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The Ecology of Arbuscular Mycorrhizal Fungi

A. Willis [a] , B. F. Rodrigues [b] & P. J. C. Harris [a]
[a] Centre for Agroecology and Food Security, Coventry University, Coventry, United Kingdom
[b] Botany Department, Goa University, Goa, India

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The Ecology of Arbuscular Mycorrhizal Fungi

A. Willis,[1] B. F. Rodrigues,[2] and P. J. C. Harris[1]
[1]*Centre for Agroecology and Food Security, Coventry University, Coventry, United Kingdom*
[2]*Botany Department, Goa University, Goa, India*

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Address correspondence to A. Willis, Centre for Agroecology and Food Security, Coventry University, Priory Street, Coventry CV1 5FB, UK. E-mail: andyewillis@gmail.com

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Arbuscular mycorrhiza is a mutually beneficial biological association between species in the fungal phylum Glomeromycota and higher plants roots. The symbiosis is thought to have afforded green plants the opportunity to invade dry land ca 450 Ma ago and the vast majority of extant terrestrial plants retain this association. Arbuscular mycorrhizal (AM) fungi perform various ecological functions in exchange for host photosynthetic carbon that almost always contribute to the fitness of hosts from an individual to community level. Recent AM fungal research, increasingly delving into the 'Black Box', suggests that species in this phylum may play a key facilitative role in below-ground micro- and meso-organism community dynamics, even more perhaps, that of a bioengineer. The ubiquitous nature of the symbiosis in extant flora and the fact that variations from the AM symbiosis are recent events suggest that Glomeromycota and plant roots coevolved. This review considers aspects of AM fungal ecology emphasizing past and present importance of the phylum in niche to global ecosystem function. Nutrient exchange, evolution, taxonomy, phenology, below-ground microbial interaction, propagule dissemination, invasive plants interactions, the potential role in phytoremediation and some of the factors affecting AM fungal biology are discussed. We conclude that it is essential to include AM association in any study of higher plants in natural environments in order to provide an holistic understanding of ecosystems.

Keywords arbuscular mycorrhiza, Glomeromycota, ecological complexity, plant community driver, soil community facilitator, keystone mutualist

I. INTRODUCTION

Arbuscular mycorrhizal (AM) fungi are ubiquitous root symbionts of more than 90% of vascular plants and over 80% of all extant terrestrial plants (Wang and Qui, 2006). Arbuscular mycorrhiza has been found in the Rhynie Chert, an Early Devonian sedimentary deposit exposed near the village of Rhynie, Aberdeenshire in Scotland, which formed 410 Ma ago (Remy *et al*., 1994). AM fungi are considered to have been indispensable in green plant colonization of terrestial habitats (Helgason and Fitter, 2005). Their primary function is thought to be contribution to plant nutrition, particularly phosphorus (P) (Bolan, 1991), often a limiting resource, and micronutrients (Clark and Zeto, 2000), especially in nutrient depleted hostile environments. There is also evidence of ammonium- and nitrate-nitrogen contribution derived from organic matter (OM) (Leigh *et al*., 2008). Secondary roles of AM fungi include reduction of root invasion by microbial soil-borne plant pathogens (Newsham *et al*., 1995), reduction in plant uptake of phytotoxic heavy metals (Göhre and Paszkowski, 2006), improved host plant water balance in periods of ample water and drought (Augé, 2001) and soil particle aggregation through the cohesive action of a Glomalean water-stable glycoprotein (Rillig and Mummey, 2006). Further effects of AM reported include reduction in insect herbivory by induced plant response (Bennett *et al*., 2009) and variation in that response relative to nitrogen (N) uptake (Gange *et al*., 2005), increase in insect pollination (Gange and Smith, 2005) and percentage increase in F_1 generation seed germination (Srivastava and Mukerji, 1995). AM are also reported to increase the density of insect herbivore parasites in trophic food webs (Hempel *et al*., 2009; Hoffmann *et al*., 2010). All of these functions are performed in exchange for host plant carbon (C). There is evidence to suggest AM fungi may play a significant role in soil N and C cycles (Govindarajulu *et al*., 2005; Jones *et al*., 2009) and make considerable contribution to terrestrial ecosystem C sinks (Wright and Upadhyaya, 1998). In addition to the above functions, AM fungi can also influence, perhaps even organize and structure, plant community patterns (van der Heijden *et al*., 2008) and soil microbiota community populations (Rillig *et al*., 2006; Toljander *et al*., 2007).

II. TAXONOMY

Taxonomy of AM fungi describes 214 species in four orders, 13 families and 19 genera, in the class Glomeromycetes of the phylum Glomeromycota (Muthukumar *et al*., 2009), surprisingly few considering their having been extant for 450 Ma (Pirozynski and Malloch, 1975) or more (Redecker *et al*., 2000). The phylum is represented worldwide in almost all major terrestrial biomes (Treseder and Cross, 2006), in bryophytes (mosses), hepatics, pteridophytes, gymnosperms and angiosperms. Almost all tropical plants are typically AM mycotrophic (Janos, 1987), a phenomenon that may be related to rapid litter decomposition and consequent high ecosystem C turnover (Cornelissen *et al*., 2001). Only the plant families Chenopodiaceae, Polygonaceae, Juncaceae, Cruciferae (Brassicaceae),

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Caryophyllaceae and Proteaecae do not consistently host AM fungi (Smith and Read, 2008). The fungal species are considered non-host plant specific in their associations (Giovanetti and Hepper, 1985), although there appear to be clear cases of preference (Vandenkoornhuyse *et al*., 2002; Croll *et al*., 2008).

Traditionally the species have been identified by morphological characteristics of spores and sporocarps, spore suspensors and subtending hyphae, but increasingly sophisticated molecular methods are now also used. PCR analysis has become a regular feature of species identification since the isolation and amplification of an AM fungi small subunit rRNA (SSU-rRNA) 18S gene sequence by Simon *et al*. (1992). Universal primers have been developed that enable AM identification to species level in both soil and root samples with negligible error, and gene-code reference libraries are readily available on CD-ROM and the internet. The subsequent development of a quantitative real-time PCR analysis technique (Alkan *et al*., 1994) has enabled expansion in research into spatial, temporal and functional symbio-biological activities of AM *in planta* and in the mycorrhizosphere (Robinson-Boyer *et al*., 2009; König *et al*., 2010).

