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Review

Diversity and ecology of soil fungal communities in rubber plantations

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ABSTRACT

Monoculture rubber cultivation and its intensive associated human activities are known to have a negative impact on the biodiversity, ecology, and biological conservation of the ecosystems in which they occur. These negative impacts include changes to the biodiversity and function of soil fungal communities, which contribute towards nutrient cycling and interact with other organisms in belowground ecosystems, and may be pathogens. Despite the important role of soil fungi in rubber plantations, these communities have been poorly studied. In this paper, we review the existing literature on the diversity and ecology of belowground fungi in rubber plantations. Various groups of soil fungi, including saprobes, symbionts, and pathogens are discussed. Additionally, the role of plantation management is discussed in the context of both pathogenic soil fungi and the promotion of beneficial soil fungi. Management practices include clone selection, tree age and planting density, application of chemicals, and intercropping systems. Our review shows the strong need for further research into the effects of monoculture rubber plantations on soil fungal communities, and how we can best manage these systems in the future, in order to create a more sustainable approach to rubber production.

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1. Introduction

The rubber tree, *Hevea brasiliensis* (Willd.) Muell.Arg., a deciduous perennial tree of the family Euphorbiaceae, is the main producer of commercial natural rubber (Priyadarshan et al.,

2009). Although the rubber tree is indigenous to the tropical rain forests in the Amazon Basin of South America, it is cultivated in tropical regions worldwide (Rao et al., 1990; Priyadarshan et al., 2009). With the introduction of the rubber tree to the world market, consumption of natural rubber in

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global markets has increased dramatically, leading to further expansion of rubber plantations (Fox and Castella, 2013). Today, rubber plantations are rapidly expanding throughout non-traditional environments in montane areas of mainland Southeast Asia, including China, Laos, Thailand, Vietnam, Cambodia, and Myanmar (Ziegler et al., 2009; Ahrends et al., 2015).

The introduction of monoculture rubber plantations has led to the spread of pathogens and diseases and resulted in a number of negative environmental impacts (Jacob and Liyanage, 1992; Jayasinghe, 1999, 2001; Ziegler et al., 2009; Xu et al., 2014; Liyanage et al., 2016). These environmental impacts include the loss of natural forests, a decline in biodiversity, a depletion of natural carbon (C) stocks, and soil degradation (Zhang et al., 2007; Li et al., 2008; De Blé court et al., 2013; Warren-Thomas et al., 2015). Reference to soil degradation includes factors such as the loss of soil organic matter and nutrients, increase in surface run off of water, a reduction in the soil water holding capacity, and a decrease in soil biological activity (Zhang and Zhang, 2003, 2005; Guardiola-Claramonte et al., 2010; Clermont-Dauphin et al., 2013; Sreekanth et al., 2013; Puttasao et al., 2015).

Soil is a complex system comprising both abiotic and biotic factors, including macro- and meso-fauna, and microorganisms (Lavelle and Spain, 2001). Fungi comprise a crucial functional component of the belowground ecosystem in terms of nutrient acquisition and cycling, C turnover, soil formation, and the formation mycorrhizal associations with plants (Fontaine et al., 2007; Van Der Heijden et al., 2008). In addition, certain species of soil fungi are known to be pathogenic, resulting in the spread of disease both above and below ground (Narayananasamy, 2011).

It was estimated that the total number of fungi worldwide is around 1.5 million species with only 70,000 species presently described (Hawksworth, 1991, 2001). Soil fungal diversity is still underestimated and the function and relationship between fungi, soil, and plants remains unclear (Bridge and Spooner, 2001; Van Der Heijden et al., 2008). The majority of below ground studies conducted in rubber plantations have focused on soil quality in terms of physical and chemical characteristics, ignoring the role of the soil microbial communities (Cheng et al., 2007; Zhang et al. 2007; Orimoloye et al., 2010; Oku et al., 2012). Despite the fact that fungal activity in soil has direct consequences for soil quality and fertility, fungi have received little attention to date (Peries et al., 1979; Deka et al., 1998; Guo et al., 2013, 2015; Krashevskaya et al., 2015). This review therefore highlights the significance and influence of soil fungi on rubber plantations.

