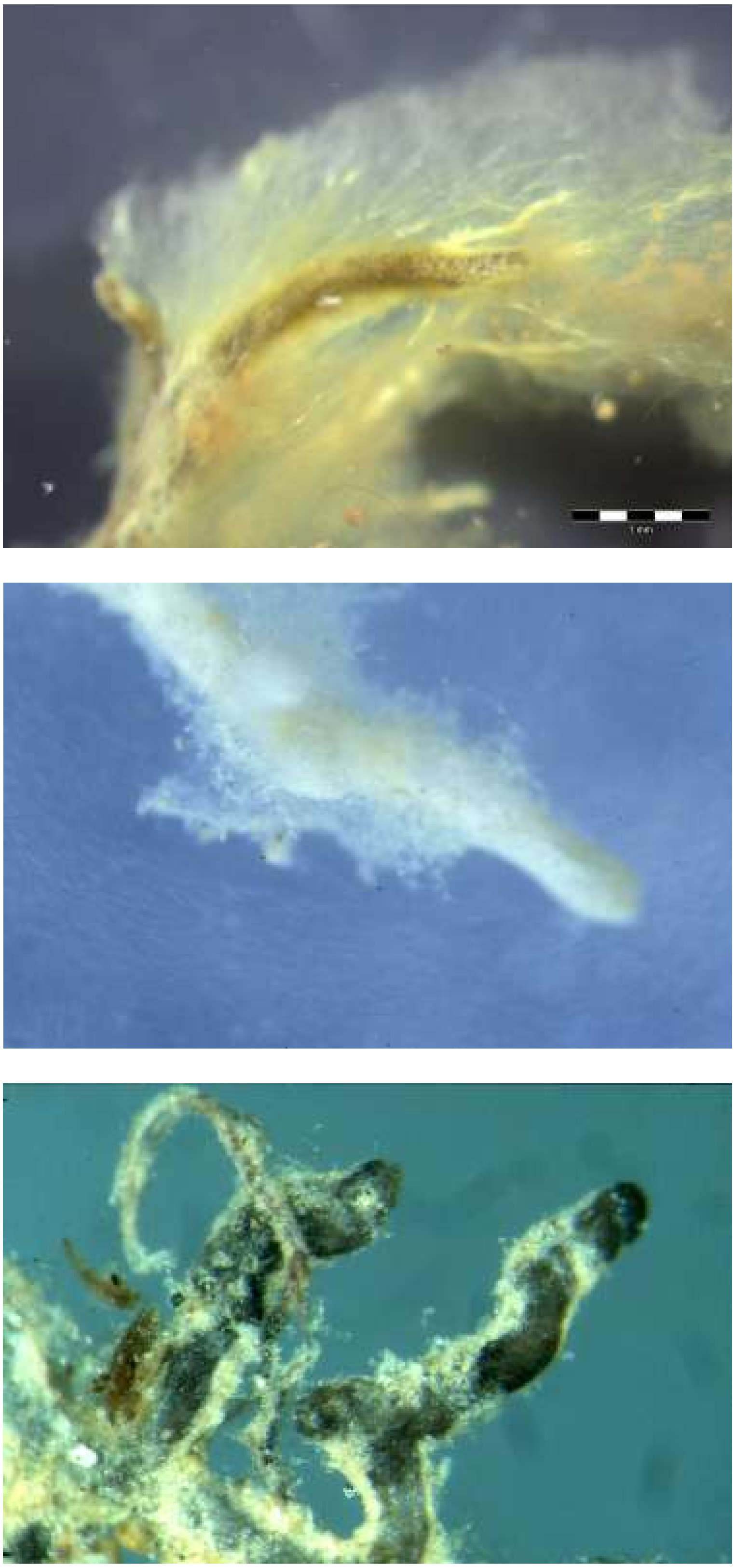

TABLE 1. Molecular identification of ectomycorrhizas associated with Dipterocarpaceae hosts in a number of studies. All values are the percentage of sequences found within the particular fungal lineage (taxonomic nomenclature follows Tedersoo *et al*. 2010). Note that studies are not strictly comparable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

	Malaysia (Five sites)	Venezuela (*Pakaraimea dipterocarpacea*)	Thailand (Eight sites)	Seychelles (*Vateriopisis seychellarum*)	Sarawak (Lambir Hills)	Sumatra (Jambi)	Thailand (Phitsanulok)	Kalimantan (Bukit Bangkirai)
	Sirikantaramas *et al*. 2003	Moyersoen 2006	Yuwa-Amornpitak *et al.* 2006	Tedersoo *et al*. 2007a	Peay *et al*. 2010	Tata *et al.* 2010	Phosri *et al.* 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	-
Cantharellalaes	-	-	-	-	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	-	-	-	-	-