III. EVOLUTION

The earliest fossil evidences of AM fungi are isolated spores from the Ordivician of Wisconsin dated at 460 Ma ago, and in Early Devonian Rhynie Chert where features similar to extant *Glomus* spp. hyphal and arbuscular structures were found in the protostelic roots of *Rhynia* and *Asteroxylon*, early vascular plant species dated at *ca* 410 Ma. As these features appear to be evolutionarily advanced, arbuscular mycorrhiza may have by then been evolving for a considerable period. It is likely that the symbiosis developed with primitive freshwater-aquatic phototrophic gametophytes (Embryophyta) long before the Ordovician invasion of dry land and the development of mycorrhizal rhizoidal bryophytes and hepatics. This is supported by evidence from Wang *et al*. (2010) describing three genes required for AM formation isolated from almost all ancient plant lineages, indicating AM presence in the common ancestor of land plants. A further indication of ancient ancestry is the AM symbiosis between the cyanobacterial species *Nostoc punctiforme* and the only living representative of the ancient Geosyphonaceae, *Geosyphon pyriformis*. Redecker and Raab (2006) suggest *Geosyphon* (Archaeosporales) is closely related to basal *Archaeospora*, branching-off earlier than *Paraglomus* (Paraglomales) in the phylogeny of the phylum. Subsequent origins of Glomerales, the largest order representative in the phylum, and Diversisporales are indicated as being monophyletic (however, see Walker and Schüßler (2002) http://invam.caf.wvu.edu/index.html [23.11.10], who suggest convergent evolution may have occurred in Diversisporales). When origins and divergences occurred is unknown but it might be reasonable to assume they were early in AM fungal evolutionary history. All genera are globally represented and dispersal of hosts and fungal symbionts was perhaps enhanced by continental drift through the formation and break-up of the supercontinents Pangea and Gondwanaland. The fossil record does not substantiate this, however, there being no reliable representation of taxa other than '*Glomus*-like'. Nicolson (1975) described AM fungi in a Late-Carboniferous gymnosperm species resembling those in extant species. Stubblefield *et al*. (1987) reported fossilized arbuscules structurally similar to modern-day AM fungi in Triassic strata in Antarctica. There are a number of reports of AM fungi in Quaternary deposits.

Even if the fossil record is extended, it is unlikely to show how and when AM fungal species diversified. Consideration of geological history, however, suggests that since origination AM fungi have survived five major extinction events, after the last of which previously slowly spreading flowering plants rapidly diversified. Genotypic change in evolving host plants on a global recovery scale after each extinction event may have driven fungal symbiont speciation beyond background levels.

Thus, 80% of all extant terrestrial plants, including species of ancient lineage, bryophytes (mosses) (Zhang and Guo, 2007) though there are contrary reports, liverworts (Duckett *et al*., 2006), hornworts (Schüßler, 2000), quillworts (Radhika and Rodrigues, 2007), club mosses (Winther and Friedman, 2008), selaginellas (Strullu-Derrien and Strullu, 2007), horsetail ferns (Dhillion, 1993) and cycads (Muthukumar and Udaiyan, 2002) and more than 90% of extant vascular plants including ancient conifers and Old World angiosperms are arbuscular mycorrhizic. There are degrees of dependence upon the symbiosis on the part of the higher plant species ranging from obligate to facultative to non-mycorrhizal mycotrophy within and between species. Emerging ecto-, ericoid- and orchid-mycorrhizas, and non-AM evolutionary developments, such as fine roots with root hairs, cluster roots and non-mycotrophic plants, are all relatively recent events occurring from the Mid- to Late-Cretaceous through the Tertiary (95–2 Ma) period (Brundrett, 2002), so it is likely that almost all plants up to this time were to some extent AM mycotrophic. AM symbiosis has thus had a considerable effect on global plant community ecosystems during extreme oscillations in environmental conditions for at least 365 Ma.

IV. HYPHAL NETWORK

There are two distinct types of AM fungi, characterized by intraradical hyphal modifications: (i) the *Paris*-type where hyphal development is exclusively intracellular, forming coils in host plant cortical cells, and (ii) the *Arum*-type, where intraradical hyphal development is mostly intercellular and forms arbuscules in root cortical cells (Figure 1). These are the characteristic tree-like structures from which AM fungi derive their name. Between these ends of the spectrum are a number of gradations, described as intermediate types (Dickson, 2004).

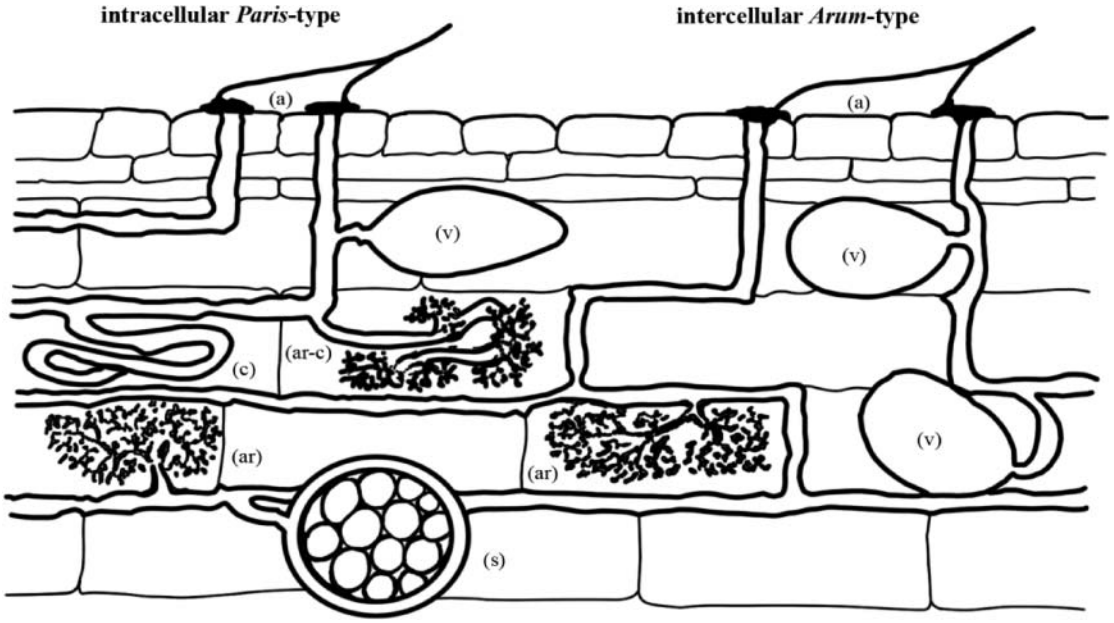

FIG. 1. Sketch of inter-radical morphological features of AM fungi. (a) = appressoria; (ar) = arbuscules of intercellular *Arum*-type AM; (ar-c) = arbusculate-coil and (c) = coil of intracellular *Paris*-type AM; (s) = inter-radical spore; (v) = vesicles.