2. Soil fungal communities in rubber plantation

Saprotrophic fungi

Given that *H. brasiliensis* is a deciduous tree, a large amount of litter is generated, which accumulates on the plantation floor throughout the year (Verghese et al., 2001). It has been reported that, annually, rubber plantations produce approximately 7 tonnes of litter per hectare. However, this litter has

been shown to decompose at a slow rate, with 16–21 % leaf weight loss in 120 d (Jacob, 2000; Verghese et al., 2001).

It is well-established that the conversion of natural forests to rubber plantations results in a decline of litter decomposition rates (Zheng et al., 2006; Zhang et al., 2013). The slow decomposition of rubber litter has been attributed to the greater amounts of recalcitrant compounds such as alkyl C and methylated hydrocarbon cis polyisoprene in comparison to forest litter (Abraham and Chudek, 2008; Zhang et al., 2013). In a study conducted by Abraham and Chudek (2008), rubber had the lowest soil microbial activity compared to pueraria, mucuna, teak and natural forest. This was attributed to the greater alkyl-C: O-alkyl-C ratio of the rubber litter. The greater microbial activity of teak soil might be due to the increased understory layer and longer planting cycles (up to 100 y) of teak, resulting in a build-up of soil organic matter (Abraham and Chudek, 2008). Thereby, this study suggested that rubber plantations should be cropped with leguminous species during the initial years.

There have been few studies investigating the fungal communities associated with rubber litter (Osemwegie et al., 2010; Seephueak et al., 2010, 2011a, 2011b). The studies of fungal diversity in the rubber litter layer, conducted by Seephueak et al. (2010, 2011a, 2011b), found 447 species of saprotrophic fungi on leaves, 497 species on branches, and 461 species on logs. These studies also established that the diversity and composition of fungal communities on rubber litter varied according to differences on decomposition stages and seasonality. Rubber litter also supported high species richness and fungal diversity. Many factors can affect the changes in fungal communities such as the physical and chemical properties of trees, tree ages, microclimate, biological interaction, substrate preference, host preferences and geographical characters (Lodge, 1997; Kodsueb et al., 2008). Therefore, more studies on fungal diversity of rubber litter in other regions should be carried out to evaluate these effects. It would also be of value to investigate the function of these decomposer fungi.

A study of mushroom diversity related to rubber agroforestry systems and secondary forests in south western Nigeria revealed a total of 435 fruiting bodies, belonging to 93 fungal species (Osemwegie et al., 2010). The greatest number of fungal taxa recorded was wood-inhabiting mushrooms, comprising 70 % of the total fungal community. Compared to secondary forest, rubber agroforestry systems had lower macrofungal diversity, whilst the young rubber plantation supported greater fungal species richness and diversity of macrofungi than the old rubber plantations. In conclusion, the conversion of secondary forest into rubber agroforestry systems has a negative impact on mushroom diversity (Osemwegie et al., 2010).

Mycorrhizal fungi

Arbuscular mycorrhizal fungi (AMF) were first described on the roots of *H. brasiliensis* by D'Angremond and Van Hell (1939). They recorded intra and extracellular hyphae as well as vesicles and arbuscules. This AMF was suggested to be *Rhizoctonia bataticola* (*Macrophomina phaseoli*) (Taub.) Butl., nevertheless, the correct identity has not yet been confirmed (D'Angremond and Van Hell, 1939). The AMF species which

have been reported to grow on the roots of *H. brasiliensis* are shown in Table 1.

Jayaratne (1982) examined the AMF species from the soils of rubber plantations throughout Sri Lanka, including a variety of tree age classes and found that AMF distribution appeared to be unrelated to the geographical distribution and ages of the rubber trees, but were rather influenced by the moisture and P content of the soils. In another study, investigating the percentage colonization of rubber tree roots by AMF, it was reported that, compared to paper mulberry, agarwood, and teak, rubber trees exhibited the highest number of AMF spores and percentage colonization (Kanyasone, 2009). These findings are confirmed by the studies of Tawaraya et al., (2003) and Dhar and Mridha (2006), who both reported that rubber trees hosted a higher diversity of AMF species, greater AMF root colonization and higher AMF spore diversity, than other trees evaluated in the respective studies. However, there have been some conflicting reports indicating that the AMF diversity and spore count can also be comparatively low in rubber plantations. Pereira et al. (2014) measured the diversity of AMF in a variety of land used systems,

including an Atlantic forest, a sapodilla plantation, a rubber tree plantation, a mahogany plantation, a eucalyptus plantation, and a cassava crop. When compared to these land use systems, with the exception of the eucalyptus plantation (which is predominantly ectomycorrhizal), the rubber plantation expressed lowest numbers of AMF. Similar results were reported by Souza et al. (2010), who found that the spore diversity of AMF in different soil management systems was among the lowest in rubber plantations. Thus there appears to be varying accounts of AMF activity and diversity in rubber plantations and it is likely that aspects such as climate, land use history, soil type and plantation age will contribute to the abundance and diversity of AMF species within the various rubber plantations samples.

