



REVIEW PAPER

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Symbiotic fungal biodiversity, structure, role and benefits to their host plants-discovering microbes with potential agricultural significance: A literature probe

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Abstract

We live in an enclosed system, the planet Earth, where every element is considered important to all other elements within it. The biosphere which constitutes the living and the nonliving things of all the Earth's ecosystems represent a highly interconnected system. The interconnectedness of every component is indicative that all biotic and abiotic constituents within the system are important and thus necessary for its resilience, sustainability, and perpetual survival. Long before human emerged as a dominant species in the planet, the Earth is considered naturally resilient and sustainable. The concepts of ecosystem biodiversity and environmental conservation started to become a necessity when anthropogenic interventions began to dominate the planet. Threats brought by industrialization, urbanization and technology advancements also began to emerge. The underlying theories in ecosystem biodiversity and environmental conservation may be put into practice to minimize the far-reaching effects of human-induced environmental degradation. In doing so, a clear understanding of the interconnections and associations between and among the living components as well as the non-living components of the biosphere is indispensable. To elucidate the obligatory interactions by all the biotic constituents of the biosphere, we should not only look into the key roles of plants, animals and other macro-organisms. More importantly, the compulsory roles of microorganisms should also be recognized. Fungi, bacteria and viruses are undoubtedly essential to plants and animals. Thus, associations among these key macro- and micro- players, negative or positive, must be taken into account. On top of these biotic relations, the impact of the abiotic components and how organisms subsequently affect these nonliving factors should not and should never be taken out of the picture.

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Introduction

Confining our focus to one major biotic interaction in the biosphere, we acknowledge fungi to play a pivotal role. According to Peay *et al.* (2008), fungi are a major component of all ecosystems globally. They are best known for their significant role as decomposers. Through the process of decomposition and as part of the carbon cycle, fungi produce wide array of enzymes to degrade complex organic materials into their simple forms so that other organisms in the ecosystem would be able to utilize it (Beare *et al.*, 1992). Additionally, fungi also have a major role in food chains and food webs. Fungal mycelia and fungal bodies may serve as a carbon and food source for other micro- and macro- organisms (Wardle, 2002). Other fungi serve as predators (Thorn and Barron, 1984). Fungi also shape community dynamics of plants through range of interactions such as serving as important plant pathogens, commensals, parasites or symbionts which directly and indirectly maintains plant species diversity (Gilbert, 2002).

Despite their known significance, there are many challenges in studying fungal communities and fungal associations. One challenge is the large spatial and temporal variability in fungal communities. Likewise, their high species richness also poses a challenge because it makes it difficult to observe taxa frequently enough to draw substantial conclusions. Moreover, the ubiquitous pattern of few dominants and many rare species has been steadily observed across different fungal lifestyles in different ecosystems (Horton and Bruns, 2001; Ferrer and Gilbert, 2003; Arnold *et al.*, 2007). Thus, in determining their actual diversity, the use of molecular tools coupled with the classic morphological assessment would certainly help in quantifying the diverse nature of fungi.

The diverse nature of fungal lifestyle and their spatio-temporal communities denote hardship not only in determining their diversity but also an implication of their complex but crucial relationship with plants and other organisms. Dhankhar *et al.* (2012) and Khalmuratova *et al.* (2015) suggested that all higher plants are hosts to one or more symbiotic

microorganisms. Unfortunately, the relationship between the microorganisms and their hosts are the least studied biochemical relationships (Sultan *et al.*, 2011). Examples of symbiotic microorganisms are the root symbiotic fungi that reside inside a healthy plant tissue without any perceptible negative physiological effect to its host (Wilson, 1995; Khalmuratova *et al.*, 2015). The positive symbiotic relationship and survival of the host and the fungal symbionts are established through various critical and wide array of metabolic processes between and among them. In relation to this, previous studies have also suggested that symbiotic fungi can be an excellent source of novel bioactive compounds such as alkaloid, benzopyranones, chinones, flavanoids, phenols, steroids, tetralones, and xanthenes (Wilson, 1995; Zeng *et al.*, 2011; Dhankhar *et al.*, 2012; Yadav *et al.*, 2014) with immense potential for agricultural, medicinal, and industrial capitalization (Tan and Zou, 2001). The ability of fungi to produce these compounds also provide us insights on their radical scavenging abilities.