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Smith and Smith (1997) in their literature survey found 41 angiosperm families to have only *Paris*-type, 30 only *Arum*-type and 21 families with examples of both. Gerdeman (1965) reported a *Paris*-type mycorrhiza in tulip tree but *Arum*-type in maize from the same fungal isolate. Coils and arbuscules were observed by Kubota *et al*. (2005) in the same root systems of cucumber and tomato. The structures are thought to be nutrient exchange sites, at least from fungus to host, including phosphate and ammonia/ammonium transporter systems via an H^+-ATPase pathway across a specialized membrane formed in cortex cells (Kobae and Hata, 2010). The sites are connected to a mycelial web in the extraradical sphere by inter- and intracellular hyphae.

Taxa other than species in the families Gigasporaceae, Paraglomaceae and Archaeosporaceae produce inter- and/or intracellular lipid-rich vesicles. These possibly act as temporary storage organs for the fungi, sometimes converting to spore-like thick-walled structures, and vesicles may be important in the efficacy of root fragments as propagules. The extraradical mycelial networks of many species have been shown to maintain viability if soils remain undisturbed, even after hot-dry or cold conditions, although the inoculum potential generally decreases with time. These networks can be extensive and Miller *et al*. (1995) reported a maximum of 111 m cm^{-3} soil in tallgrass prairie. This represents *ca* 0.002% of the soil volume based on an average mycelium diameter of 5 μm (Abbott and Robson, 1985). Hyphal lengths of <1–26 m g^{-1} have been reported in a variety of soils (Sylvia, 1992), and species differ in the degree of soil volume occupied (Abbott and Robson, 1985) and distance grown from host plant roots (Munkvold *et al*., 2004). There is no clear positive relationship between soil mycelial biomass and the quantities of nutrient transferred to hosts (Smith *et al*., 2000), nor to other AM fungi functional attributes.

There is evidence of nutrient transfer, P (Whittingham and Read, 1982; Wilson *et al*., 2006), N (Cheng and Baumgartner, 2004; Motosugi and Terashima, 2006) and water (Allen, 2007), between inter- and intra-specific host plant above-ground tissues via AM fungal hyphae, a facilitative function that may profoundly affect plant relationships (Selosse *et al*., 2006). Similarly translocated C remains within the fungal structures in recipient host roots (Bago *et al*., 2000). Interestingly Simard *et al*. (1997) reported transport of labelled-C from above-ground plant tissue to above-ground plant tissue *via* common ectomycorrhizal hyphal connections. Observations on isolates of three AM *Glomus* species made by Giovannetti *et al*. (1999) suggest that fungal genetic material may be commonly transferred through extraradical hyphal anastomosis in some taxa. Significantly, geographically separated isolates of the same species appeared not to anastomose. Intraspecific anastomosis has not been observed. There is no evidence of plant or fungal genetic material being transferred from and to host plants yet this is a potential pathway and there are many examples of symbiosis having transferred genes to the chromosomes of the host cell (Emiliani *et al*., 2009).

V. PHENOLOGY

Arbuscular mycorrhizal fungal growth and development is dynamic and rapid. The asymbiotic stage, which is the only stage in the phenology of the organism where there is evidence

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of limited saprophytic ability (Azcón-Aguilar *et al*., 1999), displays the lowest metabolic rate. The germ-tube of a spore may grow up to 20–30 mm, but if a host root is not contacted within as much as 15–20 days it may cease growth and become septated after metabolites are withdrawn. The spore may produce another germ-tube or remain quiescent until germination triggered by root proximity occurs, a strategy that conserves spore energy resource. At the pre-symbiotic stage, root exudate encourages germ-tube growth toward the root (Sbrana and Giovannetti, 2005) and triggers fan-shaped germ-tube branching (Tamasloukht *et al*., 2003) stimulating multiple entry points into the root. It may be that the spore is not the principal infective unit in thriving habitats, however, mycorrhizal root fragments and active hyphal networks being more effective (Smith and Read, 2008). Appressoria are formed at pre-determined intracellular points of contact with the root that have responded to fungal-derived signals to form prepenetration apparatuses (PPA) (Genre *et al*., 2005) through which penetration into the cortex occurs. Arbuscules are dichotomously highly-branched hyphae in entire surface contact with accommodating plant cell plasma membrane where the periarbuscular membrane (PAM), the site of nutrient exchange, is formed. The structure thus has a vastly increased exchange area. Arbuscules develop within 1–6 days of penetration into cortex cells (Harley and Smith, 1983). When fully developed they occupy, for example, 35% and 36% of the cells in wheat and oats, respectively (Alexander *et al*., 1988). After 4–15 days, the arbuscules degenerate and the host cell returns to its original state (Harley and Smith, 1983). Kobae and Hata (2010) recorded only 2–3 days of active phosphate transport in transgenic rice host roots before arbuscule degeneration. Further arbuscules develop as intercellular hyphae spread through the root and continue to penetrate receptive cortical cells. Re-entry into previously occupied cells has been observed. Total percentage of root length occupied by arbuscules varies with fungal species (Fitter, 1985), season (Bohrer *et al.,* 2004), edaphic factors (Clark, 1996; Posada *et al*., 2007), soil hydrology (Schreiner *et al*., 2007) and soil temperature (Smith and Read, 2008). The extent of root colonization also varies with soil biota interactions (Dauber *et al*., 2008) and with host plant species (Klironomos, 2003), host phenological stages (Pongrac *et al*., 2007) and C allocation (Muthukumar and Udaiyan, 2000). There is comparatively little similarly detailed description of *Paris*-type coils in the literature. van Aarle *et al.* (2005), investigating *G. intraradices* in two different plant species, reported levels of metabolic activity in *Paris*-type colonization in one plant similar to that in *Arum*-type in the other. Kobae and Hata (2010), by a novel fluorescence technique in dual-type *Gigaspora rosea* colonization of rice, found no evidence of a specific P_i transporter that was upregulated on membrane surrounding the fine branches of arbuscules and smaller arbuscular structures in arbusculate coils, on membrane surrounding coils, the hyphae of arbusculate coils, or arbuscule trunks.