Inoculation of rubber seedlings with various AMF species has been proposed as one strategy to facilitate seedling establishment and improve the survival rate of young rubber trees (see Table 2). There is conflicting evidence as to what effect the inoculation of rubber tree seedlings has on the growth and survival of these seedlings. Studies by Jayaratne et al. (1984) and Moraes et al. (2010) reported no significant

Table 1 – Arbuscular mycorrhizal fungi that have been recorded on *Hevea brasiliensis*.

Fungal species	Methodology	Location	References
<i>Rhizoctonia bataticola</i> (<i>Macrophomina phaseoli</i>)	Not specified	Not specified	D'Angremond and Van Hell, 1939
<i>Rhizophagus</i> , <i>Rhizoctonia</i> and <i>Endogone</i>	Not specified	Not specified	Institut National Pour L'Étude Agronomique Du Congo Belge 1955; Hutchison, 1958; Jayaratne, 1982
<i>Glomus fasciculatus</i> , <i>G. microcarpus</i> , <i>G. multicutis</i> , <i>G. macrocarpus</i> var. <i>geosporus</i> , <i>G. mosseae</i> , <i>G. monosporus</i> , <i>Glomus</i> sp., <i>Acaulospora elegans</i> , <i>A. scrobiculata</i> , <i>Gigaspora nigra</i> , <i>G. gigantea</i> , <i>Gigaspora</i> sp., <i>Sclerocystis sinuosa</i> , <i>S. coremioides</i> , <i>S. clavispora</i> , <i>S. rubiformis</i> , <i>Complexipes moniliformis</i>	Spore examination from soil	Kegalle, Kurunegala, Matale, Kalutara Galle, Moneragala of Sri Lanka	Jayaratne, 1982
<i>Acaulospora</i> sp., <i>Sclerocystis</i> sp. and <i>Gigaspora</i> sp.	Spore examination from soil	Malaysia	Ikram and Mahmud, 1984
Not determined	AMF colonization of roots	A peat swamp forest of Central Kalimantan, Indonesia	Tawaraya et al., 2003
<i>Glomus</i> sp., <i>Acaulospora</i> sp., <i>Scutellospora</i> sp. and <i>Gigaspora</i> sp.	- AMF colonization of roots	Madhupur forest, Bangladesh	Dhar and Mridha, 2006
Not determined	- Spore examination from soil - AMF colonization of roots	Luang Prabang, northern Lao PDR	Kanyasone, 2009
<i>Acaulospora scrobiculata</i> , <i>Glomus ambisporum</i> , <i>G. etunicatum</i> , <i>G. macrocarpum</i> , <i>G. geosporum</i>	- Spore examination from soil - Diversity of AMF (spores) - Chemical analysis of soil	Rolimde Moura, Rondonia, North Region of Brazil	Souza et al., 2010
<i>Acaulospora excavate</i> , <i>A. foveata</i> , <i>A. mellea</i> , <i>A. morrowiae</i> , <i>A. scrobiculata</i> , <i>A. tuberculata</i> <i>Acaulospora</i> sp., <i>Ambispora apendicula</i> , <i>A. gerdermanii</i> , <i>Glomus gigantea</i> , <i>G. aggregatum</i> , <i>G. glomerulatum</i> , <i>G. macrocarpum</i> , <i>G. trufemii</i> , <i>Cetranspora pellucida</i>	- Diversity of AMF - Physicochemical characterization of soil	Atlantic forest in Goiana, Pernambuco, Brazil	Pereira et al., 2014

Table 2 – Arbuscular mycorrhizal fungi that have been used to inoculate *Hevea brasiliensis* roots.