In addition to symbiotic fungi's antioxidant potentials, they also play an important role in plants' resistance to diseases, to environmental stresses as well as plant growth promotion (Evans, 2008; Selim *et al.*, 2012). These symbiotic fungi produce variety of essential plant hormones and growth regulators such as gibberellins (GAs), and auxins (IAA) (Zhang *et al.*, 1999; Hermosa *et al.*, 2012). Fungi generally influence plant fitness by improving nutrient uptake and increasing plant resistance to drought (Smith and Read 1997; Read, 1999; Fernandez and Fontenla, 2010). It is therefore generally expected that the symbiotic association of epiphytic ferns to fungi may be an important adaptation for these plants. (Benzing, 1990; Lesica and Antibus, 1990; Janos, 1993; Rains *et al.*, 2003). However, little is known about symbiotic associations of fungi in these epiphytic ferns (Bermudes and Benzing, 1989; Allen *et al.*, 1993; Janos, 1993; Michelsen, 1993).

Finally, there were earlier reports about symbiotic fungi reducing insect attacks to their respective host

plants (Webber 1981; Funk *et al.*, 1983; Lasota *et al.*, 1983; Gaynor and Hunt, 1983; Clay *et al.*, 1985; Hardy *et al.*, 1985; Latch *et al.*, 1985).

Discussion

Ecological Significance and Biodiversity of Ferns

The lycophyte and fern clade include all plants that are spore-bearing or "seed-free". The members of this clade are lumped together historically under pteridophytes and "fern and fern allies" (Smith *et al.*, 2006). A revised classification for extant ferns by Smith *et al.* (2006) recognized four monophyletic classes, 11 monophyletic orders and 37 families, 32 of which are strongly supported as monophyletic. In relation to this, Delos Angeles and Buot (2012) mentioned that around 1100 species under 144 genera and 39 families of Pteridophytes have been reported in the Philippines which recognize 4 classes, 11 orders and 37 families of fern.

These ferns emerged from the aquatic environment and later became dominant in the tropical lowland and wetland forests and have been important component of terrestrial vegetation since the Late Devonian (Odland *et al.*, 1995; Vogel *et al.*, 1999; Lehmann *et al.*, 2002; DiMichele and Phillips, 2002). Presently, majority of fern species are often found in tropical regions (Poulsen and Nielsen, 1995). But it is also noteworthy to say that ferns can also be found in several extreme environments and disturbances which are indicative of their opportunistic and colonizing lifestyle consistent of their scrambling ground cover, tree habit and liana-type body plan (DiMichele and Phillips, 2002).

Ferns have different ecological types suggestive of their diverse morphological characteristics and growth forms. They can be minute epiphytes or can grow as large trees. There are climbing ferns with long internodes which also have branched, thick and creeping rhizome. In contrast, the long creeping branching patterns together with having fine to filiform rhizome are the general attributes of epiphytic ferns. Their reduced root system could be relevant to their hygrophilous epiphytic strategy

(Lehmann *et al.*, 2002; Dubuisson *et al.*, 2003). With such aforementioned characteristics, ferns can be used address important concerns on local or global biodiversity and environmental conservation initiatives (Pearson, 1995).

Ecology and physiological adaptations of vascular epiphytes

Approximately 20,000 to 25,000 species of vascular epiphytes have been recorded where majority is found in the tropics (Benzing, 1990; Zotz and Hietz, 2001). In its simplest definition, epiphytes are those plants that grow on other plants. They live most of their lives attached to other plants without soil contact. They absorb nutrients and water from their environment and they are non-parasitic (Benzing, 1990; Silvera and Lasso, 2016). Epiphytes are ecologically important because they support large amount of animal life and they also contribute to the hydrology and nutrient cycling in an ecosystem (Stuntz *et al.*, 2002). They may be found on forest understorey or on the periphery of tree crowns. Such variations in growing sites indicate complexity due to environmental constraints experienced by the plants as they dwell in their respective and supposedly stressful growing sites or 'epiphytic habitat' (Benzing, 2000; Zotz and Andrade, 2001).

Water deficiency is one of the most important abiotic stresses in an epiphytic habitat (Zotz and Heitz, 2001). Epiphytes typify various adaptive mechanisms to cope with water stress. Poikilohydry, leaf, stem and root succulence (Ng and Hew, 2000), 'shootlessness' (Benzing *et al.*, 1983), drought-deciduousness (Benzing, 1990), early stomatal closure, low water loss in cuticle, osmotic adjustment, adaptive leaf scales and cell wall (Hietz and Briones, 1998) and the crassulacean acid metabolism (CAM) are just few of their various ecophysiological adaptations that appear to contribute to the successful life style of epiphytes in drought and light-stressed environment without any physiological damage (Hietz and Briones, 1998).