The extraradical mycelia branch and extend into the rhizosphere and beyond when arbuscules have been formed (Smith and Read, 2008). This implies that photoassimilates are exchanged *via* the PAM. Mosse and Hepper (1975) reported extraradical hyphal growth immediately upon colonization of root in monoxenic culture, before the formation of arbuscules, which suggests intraradical hyphae may also be exchange sites for host plant C. Runner hyphae extend alongside and around the root apically and distally, re-inoculating. Nutrient absorbing feeder hyphae extend out into the matrix bridging rhizosphere nutrient depletion zones. They branch dichotomously up to eight times narrowing in diameter from *ca* 20 to 2 μm (Friese and Allen, 1991) enabling uptake of nutrient resource from the smallest soil crumbs inaccessible to root hairs. The extensive mycelial web formed interconnects the root systems of plants of different species, genera and families directly or through hyphal anastomosis (Giovannetti *et al*., 2006). The life cycle is completed with the production of spores (Figure 2).

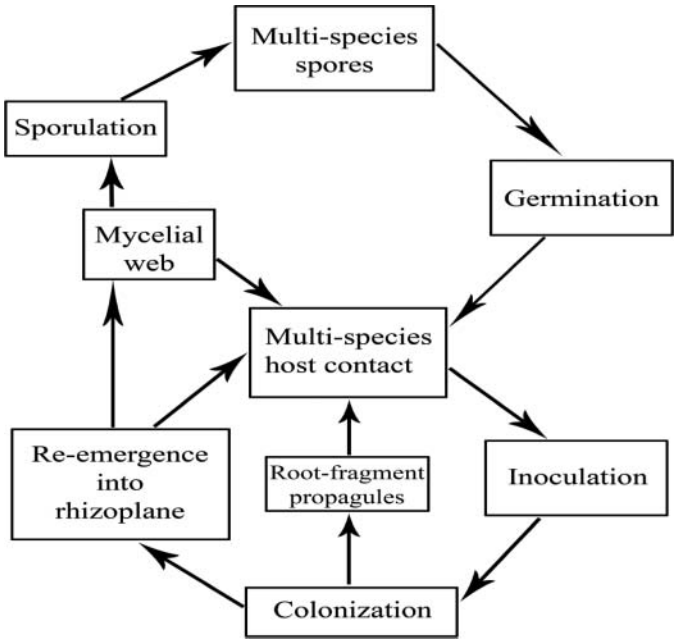

FIG. 2. General schematic of AM fungi life-cycle. Root fragments may propagate from inter-radical spores, vesicles or hyphae. Species temporal and spatial variations occur in response to differing and changing inter- and extra-radical environmental influences.

Glomeromycota spores are multi-nucleate, heterokaryotic (Hijri and Sanders, 2005), and formed asexually (Pawlowska, 2005). These are unusual features that raise intriguing questions about speciation (Redecker and Raab, 2006) and adaptation to change. Microscopical determination of variation in wall morphology, shape, color, size and reaction to staining compounds such as Melzer's reagent and Sudan Black B, has been the traditional method of classification, now enhanced by molecular methods. The spores are multi-walled and large, generally visible to the naked eye, and range from <40 μm in the smallest species to >800 μm in *Gi. gigantea*. All spores contain hundreds-to-thousands of nuclei that may not be genetically

identical, and lipid globules from which developing germ-tubes in the pre-symbiotic stage draw the majority of their required energy. Spores are formed singly, in clusters or in sporocarps in the soil, and in some species within root tissue. Numbers are typically 1-<50 g^{-1} soil (Sjöberg *et al.*, 2004). Rarely are more than 20–25 taxa reported in field studies. Density and distribution vary both spatially and temporally within and between species, with soil types and with host plants species diversity. An AM fungal species spatial sporulation-patch framework was observed by the authors during research in sand dunes on the west coast of India where fresh spores of *Scutellospora gregaria* were the most abundant in a 0.25 m^2 *Zoysia matrella* patch at the end of the monsoon season in one year, with few found in the same period of the following year when a *Gigaspora* species was dominant (Willis and Rodrigues, unpublished). Viability longevity may be enhanced by a dormancy mechanism that is little understood, but is assumed to assure longer-term survival.

Experimental evidence strongly suggests all AM fungal species are adapted to locality, with isolates from one geographical location often exhibiting poorer functional performance in other areas (Pellegrino *et al*., 2010; Antunes *et al*., 2011). As a consequence, consideration should be given to the source of spores used as inoculum in sustainable agricultural practice and in ecological restoration.

VI. SOIL AGGREGATION

There is considerable evidence that the Glomalean hydrophobic glycoprotein glomalin is involved in soil-crumb aggregation (Wright and Upadhyaya, 1998). Large quantities of this recalcitrant material are deposited from active extraradical hyphae and released during degeneration, and act as a mucilaginous glue contribution to binding soil matrix. Soil micro-aggregates are bonded more tightly than macro-aggregates (>250 μm) (Smith and Read, 2008), perhaps suggesting greater glomalin deposition from the larger surface areas of small diameter hyphae. The colonization of soil by microbiota and subsequent incorporation of detrital organic materials develops and maintains a structurally water-stable living soil.