AMF species	Other treatments	Leguminous crops	Growth responses	References
<i>Glomus fasciculatus</i> , <i>G. mosseae</i> , <i>Gigaspora margarita</i> Multispecies AMF	- Phosphorus level - Sterilized and unsterilized soil With and without phosphorus application	<i>Pueraria phaseoloides</i> <i>Calopogonium caeruleum</i>	No significant differences between AMF inoculated and non-inoculated one Improve growth and increase the uptake of phosphorus	Jayaratne et al., 1984 Ikram et al., 1992
Ten AMF species	Phosphorus level	No	Improve growth and phosphorus uptake in sterilised soil	Ikram et al., 1993
<i>Glomus mosseae</i>	No	No	After 9 m, dry weights of shoots and roots of inoculated plants were greater than those of controls by 27 and 17 %, respectively	Schwob et al., 1998
Mixed species, with <i>Glomus</i> and <i>Acaulospora</i> as dominant genera	Phosphorus level	<i>Macaranga denticulata</i>	- Increased shoot and root dry weight, number of branches, stem diameter, height - Enhance growth response when decreasing P levels	Kanyasone, 2009
<i>Glomus macrocarpum</i> , <i>G. claroideum</i> , <i>G. etunicatum</i> , <i>Gigaspora margarita</i> , <i>Scutellospora gregaria</i> , <i>S. margarita</i>	No	No	- No increase in height, diameter and number of leaves - Low level of mycorrhizal infection and number of spores in three and six months of transplanting	Moraes et al., 2010
<i>Glomus mosseae</i>	No	<i>Pueraria</i> sp.	Dry matter yield and N uptake by roots and shoots, root nodules of <i>Pueraria</i> sp. were significantly higher in <i>G. mosseae</i> inoculated soils than in uninoculated one	Rahman et al., 2011
<i>Rhizophagus irregularis</i> MUCL 41833	Compared with <i>Urtica dioica</i> seedlings (synthesize antifungal compounds of the hevein family)	<i>Medicago truncatula</i> A17 (mycelium donor plant)	<i>M. truncatula</i> presented lower root colonization in the presence of <i>H. brasiliensis</i> or <i>U. dioica</i> than control plants (grown alone)	Sosa-Rodriguez et al., 2013a
<i>Rhizophagus irregularis</i> MUCL 41833	Indole-3-butyric acid (IBA), 2-morpholinoethanesulfonic acid monohydrate (MES) buffer and carbon dioxide (CO ²)	<i>Medicago truncatula</i> A17 (mycelium donor plant)	- Root colonization was obtained after several weeks of <i>in vitro</i> culture - The highest levels of root colonization were obtained when plantlets were mycorrhized under a high CO ² concentration (1,000 μmolmol ⁻¹) with MES (10 mM) added to the growth medium	Sosa-Rodriguez et al., 2013b
<i>Rhizophagus irregularis</i> MUCL 41833	Taproot pruning and addition of activated charcoal (AC)	<i>Medicago truncatula</i> A17 (mycelium donor plant)	- After 13 weeks of culture, the plantlets grown with the addition of AC were significant higher in total root length, total root colonization, production of arbuscules and intraradical spores/vesicles - The pruned plantlets caused lower percentages of total root colonization and intraradical spores/vesicles	Sosa-Rodriguez et al., 2014

Table 3 – Fungal pathogens known to cause root disease on *Hevea brasiliensis*.

Fungal species	Disease symptoms	References
<i>Rigidoporus microporus</i> (Fr.) Overeem	White root rot	Petch, 1905 as <i>Fomes semitostus</i>
<i>Phellinus noxius</i> (Corner) G. H. Cunn.	Brown root rot	Murray, 1938
<i>Ganoderma pseudoferreum</i> (Wakef.) Over. and Steinm.	Red root rot	Petch, 1921 as <i>Fomes pseudoferreum</i>
<i>Ganoderma lucidum</i> (Leys. ex Fr.) Karst.	Red root disease	Bryce, 1921
<i>Macrophomina phaseolina</i> (Tassi) Goid.	Macrophomina root disease	Small, 1927 as <i>Rhizoctonia bataticola</i>
<i>Phellinus lamaoensis</i> (Murr.) Heim	Brown root disease	Petch, 1905 as <i>Hymenochaete</i> sp.
<i>Poria hypohrunnea</i> Petch.	Poria root rot	Petch, 1921
<i>Rosellinia bunodes</i> (Berk. & Br.) Sacc.	Rosellinia root disease	Park, 1937
<i>Sphaerostilbe repens</i> Berk. & Br.	Sphaerostilbe root disease	Petch, 1907
<i>Ustulina deusta</i> (hoffm. ex Fr.) Lind	Ustulina root rot	Petch, 1921, as <i>Ustulina zonata</i>
<i>Xylaria thwaitesii</i> Cooke	Black root disease	Petch, 1923

differences in the growth responses of the inoculated seedlings and the control plants. Whereas a number of other studies have shown improved seedling growth resulting from AMF inoculation, which was attributed to the improved nutrition of these seedlings (Ikram et al., 1992, 1993; Schwob et al., 1998; Kanyasone, 2009).