Majority of all species over the globe that utilize CAM are epiphytic (Winter and Smith, 1996). Epiphytic

plants prefer CAM because it is a water-saving mode of photosynthesis as they take up CO₂ from the atmosphere at night improving their capacity to capture carbon in a water-limited environment (Ting, 1985; Winter and Smith 1996). In line with this, reports showed that there is a relative increase in CAM taxa from wetter to drier environments. Likewise, an increase of the proportion of CAM taxa from shaded to light-exposed areas in a forest ecosystem (Griffiths and Smith, 1983; Zotz and Ziegler, 1997) indicative of the importance of this water-conserving pathway in an epiphytic habitat.

Epiphytes also experience lesser nutrient uptake when compared to ground rooted plants. Since they are not in contact with the soil, epiphytes lack access to important nutrients they can get from it (Benzing 1990). Epiphytes are commonly subjected to phosphorus and nitrogen limited environment which may be due to constant input of water and excessive rain that may wash out nutrients from the plants' surfaces (Zotz and Richter, 2006; Zotz and Asshoff, 2010; Wanek and Zotz, 2011;). To cope with this ecophysiological nutrient concerns, different epiphytic groups use diverse nutrient uptake mechanisms (Silvera and Lasso, 2016). Epiphytes may receive nutrient inputs from the atmosphere in the form of intercepted rain dust and mist. Epiphytes may also receive nutrients unleashed from ground-rooted plants through decomposition or leaching. Other means of getting nutrients from the epiphytic habitat is through dinitrogen fixation and from the remains of animals (Benzing, 1990). The problematic nature of nutrient scavenging in epiphytes is supported by various adaptive morphological structures to promote uptake of water. Some of these morphological features include phytotelmata, orchid velamen radicum, bromeliad trichomes and litter-trapping leaf arrangement (Stutz *et al.*, 2001).

Aside from unique morphological characteristics, epiphytes are also known to be symbiotically associated with other micro- and macro- organisms adding to their adaptive mechanisms to support them in their stressful habitat. Reports have also shown

that epiphytes are associated with animals, majority by which are ants. They live in cavities shaped by some plant organs. In return, the colonies or nests by these ants provide the plants a "rooting substrate" (Davidson and Epstein, 1989; Stutz *et al.*, 2001). There were also many reports showing relationship of epiphytes to fungi. Mycorrhizae were recorded to be in symbiotic relationship with epiphytes such as orchids and bromeliads suggesting their relative importance in the nutrient acquisition of epiphytes (Gemma and Koske, 1995; Lesica and Antibus, 1990; Richardson and Currah, 1995).

Epiphytes are considered as bioindicators of climate change due to their growth sensitivity to microclimate changes since they lack access to permanent water source and nutrients. In addition, they are also considered as important component of ecosystem and watersheds due to their capacity to intercept cloud and for water which eventually increases net water input in the area. Thus, epiphyte conservation program management and implementation highly depends upon the understanding of the physiological responses of epiphytes to environmental change (Silvera and Lasso, 2016).

Epiphytism in Ferns: Ecology and Physiological Adaptations

Twenty nine percent (29%) of fern species are epiphytes making them the second group of vascular plants when it comes to epiphyte diversity (Kress, 1986). As previously mentioned, epiphytic habitat is restrictive due to environmental stresses such as water scarcity, light intensity and lack of nutrients. In response, myriads of unique physiological operations can be exhibited by different epiphytic fern species in order to cope with these critical environmental issues. The *Pleopeltis polypodioides*, also known as "resurrection fern" is poikilohydrous or can revive after a long period of desiccation (Dubuisson *et al.*, 2009).

Dubuisson *et al.* (2009) elaborately discussed the three groups of epiphytic ferns categorized according to their tolerance level to drought: hygrophytes,