Glomalin C fraction can range from 9–22%, residence time in soil from 6–42 years, and may represent >5% of total soil C (Rillig *et al*., 2001a). AM fungi thus have immense influence upon soil C cycles. Rillig *et al*. (2005) conducted long-term mesocosm research with single AM fungal species isolates. They reported differences in aggregation that they attributed to the influences of different associative microbiotic communities. In a mixed AM community, this may indicate a highly complex biotic heterogeneity in mycorrhizosphere soils. Interestingly researchers consistently report higher values of available P in the smallest aggregates, in Ultisols (Thao *et al*., 2008) and in highly weathered laterite soils (Wang *et al*., 2001), regions in the matrix unavailable to plant roots and root hairs but available to hyphae, an exploitation advantageous to AM fungi and consequently host plant fitness.

VII. PROPAGULE DISSEMINATION

Evidence clearly indicates that germinating spores and active AM mycelial webs colonize plant roots within the immediate mycorrhizospere and that each web overlaps and interacts with all others in the vicinity, spatially becoming a 'global' network. A strategy for dissemination of viable AM fungal propagules over distance is less clear. There are reports of spores being vectored by insects and small mammals, and possibly by water and wind over long distances. The latter would certainly have been an advantage in the spread of early seed-bearing plants with long distance dispersal mechanisms. However, no viable spores to date have been recovered from an apparatus devised to capture wind-borne AM fungal propagules at a 0.5-m height over an 18-month period at Goa University (Willis and Rodrigues, unpublished data). Wind-borne AM hyphal fragments are reported to be non-viable. This is supported by the consistant failure of hyphal fragments collected from the apparatus to colonize host roots in trap culture. The question of wind-borne viable propagule dissemination was re-visited after observations made on fresh iron-ore mine spoil mounds where there was spontaneous sporadic growth of herbaceous AM fungal colonized plants. The plants may have been inoculated by raindrop splash from a nearby, lower, line of colonized plants developed from dump-truck wheel deposits (India west coast monsoon rains can be very heavy at times) or perhaps by inoculated root-invaded leaf litter carried in from adjacent restoration plantings. Aristizábal *et al.* (2004) reported AM hyphal and vesicle colonization of leaf litter in Colombian montane sites, and litter containing AM colonized roots used as inoculum in trap culture at Goa University soon heavily colonized host roots (Willis and Rodrigues, unpublished data).

The sporadic spontaneous mycorrhizal plant growth pattern observed in the mine spoil indicates an epi-central plant community development strategy in primal, hostile and nutrient-poor soil environments, but only on a limited scale initially. The niche in which a viable spore or root fragment is deposited by chance necessarily needs to be an environment which facilitates AM development. This should include actively growing plant roots, an N source and associative saprotrophic microbial populations which contribute to labile nutrient pools. Where AM development occurs, the surviving plants will contribute to soil nutrient status through rhizodeposition, litter-fall and root death leading to a gradual below-ground increase in hyphal networks. This accretion strategy may be the principal form of AM fungal dissemination.

Supporting evidence for the hypothesis is limited but there are data which, by inference, may substantiate the notion. A database constructed from reports of worldwide SSU-rRNA AM fungi sequences by Öpik *et al*. (2010) indicated limited distribution ranges of most taxa but geographically wide ranges where host taxonomic range is also wide, distribution patterns which may well have arisen from an accretion process. Similarly, AM inoculated mixed-species herbaceous and woody 'primer' plants, spaced as fertile islands in managed

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re-instatement programmes in impoverished landscapes, spread and interact with each other through rhizosphere accretion.

Growth of hyphal networks varies with AM fungal species but can be rapid and extensive, found mostly in the top *ca* 20 cm volume of soil. Allen *et al*. (2003) estimated, in *Glomus* spp. studied, every 1 mm of new root growth equated to formation of 122 cm of hyphae. Roots can expand at the rate of several cm day^{-1}. Any successive AM mycotrophic plant propagules arriving within a developing or established mycorrhizosphere have immediate access to the benefits of the symbiosis, exponentially increasing the productivity of the network season by season, year by year. The arrival of novel AM fungal and host species would contribute to the development (or disturbance) of complex multi-species above- and below-ground communities.

If accretion is the primary method of AM dissemination it may help in explaining within-species spore tolerance or adaptation to environment. Often it is found spores of the same AM fungal species collected from geographically different locations have differing influences on plant fitness. As the fungi encounter variation in heterogeneity of local environments during expansion, isolates, those species that generally perform better than reference species in 'home' soils, may commonly develop.

VIII. TRANSPORT

Both intra- and extra-radical hyphae are generally non-septate. Formation of septa has been noted in hyphal-branching structures immediately prior to root contact (Giovannetti *et al*., 1993), in the process of repair (de la Providencia *et al*., 2005), at arbuscule degeneration, on separation of functional and degenerating intraradical hyphae (Kinden and Brown, 1975), and during germ-tube retraction. Septa in sub-tending hyphae are an important feature in morphological spore identification in some species. The transport of materials within hyphae is bi-directional (Smith and Gianinazzi-Pearson, 1988). Soil derived nutrients are transported to the host while the C assimilates from the host utilized by the fungus are distributed throughout the mycelial web and hyphosphere. Nutritionally the symbiosis might be described as a loop, a bottom-up or top-down (or both) feedback system whereby each partner benefits. The fungus delivers nutrients from the available pool in excess of its own minimal maintenance requirements and thus enhances the fitness of the host. Similarly the host provides C in excess of its own minimal maintenance requirements and thus enhances the fitness of the obligate symbiont. Where the fungal partner delivers nutrients to the host, physiological changes such as increase in transpiration and photosynthetic rates occur (Allen *et al*., 1981), enabling the host to return excess C to the fungus. Where, however, the host has sufficient nutrients from other sources such as agricultural P fertilizers, C supply to the fungus is reduced, and colonization and diversity is decreased (Johnson and Pfleger, 1992). Optimally, in both natural and sustainable agriculture systems, the partners would benefit most where each is able to simultaneously and constantly deliver nutrient to the others requirements effecting a balance or equilibrium. Environmental change, which may occur at the niche level, in localized disturbance, and in global ecosystem oscillations, necessarily moves the relationship away from this equilibrium. Each partner reacts compensatively to maintain fitness, yet still within a framework of synergism.