A number of studies have indicated that the development of the AMF symbiosis on the roots of *H. brasiliensis* is very slow (Schwob et al., 1998, 2000; Sosa-Rodriguez et al., 2013b). It has been suggested that the delay of root colonization by AMF might be due to defence responses in the roots of the rubber trees, such as the production of antifungal enzymes and inhibitory or antifungal compounds (Schwob et al., 2000; Sosa-Rodriguez et al., 2013a). Schwob et al. (2000) proposed that the roots of rubber trees might release enzymes such as cinnamyl alcohol dehydrogenase and cell wall → bound peroxidases to defend against AMF in the early stages of colonization. The exudation of antifungal compounds such as hevein from *Hevea* roots inhibits the growth of fungal pathogens, and this may account for the delayed root colonization by AMF species (Van Parijs et al., 1991). This was confirmed by Sosa-Rodriguez et al. (2013a), who reported that hevein-producing plants, such as *H. brasiliensis* and *Urtica dioica*, had lower AM root colonization rates than the control plants in the study.

Fungal pathogens

The greater biodiversity found within tropical regions is impacted by the larger number of pathogen species (Ploetz, 2007). Tropical perennial crops, such as rubber plantations, are commonly subject to a large number of diseases (Ploetz, 2007). Due to their long-term growth, and often more than one generation of rubber trees within a plantation, there is build up in the amount of pathogen inoculum within the plantations, leading to the development of disease epidemics (Ploetz, 2007). Further compounding this, the perennial crop systems continuously remove nutrients from the soils, resulting in a decline of soil fertility (McMahon, 2012). Soil nutrient deficiencies are known to increase a plants' susceptibility to infection (McMahon, 2012).

Rubber trees are subject to a wide variety of fungal pathogens (Nandris et al., 1987). Fungal root diseases cause severe losses in rubber plantations through damaged roots, disrupting the absorption of water and nutrients from the soil.

Furthermore, fungal root diseases are usually only apparent once infection has spread to a point where the root material is dead or past the point where effective treatment is possible (Guyot and Flori, 2002). There are numerous fungal pathogens known to infect rubber tree roots (Table 3). The three most important fungal root diseases are white root rot (*Rigidoporus microporus* (Fr.) Overeem), brown root rot (*Phellinus noxius* (Corner) G. H. Cunn.), and red root rot (*Ganoderma pseudoferreum* (Wakef.) Over. and Steinm.) (Jayasinghe, 2001; Ogbebor et al., 2010). *R. microporus* (synonym *R. lignosus* (Kl.) Imazeki) is, economically, the most important disease in rubber trees due to the fact that it causes a serious loss of rubber yield worldwide (Jayasinghe, 2001; Omorusi, 2012). *P. noxius* and *G. pseudoferreum* have a lower impact on the economics of rubber plantations as they are generally slow growing and have a low impact on tree growth and latex production (Jayasinghe, 2001). Often the symptoms of these two diseases are only seen years after infection has taken place.

R. microporus is known to infect rubber trees throughout the tropics, however it is one of the major diseases impacting rubber plantations in South-east Asia (Hashim and Malik, 2006; Omorusi, 2012). *R. microporus* produces abundant white mycelium, and flattened rhizomorphs 1–2 mm thick, which inhabit the soil and attach themselves to the root surface. The infection of healthy trees occurs by contact with disease sources, such as infected roots and woody debris. After contact has been made, the rhizomorphs can expand through the soil and infect surrounding healthy trees (Nandris et al., 1987). The infection process begins when the mycelium penetrates the root system and colonizes cell tissue (Omorusi, 2012). This pathogen degrades cell wall structures by producing several extracellular enzymes, a process which is strictly controlled by conditions of partial anoxia in soil (Nandris et al., 1987). In the early stages of root penetration, cellulolytic enzymes from fungi play an important role in utilizing carbohydrates. The degradation of lignin and hemicellulose may begin at the same time as with cellulose, or later. Enzymes such as laccase play an important role in lignin degradation and the facilitation of host cell penetration (Geiger et al., 1986; Nicole and Benhamou, 1991). Young trees (during the first 12 m after planting) are more susceptible to *R. microporus* than mature trees, where root lignification is more advanced (Nicole and Benhamou, 1991).