mesophytes, and xerophytes (Benzing, 1990). The first group, hygrophytes, are niched in tropical rainforest where rain is profuse because they are drought intolerant. They directly absorb rainwater or flowing water on branches and their dehydration is limited by high moisture. The fern family Hymenophyllaceae is a typical example. Mesophytic ferns are also found in places where water is relatively available. Their adaptations include creating a soil suspension to accumulate humus and entrap moisture and nutrients. The fern *Asplenium nidus* (Aspleniaceae) is of this kind. Similar growth can also be found in species belonging to family Polypodiaceae. However, there are two specialized species of Polypodiaceae that respond to limited access of nutrient and water through a mutualistic relationship with ants. The *Drynaria* species use specialized humus-collecting blades and some *Aglaomorpha* species have basally enlarged fronds (Janssen and Schneider, 2005). The *Platyserium* species possess agglomerated sterile fronds forming a nest to capture flowing water. The *Microgramma* species bear specialized culinary urn-like structures that absorb captured water. Species in the genus *Lecanopteris* form cavities in shoots to house ants and help in water and nutrient access (Gay, 1993). On the other hand, xerophytic-epiphytic ferns display adaptive traits to endure drought. Epiphytic ferns that are considered xerophytes have adaptive traits like sclerophylly for limiting water loss, and succulence for storing water and nutrients. Moreover, shedding of leaves when dry, and possessing stout blades covered by a thick cuticle are other xeromorphic attributes of fern epiphytes. A good example of epiphytic fern with xeromorphic feature is the bracken fern (*Pteridium aquilinum*) and some members of the Davalliaceae-Polypodiaceae clade (Dubuisson *et al.*, 2009).

Fungal structure, metabolism and ecology

All fungi are chemoheterotrophic. They synthesize organic compounds from organic sources in their environment particularly for their growth and development as well as for energy consumption. Fungi obtain nutrients through the process of

absorption. During absorption, they use extracellular enzymes to facilitate breaking down of large molecules into smaller ones. In addition, fungi are restricted in relatively moist ecosystems to sustain their active development (Tariq, 2006).

Most fungi grow as tubular filaments (hyphae) which can grow as interwoven masses (mycelium). Fungi have chitin to strengthen the walls of hyphae. In terms of dispersion, fungi generally release spores that are usually windblown. Being heterotrophic, some fungi live as saprophytes, getting their nourishment from the environment. These kinds of fungi are essential in the decomposition and recycling of nutrients in the environment. On the other hand, some fungi live in a mutually beneficial symbiotic association with other organisms, often are plants (Kimball, 1994).

Symbiotic fungi's ecology and functional roles

Fungal symbionts have fervent effects on plant ecology, fitness and evolution as they shape plant community dynamics (Clay and Holah, 1999; Brundrett, 2006). Likewise, they manifest great impacts on the associated organisms (Omacini *et al.*, 2001). One basic characteristic of fungal symbionts is being found entirely within the external or internal plant tissues; either in leaves, roots and stems (Stone *et al.*, 2004; Rodriguez *et al.*, 2008).

Tian *et al.* (2014) mentioned that due to the fact that they steadily interact with their host, it is obvious that they have ensuing influence on each other's metabolic processes and by-products. In their experiment on fungal symbionts, they (Tian *et al.*, 2014) observed that the fungus specifically metabolized glycosylated flavonoids of the plant leading to the production of aglycone moieties. These metabolically produced flavonoids appear to have beneficial effects on the hyphal growth of the symbiont which indicates their valuable impact as signaling molecules in the plant-symbiont mutualism.

Functional roles of symbiotic fungi in insect-pests control

The use of natural and biological pest control initiatives has gained much attention as a way to

reduce the use of chemicals in agriculture (Alves, 1998; Melo and Azevedo, 1998; Azevedo *et al.*, 2000). Agriculture in itself is antiecolological. The use of pesticides, insecticides and fungicides which aim to control pests and pathogens also eliminates important insect species crucial in the biodiversity of the surrounding environment. In the last 20 years, symbiotic fungi have received considerable attention due to their uncovered capacity to protect hosts against insect-pests and pathogens. It was also found that they have other important attributes such as helping plants adapt to stressful environmental conditions, altering plants' physiological properties, and produce phytohormones with biotechnological interest (Azevedo *et al.*, 2000).

Early reports by Webber (1981) found out that in the presence of symbiotic microorganisms, insect attacks have been reduced in their respective hosts. On his (Webber, 1981) attempt to report an example of plant protection by symbiotic fungus, he found out that the fungal symbiont *Phomopsis oblonga* protected elm trees against the beetle *Physocnemum brevilineum*. The repellent effect observed was associated to the toxic compounds produced by the fungi. Other early observations include: the protection of perennial ryegrass *Lolium perenne* L. against the sod webworm (Funk *et al.*, 1983), stem weevil, *Listronotus bonariensis* (Gaynor and Hunt, 1983), and *Spodoptera frugiperda* insect pest affected by symbiotic fungi like *Balansia cyperi* (Clay *et al.*, 1985; Hardy *et al.*, 1985); protection of white spruce *Picea glauca* against Homoptera *Adelges abietis* when galls are infected with the symbiotic fungus *Cladosporium sphaerosperium* (Lasota *et al.*, 1983); protection of *Lolium* with two symbiotic fungi, *Acremonium lolii* and a member of the genus *Gliocadium* (Latch *et al.*, 1985); and protection of *Acremonium* on the genera *Lolium* and *Festuca* against aphids (Latch *et al.*, 1985). These earlier reports show the diversity of control mechanisms exhibited by fungal symbionts.