IX. PHOSPHORUS

All species of AM fungi contribute inorganic P (P_i) to their hosts, particularly in a P limited environment. The extent of P supply varies depending on the colonizing fungal symbiont species (Smith *et al*., 2010). There is evidence of hydrolysation of organic P (P_o) by AM extraradical hyphae at the hyphal tip (Koide and Kabir, 2000), but there are very limited quantities of AM fungal derived phosphatase in soils adjacent to hyphae (Joner *et al*., 2000). Other soil microorganisms, bacterial and fungal, with abundant hydrolysis capacity, release copious quantities of P_i into the labile pool that AM fungi trans-membrane transport into extraradical 'feeder' hyphae (Karandashov and Bucher, 2005), convert to polyphosphate long-chain and granular fractions (Solaiman *et al*., 1999), and transport to the intraradical exchange sites by cytoplasmic streaming (Cox *et al*., 1980). Cox *et al*. (1980) quantitatively assessed mean P flux in extraradical hyphae at 2.7×10^{-8} mol P cm^{-2} s^{-1}.

Temporal aspects of plant nutrient demand require attention when considering the supply role of AM fungi. Harper (1977), for example, suggested "there is evidence in cereals (which exemplify annual strategies) that 90% of total nitrogen and phosphorus content of the mature plants has been absorbed before the plant has achieved 25% of its final dry weight" and Radhika (2008) found two of the commonly occurring herbs studied had maximum root and shoot P concentrations during flowering stage and a third species during the vegetative stage.

X. CARBON

Carbon supplied from the host to the fungal symbiont is derived from plant sugars and is thought to be transported by passive efflux. The intraradical hyphae and/or arbuscules take up hexose, a substantial amount of which is used in lipid, trehalose and glycogen synthesis before translocation to extraradical mycelia (Bago *et al*., 2000; Bago *et al*., 2003). Up to 20% of total photosynthate, always of recent assimilate partitioned to roots, may be supplied to the fungus. Movement of lipid bodies from intraradical to extraradical hyphae has been imaged by real-time immunofluorescence technique (Bago *et al*., 2002*a*). Other work has also shown movement in the opposite direction (Bago *et al*., 2002b). Much of this C is utilized in fungal maintenance and growth and there is evidence that the AM mycelial web releases C into the mycorrhizosphere (Toljander *et al*., 2007), just as roots exude into the rhizosphere soil matrix, influencing biota populations (Jones *et al*., 2009). Estimates of soil C derived from AM fungal extraradical hyphae range from 50 to 900 kg ha^{-1} (Zhu and Miller, 2003). Rillig (2004) reported

1.45 Mg C ha^{-1} complexed in glomalin in the top 10 cm of soil in a lowland tropical forest.

XI. NITROGEN

Comparatively recent investigation has shown AM fungi to play an important role in the transport of N from OM and leaf litter (Leigh *et al*., 2008) to host plants. Unlike with P, AM fungi do not enhance the acquisition of N when present at low levels in soil (Reynolds *et al*., 2005) but can make a significant contribution to plant N requirement (Hodge and Fitter, 2010), particularly in dry soils where mobility to the direct pathway *via* roots is restricted (Tobar *et al*., 1994). The hyphal pathway converts inorganic N taken up from the labile pool into amino acids, and translocates it principally as arginine from extraradical to intraradical hyphae (Govindarajulu *et al*., 2005). Here the N is converted to inorganic N compounds before passing to the host. A recent report by Guether *et al*. (2011) describes the characterization of an organic N transporter in *Lotus japonicus* roots induced by mycorrhization that may be involved in active transfer of organic N compounds, principally energy rich amino acids, to the plant.

An increased P was consistently associated with an increase in N accumulation in mycorrhizal *Vicia faba* under low P conditions (Jia *et al*., 2004). As with all other aspects of mycorrhizal ecology, however, N relations are complex. Jurkiewicz *et al*. (2010) found that *G. intraradices* performed well in the colonization of *Arnica montana* in high N soil, but no mycorrhization occurred when N was low. Blanke *et al*. (2005), on the other hand, reported strong colonization by AM fungi in P-polluted N-deficient soils and reduced mycorrhization in comparable P level soils with higher N concentrations. AM fungal extraradical hyphae are thought to contribute indirectly to leguminous plant N status but only in reduced P conditions, supplying essential P and micronutrients to nitrogen-fixing organisms (Smith and Read, 2008).

XII. MICRONUTRIENTS

The symbiosis also contributes micronutrients to the host plant. Suzuki *et al*. (2001), using a multitracer technique, detected the uptake and transport to hosts of sodium (Na), zinc (Zn), selenium (Se), rubidium (Rb) and strontium (Sr) by AM fungal hyphae. Bürkert and Robson (1994) observed Zn uptake to varying degrees in three fungal species and Caris *et al*. (1998) reported uptake of iron (Fe) in sorghum (but not in peanut) by *G. mosseae*. Marschner and Dell (2006) found that AM symbiosis could account for up to 60% of plant copper (Cu) and 10% potassium (K) requirements in experimental chambers. Clark and Zeto (2000) found that K, calcium (Ca) and magnesium (Mg) uptake was enhanced by mycorrhization in acidic soils and Li *et al*. (2006) reported an increase in plant shoot Cu in calcareous soil, relative to P uptake. Allen and Shachar-Hill (2009) found that uptake of sulphur (S) in monoxenic culture of *Daucus carota* with *G. intraradices* was halved when supply of the nutrient was increased above growth limiting levels.

XIII. COLONIZATION

Several species of a number of genera of AM fungi may colonize a host root simultaneously (Bever *et al*., 2001). Although these species are, by definition, competitive with each other (Wilson, 1984; Smith and Read, 2008) there may be complementarity, as suggested by Jansa *et al*. (2008). Variation in colonization strategy is displayed at the taxonomic level (Hart and Reader, 2002) with each species possibly contributing differing functions to the symbiosis to varying degrees. Arbuscular mycorrhizal communities within a host can change significantly over time. The species that dominate in saplings have been shown to become minor species as the host plant develops and grows while formerly rare or previously undetected species can become dominant (Husband *et al*., 2002). This may represent r- and K-strategies, a colonization/persistence trade-off (Hart *et al*., 2001) on the part of some of the fungal species but it may also suggest that the hosts' functional demands of the symbiont may change with time. For example, P and N demand may be of primary importance during early stages of plant development, particularly in nutrient deficient and hostile environments, whereas difficulties in transpiration may be of primary concern in mature canopy trees.