Damaged roots are covered by an abundance of white mycelium, initially brownish and later chalky whitish, hence

the common name of white root rot (Omo-ikerodah et al., 2012). In the late stages of infection, the fungi produce a brownish-orange basidiocarp, with a bright yellow margin when fresh, while the lower surface becomes reddish-brown around the base of the trunk (Omorusi, 2012). At this stage of infection, leaves of the rubber tree begin to turn yellow. Finally, the disease destroys the canopy and root system, killing the tree, which will eventually fall over (Omo-ikerodah et al., 2012).

P. noxius is also widespread in tropical regions, including India, Indonesia, Malaysia, Sri Lanka, Thailand, Vietnam, China, the Ivory Coast and Nigeria (Jayasinghe, 2001). Although the fungus causes a severe loss of yield in rubber plantations, these losses remain less than those incurred by *R. microporus* (Nandris et al., 1987; Farid et al., 2009). Unlike *R. microporus*, *P. noxius* produces rusty brown mycelium that attaches to soil particles on the root surface (Nicole et al., 1995; Farid et al., 2009). In the later stages of infection, *P. noxius* produces bracket sporocarps, which are uniformly dark brown, but rarely occur in plantation areas (Nicole et al., 1995; Jayasinghe, 2001). The infection mechanism of *P. noxius* develops in a manner very similar to that of *R. microporus* in terms of the production of extracellular sheaths and the type of extracellular enzymes used by the fungus (Nicole et al., 1995). On the other hand, the mycelial growth rate of *P. noxius* on the root surface of *Hevea* sp. is slower than *R. microporus* (Nandris et al., 1987). The result is that *P. noxius* seldom causes the death of plantation trees (Jayasinghe, 2001). Furthermore, Farid et al. (2009) revealed that, compared to other host trees, *H. brasiliensis* is more susceptible to *R. microporus* than to *P. noxius*.

G. pseudoferreum is widely distributed in China, Indonesia, Malaysia and Nigeria (Rao, 1975; Ogbebor et al., 2010; 2013a). *G. pseudoferreum* produces red-brown mycelium and fruiting bodies, of which the upper surface is a shiny dark red, with a narrow white margin, whereas the lower surface is ash-light-yellow with a prominent creamy-white fringe (Ogbebor et al., 2013a). The symptoms of infection are similar to those of other root rot diseases, nevertheless this is a slow growing fungus, mostly causing infection in mature rubber trees (Rao, 1975).

The control and treatment of root disease require an approach that integrates both cultural and chemical methods. Normally, all infected dead plant materials are removed, burnt and fungicides are applied to the soils surrounding the infected area, to prevent the spread of the fungus to surrounding trees (Omorusi, 2012). However, these methods are expensive (Guyot and Flori, 2002; Jayasuriya and Thennakoon, 2007) and pose a risk to the environment (Jayasuriya and Thennakoon, 2007). Consequently, alternative control mechanisms are being sought, such as the use of antagonistic microorganisms. Many studies have screened the soil microbiota in rubber plantations and have isolated antimicrobial compounds that work against root rot fungi (Zakaria, 1989; Jacob et al., 1991; Wijesundera et al., 1991; Jayasuriya and Deacon, 1995; Jayasuriya et al., 1996; Jayasuriya and Thennakoon, 2007; Ikediugwu and Monday, 2012). Among these, *Trichoderma* spp. is well-known for its use as a biological control agent for various pathogens (Ikediugwu and Monday, 2012). In Sri Lanka, all *Trichoderma* species isolated from the soils in rubber

plantations were found to be effective inhibitors of the growth of *R. microporus*, an effect attributed by their production of degrading enzymes such as glucanase and chitinase (Wijesundera et al., 1991). Jacob et al. (1991) reported that rubber seedlings grown in soils containing *Trichoderma viride* and *T. hamatum* showed improved growth, when infected by *P. noxius*, as compared to the rubber seedlings grown without these *Trichoderma* species. Similarly, in a study conducted by Zakaria (1989), the biological control application of *Trichoderma harzianum*, combined with the use of fungicides and organic matter, proved to be most effective in treating *Ganoderma* root disease.