The protection exemplified by fungal symbionts is more complex than what we probably expect. Symbiotic fungi synthesize alkaloids during plant infection reducing the survival of *S. frugiperda* in

Graminae and Cyperaceae (Cheplick and Clay, 1988). In another study by Ju *et al.* (1998), it was found that the extracts of *Poa ampla* associated with *Neotyphodium typhnium* were effective against mosquito larvae but not the extracts obtained direct from the fungi alone. This indicates that the host protection process displayed by symbiotic fungi against insects seems to be general where there has to be a symbiotic interaction for the protection to take effect.

The capacity of symbiotic fungus to repel insects, reduce growth and development and even increase pest death rate was correlated with toxin production (Azevedo *et al.*, 2000). Fungal symbionts' mode of action is basically to render the plants unpalatable to several types of pests like aphids, grasshoppers, beetles, and others (Carroll, 1988; Clay, 1988). For example, Miller (1986) showed that the protection of Canadian fir against spruce budworms resulted from the production of toxic secondary metabolites by the symbiotic fungi. It was also established by Prestidge and Gallagher (1988) the production of a strong toxin, lolitrem B by the fungus *A. lolii* in *Lolium perenne* which significantly reduced insect attacks. It was indeed accepted that the production of toxin by the symbiotic fungi was a plausible explanation for the interactions resulting in natural insect control (Azevedo *et al.*, 2000).

Functional roles of symbiotic fungi in growth-limiting and drought stress

There were systematic speculations that fungal-phototrophic organism symbioses allowed terrestrial biosystems colonization by primitive plants. This mutualistic relationship helped plants acclimate to new environmental stresses such as desiccation, increased solar radiation exposure, and extreme temperature fluctuations (Selosse and Le Tacon, 1998). There has been many studies showing that fungal symbionts can enhance drought, salt, and soil temperature tolerance of their host plants (Cheplick, 2004; Rudgers and Swafford, 2009; Bayat and Mirlohi, 2009; Hubbard *et al.*, 2012; Hubbard *et al.*, 2014).

With increasing tendencies of climate change affecting agriculture, knowledge and practical applications about fungal symbionts conferred drought tolerance has become significantly important. By affecting plant morphology and growth, as well as biochemical and physiological responses to stress, symbiotic fungi can promote channels of drought avoidance, drought tolerance and drought recovery in their host plants (Malinowski and Belesky, 2000).

Environmental stresses such as drought affect majority if not all of a plant's life stages. Seed germination for instance, is a critical life stage for plants survival. If inflicted by drought, it would certainly affect not only the percentage of seeds' survival percentage but also the quality of the surviving seedlings. In the study conducted by Hubbard *et al.* (2012), they hypothesized that fungal symbionts would improve wheat seed germination under heat and drought stress. The fungal symbionts tested dramatically increased the percent of germination and other values such as energy of germination and hydrothermal time. Wheat susceptibility to heat and drought were also diminished, thus indicating that when colonized by the most effective symbiotic fungi, wheat seeds' capacity to tolerate stress will be induced. Hubbard *et al.* (2014) went to support their above results by subjecting the growing wheat to drought tolerance. Similar results were obtained. Hubbard *et al.* (2014) found out that fungal symbionts has the potential to improve wheat adaptation to heat and drought as it gave a positive impact on the growth ecophysiological and reproductive responses of wheat when exposed to heat and drought.

Rudgers and Swafford (2009) also tested the benefits of a fungal symbiont in wild rye under drought stress. They hypothesized that fungal symbiosis with wild rye would promote host tolerance to drought. It was found out that wild rye without fungal symbiosis has 23% less aboveground biomass under drought. Moreover, Bayat and Mirlohi (2009) conferred with the above observations.

Their (Bayat and Mirlohi, 2009) experiment on the effects of symbiotic fungi on tall fescue subjected to drought revealed that fungal symbionts considerably contributes to host grass water stress tolerance in terms of relative water content, cell membrane stability, proline and chlorophyll contents in plant leaves. There were however other studies showing that fungal symbionts were the one benefited in their relationship with their plant hosts. In the study conducted by Cheplick (2004), he ascertained that the relationship between ryegrass and its fungal symbiont primarily benefits the fungus and not the host under many environmental conditions.

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