Symbiotic events occurring in a woody host species may be quite different from those in an adjacent herbaceous species. Even among mixed herbaceous species occurring events may be dissimilar even though their roots occupy common soil volume (Vandenkoornhuyse *et al*., 2003). Events in two adjacent plants of the same species may be quite different, particularly where an AM fungal species might also exhibit functional variability (Smith *et al*., 2004). If, as has been recently suggested, the primary driver of local adaptation of AM fungi is edaphic resource availability (Johnson *et al*., 2010), it is feasible that ecological activity in the symbiosis is as heterogenous as the between- and within-soils matrices occupied. Perhaps plasticity derived from the inherent heterokaryotic nature of multiple nuclei is a strategy enabling isolate-variable AM fungal fitness in almost any habitat, or niche.

XIV. MICROBIAL INTERACTIONS

Fungi are thought to have originated some 760 Ma −1.06 Ga ago and Ascomycota 500–650 Ma ago (Lücking *et al*., 2009). Glomeromycota arose from non-septate Zygomycotina, an earlier sister clade to septate Asco- and Basidio- mycotina, and are ancestrally symbiotic with all extant plant clades. This suggests the phylum evolved along with phototrophic charophytes, green algae which include the closest living relative of embryophyte plants, in primeval fresh-water and muds for perhaps as long as 300–540 Ma before the advent of the invasion of dry land. It is not possible to deduce whether AM fungi had, and subsequently lost, saprotrophic ability, or evolved to take advantage of a

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symbiotic C source from the outset. Neither is it clear which of the many functions now known to be attributable to AM fungi were then imparted toward phototroph fitness.

At the origins of AM fungi there would have already existed considerable archaean and bacterial species diversity. Blue-green bacterial stromatolites have been dated as far back as 3.45 Ga and fossilized biofilm along with spherical and rod-shaped structures are present in 3.3–3.5 Ga old cherts in the South African Onverwacht Group (Westall *et al*., 2001). Interactions with these organisms must have been as much a part of successful evolution of Glomeromycota as adaptation to the symbiotic habit.

Much of the data on AM fungal interactions with other microbial soil organisms, particularly rhizobacteria, has been obtained from trap-culture or *in vitro* studies. Care should be taken in interpreting these data as they may not fully represent the complexities of the multi-trophic environment of soils. Nevertheless insight into many significant saprotrophic and synergistic associations has come to light. Increased supply of P to plants *via* AM hyphae has been observed in a large number of experiments where species of phosphate-solubilizing bacteria have been cultured along with the fungus. Similarly, detrital decomposers and nitrogen-fixing bacteria have been shown to enhance plant N nutrition *via* AM mycelial uptake. It might be concluded that the fungus is 'simply in the right place at the right time' but investigation by a number of researchers strongly suggests at least some species of AM fungi promote selection and proliferation of specific bacteria in the mycorrhizosphere and of those attached to extra-radical hyphae. This may result in an enhanced AM fungal mycelium-available nutrient status in the labile pool. Mycorrhiza helper bacteria (MHB), species that assist mycorrhization and functioning of the symbiosis including plant root pathogen protection, have been investigated. Species of plant growth promoting rhizobacteria (PGPR) encourage the mycelial growth of AM fungi and, to a lesser extent, diazotrophic endophytic plant growth promoters in both fungal organs and plant roots, which may also be involved in interaction activity. Interestingly there is clear indication that while there is little or no specificity between host plants and AM fungi there may be specificity between bacterial species and AM fungal species. It is thought specific bacterial diversity is a response to subtle changes in rhizo-deposited photosynthates by the fungi. For a comprehensive review of the plant growth promoting interactions between bacteria and AM fungi, see Artursson *et al*. (2006).

Soil fungi other than Glomeromycota have antagonistic, synergistic and neutral interactions with AM fungal species. Fracchia *et al*. (1998) found one species inhibiting AM fungal spore germination and germ-tube growth while all others observed enhanced growth and root colonization of *G. mosseae*. The AM fungal species had reciprocal effects upon the associated saprophytic fungi. Further complexity was observed with variation in both host species and light levels. These saprotrophs also contribute AM-available and hence plant-available nutrients to the labile pool. It is possible there is synergistic activity, directly or indirectly, between AM fungi and dark septate endophytes (DSE), root inhabiting species of Ascomycetes and Basidiomycetes characterized by distinctive coil, knot and hyphal structures in cortex cells which may themselves be symbiotic with higher plants. Observations made by Willis and Rodrigues indicate a clear reduction in root hair density, a universal phenomenon in the AM symbiosis, when roots are colonized by DSE, even in the absence of AM fungi (unpublished).

XV. INVASIVE PLANTS

Invasive plants, those which threaten native biological diversity, employ a variety of tactics to gain a foothold and thrive in new territories (Sakai *et al*., 2001), including interactions with AM fungi. Marler *et al*. (1999), in a greenhouse experiment, concluded the invasive European mycorrhizal forb spotted knapweed (*Centaurea maculosa*) was "strongly enhanced" in interspecific competition with the North American native grass species *Festuca idahoensis* only when mycorrhizae were present. Intraspecific competition was weak. They reported, in interspecific competition without AM fungi, *F. idahoensis* biomass gains up to 171% higher than with AM fungi, and *C. maculosa* plants 66% larger in interspecific competition with AM fungi as against without. Walling and Zabinski (2004), in a split-pot experiment with single plants on one side and P amendments in bare soils on the other, found greater extraradical hyphal mass in association with *C. maculosa* than with *F. idahoensis*, which suggests an increasing mineral nutrient exploitation potential. This is supported by previous work from Zabinski *et al*. (2002) that showed P concentrations in *C. maculosa* grown in a 28-μm membrane split-pots excluding fine roots but not AM hyphae, adjacent to native grass species, were increased. Mummey and Rillig (2006) described a significant (ave. 24%) reduction in extraradical hyphal lengths in *C. maculosa* dominated sites as against native grass species dominated sites in the field. They didn't differentiate between living and dead hyphae and so could draw no conclusions about AM fungal function but suggested the resulting decrease in glomalin deposition and its effect on soil structure may be a factor accounting for greater erosion losses that occur in *C. maculosa* dominated communities (Lacey *et al*., 1989).