Given that symptoms are only recognizable later on in the development of these fungal diseases, most diseases are only detected once it is too late for effective treatment, at which point the mycelium has already progressed through the soil and infected other trees. For this reason, the early detection of root fungal disease is essential. Current practice involves digging a trench in the soil around the tree base to observe the presence of rhizomorphs and then identification of the pathogen (Ogbebor et al., 2013b). Nevertheless, this method can be difficult to apply in large field plantations. Louanchi et al. (1996) developed an early warning assay, namely the double antibody sandwich-enzyme linked immunosorbent assay (DAS-ELISA), which can be used to detect *R. microporus* in rubber plantations. Furthermore, rubber material, which has been mulched and soaked with water and sugar solution, has been shown to be effective for the identification and early detection of *R. microporus* (Ogbebor et al., 2013b). Dried seed pods from the rubber tree, displayed the highest percentage colonization of *R. microporus* 5 d after incubation. This method is cost effective and easy to implement in the field (Ogbebor et al., 2013b).

Given that there remains no effective method to control and treat fungal root diseases in rubber trees, and no resistant clones have been bred against these diseases, it is important to understand how these diseases spread and where they originated from (Oghenekaro et al., 2014). In Asia, a few studies have been conducted on the biology and molecular phylogeny of root disease fungi (Liyanaage et al., 1977; Kaewchai et al., 2009, 2010). Oghenekaro et al. (2014) revealed using phylogenetic analyses, that *R. microporus* isolates from Africa, Asia and South/Central America formed three distinctive clades and isolates collected from rubber trees were found to be closely related to those found on other hosts. The pathogen *R. microporus* is thought to have jumped host to *H. brasiliensis* from native trees. Therefore, to understand the characteristics of root fungal diseases and improve a sustainable management practice, it is important to characterize fungal root pathogens using population genetics and phylogeographic studies (Oghenekaro et al., 2014).

3. Diversity and community composition of soil fungi in rubber plantations

Investigations of soil fungal diversity and community composition in rubber plantations have rarely been reported, although a few key studies have highlighted the impacts of rubber plantations on these communities. Puangsombat

et al., (2010) reported that the number of fungal species and the fungal diversity index was lowest in rubber plantations, when compared to other land uses, such as secondary dry evergreen forest, *Dalbergia* plantations, grasslands and pineapple fields. Puangsombat *et al.* (2010) suggested this might be due to biannual herbicide application in rubber plantations. Peries *et al.* (1979) found that the distribution and abundance of fungi in rubber plantations were distinct among sites with different soil pH. Peries *et al.* (1979) reported that species of *Penicillium* were more abundant in acid soils, than in neutral soils, and *Fusarium* species were more frequently found in neutral soils than acid soils. This study suggested that the composition of soil fungi in rubber plantations might be more strongly influenced by soil edaphic factors than the rubber trees (Peries *et al.*, 1979). Abundant populations of filamentous yeasts were also detected in soil found in rubber plantations, which might be associated with high carbohydrate leachates from the rubber tree roots (Deka *et al.* 1998). However, these studies were based on dilution plating techniques, which limits the results of this study to only those fungi which can be cultured by this method.

Phospholipid fatty acid has been used to study soil microbial communities in rubber plantations (Guo *et al.*, 2013, 2015; Krashevskaya *et al.*, 2015). The relative abundance of fungi was significantly higher in rubber plantations than in grass soils (Guo *et al.*, 2013) and in rainforests (Krashevskaya *et al.*, 2015). This might be associated with the application of fertilizer in rubber plantations, which can enhance the size of the fungal population (Kerekes *et al.*, 2013, Krashevskaya *et al.*, 2014). Krashevskaya *et al.* (2015) showed that saprotrophic fungi and AMF were not significantly affected by the conversion of rainforest to rubber plantations, whereas some groups of bacteria were significantly affected by this conversion. However, assessing soil microbial communities using PLFA techniques limits the assessment to that of species composition and biomass, but fails to elucidate community functions and responses to external factors.

Thus, in order to further our understanding of soil fungal communities in rubber plantations, in depth studies using a variety of molecular based techniques are required, yet few studies have used these approaches in rubber plantations. For example, Schneider *et al.*, (2015) used molecular techniques to investigate the impacts of conversion from rain forest to oil palm and rubber plantations, on soil prokaryotic communities. Unfortunately this study did not include soil fungi within the scope of the work, and an in depth understanding of how soil fungal communities respond to the conversion of rainforests to rubber plantations continues to elude us.

4. Management practices affecting soil fungal communities

Rubber plantations are grown in a number of areas worldwide, with varying biotic and abiotic factors throughout these regions. However, most rubber plantations are typically of poorer soil quality and often have a lower soil fungal diversity than surrounding natural forests (Osemwegie *et al.*, 2010; Zhang *et al.*, 2013). Various management practices within

rubber plantations can affect the soil fungal communities. Thus, a broader understanding of these practices and the related effects are necessary to better manage plantation soils. Soil fungal communities can also be used as an indication of soil quality and as a measure of the various impacts of management practices in rubber plantations (Jangid *et al.*, 2011; Lin *et al.*, 2012).

The application of herbicides and fungicides in agricultural soils can have a negative impact on soil fungal communities (Kunishi and Bandel, 1991; Sebiomo *et al.*, 2013). This can lead to deleterious effects in the nutrient cycling processes and also reduce the abundance and diversity of symbiotic fungi. It has been shown that soil fungal populations in a variety of land use types, i.e., turfgrass, forest, and agricultural soils, were negatively affected by the application of the fungicide chlorothalonil (Sigler and Turco, 2002). Ratcliff *et al.* (2006) however, demonstrated that there were few changes in fungal communities of forest soils when the herbicide glyphosate was applied. Consequently, further clarification is required to determine what overall effects different chemical herbicides and fungicides have on the soil fungal communities in rubber plantations.

In addition to herbicides and fungicides, chemical fertilization can have a negative effect on the AMF population. The high and intensive inputs of inorganic fertilizers that are regularly applied in rubber plantations have been shown to reduce the population of AMF. According to Wang *et al.* (2009), high levels of N, P, and K, resultant of fertilization schemes, decrease the growth, colonization, and reproduction of AMF. Deka *et al.*, (1998) revealed that applied fertilizer in rubber plantations causes a negative effect on the AMF populations, as indicated by lower percentage of AMF root infection. Therefore, alternative, more sustainable mechanisms of adding nutrients to these systems, such as the planting of leguminous cover crops between the rows of rubber trees, should be investigated and implemented (Verheye, 2010).

There are a number of species with which rubber plantations can be intercropped, depending on the age of the rubber plantations. Younger rubber plantations are often intercropped with banana, pineapple, cassava, tea, and sugarcane, nevertheless, once the canopy closes, shade tolerant species are required (Rodrigo *et al.*, 2001; Pinto *et al.*, 2005; Zhang *et al.*, 2007). Intercropping has been shown to improve soil quality and biodiversity within monoculture systems, such as rubber plantations (Rodrigo *et al.*, 2001; Pinto *et al.*, 2005; Zhang *et al.*, 2007). Tree-based intercropping systems have also been shown to be successful in improving the quality of soil in rubber plantations, enhancing the soil C content and biodiversity of the soils (Thevathasan and Gordon, 2004; Lacombe *et al.*, 2009). Monocropping systems are known to have negative effects on the abundance and diversity of soil fungi, thus the inclusion of trees into monoculture rubber systems will ultimately lead to an improvement in the diversity and activity of fungal, and more specifically, mycorrhizal species (Bainard *et al.*, 2011).

5. Conclusion and perspectives

The number of studies investigating soil fungi in rubber plantations is still limited, in spite of the essential role that fungi

play within an ecosystem. Many of these studies have extrapolated the findings from other monoculture systems and imposed these results into rubber systems, thus emphasizing the need for more research on this topic.

In order to fully understand the impact that these rubber-farming systems are having on the related fungal communities, we need to first investigate the true nature and diversity of the fungal communities in question. There is a need for further research investigating the composition and dynamics of these soil fungi, on both a spatial and temporal scale. Questions addressing topics related to plantation management, chemical use, and the role of mixed planting systems are likely to provide insights into how we can improve the diversity of beneficial soil fungi and hopefully diminish the negative impacts of pathogenic fungi, as well as alleviating the effects of monoculture systems.

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