Further research by Callaway *et al*. (2003) investigated the effect of invasive *C. melitensis* on two co-occuring native grass species *Avena barbata* and *Nassella pulchra* where application of the fungicide benomyl had reduced AM fungal abundance. They reported *C. melitensis* biomass reduced by $>50\%$ in fungicide untreated soils as against treated when grown alone, little change in biomass when grown with *A. barbata* whether fungicide treated or not and an almost 5x increase when grown with *N. pulchra* where the resident AM fungal population had remained fungicide untreated.

Callaway *et al*. (2008) attributed inhibition of native AM fungi in N. American forest soils by the European

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non-mycorrhizal invader garlic mustard (*Alliaria petiolata*, Brassicaceae) to a 'novel weapons' effect, specific biochemicals released into the rhizosphere to which AM fungi in home soils are immune. The inhibition of native AM fungal species corresponded with severe adverse effects on the native plants community. In prior *A. petiolata* work in a series of experiments, Stinson *et al*. (2006) described an indirect effect of allelopathic suppression of AM spore germination and colonization and its adverse effect on mycorrhizal-dependant canopy tree seedling recruitment. Burke (2008), also investigating *A. petiolata* interactions with AM fungi, on this occasion in three N. American native woodland herbaceous species, found the invasive selectively affected inhibition of a significant indicator *Acaulospora* AM fungal species in one of the native plants, while the AM fungal communities in the other two plants were unaffected. In a different experimental approach, Anderson *et al*. (2010) removed *A. petiolata* from an invaded site, finding increase in mycorrhizal inoculum potential and cover of native plants species within a two-year period.

Barto *et al*. (2010) conducted a novel laboratory experiment introducing *A. petiolata* root and leaf extracts at lower, more realistic levels than in previous investigations, to another N. American native woodland-floor plant, *Impatiens pallida*. They defined four different growth stages: germinating seeds in the absence of AM fungi; seedlings growing where AM fungi were excluded (pre-symbiosis phase); germinating seeds and subsequent development with AM fungi (symbiosis formation phase); and plants which had been colonized by AM fungi for four weeks (symbiosis growth phase). Their results showed a *ca* 50% reduction in seed germination in the absence of AM fungi; reduction in root length and inhibition of root-foraging structure development in the pre-symbiosis phase; growth rates of height, root and rhizosphere areas unaffected by the extracts in the symbiosis formation phase; and growth rate, root and shoot dry masses and root to shoot ratio unaffected by *A. petiolata* extracts in the symbiosis growth phase. They concluded that a pre-established AM fungal symbiosis in *I. pallida* ameliorates allelopathic effects of *A. petiolata* and restoration of invaded areas more successful if colonized plants are used rather than the traditional method of sowing seed.

The examples cited are few (for a comprehensive review see Pringle *et al*., 2009) but clearly they show AM fungi can contribute to the success (and failure) of invasive plants establishment. The evidence suggests in undisturbed terrestrial environments many invasive plants are only able to gain purchase in new habitats by altering native AM fungal population density and diversity, with consequential effects on native plant communities. It also lends considerable support to the proposal that Glomeromycota mediate in manipulation of plant community structure.

Invasive plants regularly proliferate in disturbed areas, rapidly modifying soil biotrophic communities, to the exclusion, perhaps, of endemic primary colonizer species. Ensuing plant community succession is biased at the outset. This strategy emphasizes the importance of plant species selection at the very beginnings of managed indigenous plant community restoration.

XVI. PHYTOREMEDIATION

Plants display a number of methods of averting possible stress due to heavy metals (HM) in contaminated soils. For an overview at the molecular level see Hall (2002). There is evidence that some species of Glomeromycota in certain circumstances have a beneficial influence on plants growing in soils contaminated with HM by impeding uptake. Other species encourage a higher rate of uptake that, if it occurs in tolerant plants, may aid detoxication of the contaminated soils by the process of phytoremediation.

González-Chávez *et al*. (2004) found that glomalin in hyphae and in soils had sequestered the "potentially toxic elements (PTEs)" Cu, cadmium (Cd) and lead (Pb). Interestingly they found no differences in sequestration by Cu tolerant over non-tolerant *G. mosseae* isolates *in vivo*. Hyphal wall sequestration has also been reported (Joner *et al*., 2000) with HM binding to chitin. Chen *et al*. (2005) described a correlation between Pb sequestration and increased vesicle numbers. Ultra *et al*. (2007) reported a reduction in arsenic (As) toxicity symptoms in *Glomus* inoculated sunflower plants. They also found that As was converted to organic forms in the mycorrhizosphere, suggesting an active reducing mechanism by the AM fungus. A further mechanism is described by Göhre and Paszkowski (2006) where a number of AM fungus produced chelators within the cytosol bind the metals which are then pumped out by HM transporters. Tullio *et al*. (2003) found that AM isolates from Cd polluted sites impeded translocation of Cd to a greater extent and colonized barley roots to a greater extent than spores from non-polluted sites.

Experimental work in pots reported by Weissenhorn *et al*. (1995) clearly showed the complexity of AM fungal involvement in HM translocation in plants. They conducted a multifactorial study of the translocation of Zn, manganese (Mn), Cu, Cd and Pb from soils surrounding a disused smelting plant in maize plants at different light intensities. They found lower levels of HM (Cd, Cu, Zn, Mn) translocation where spores were from the contaminated soils and higher levels of inoculation compared to imported spores at increased light levels, again suggesting fungal adaptation or at the least, spore tolerance. In the highest levels of light-enhanced inoculation and plant biomass, however, AM isolates from the contaminated soils increased Cu and Zn root-to-shoot translocation. Shen *et al*. (2006) noted an interactive effect of Zn and Cd in mycorrhizal plant growth.

Although there appears to be spore tolerance to HM, abundance itself may be adversely affected. Ortega-Larrocea (2001) found a significant reduction in *Glomus* spores in clay-deep vertisols where the HM chromium (Cr), nickel (Ni), Cu, Zn and Pb had accumulated in agricultural fields after 90 as compared to 5 years of wastewater irrigation.

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Clearly there is no commonality in the role of AM fungi in either HM sequestration or phytoremediation. There is, however, obvious potential. In certain circumstances and with careful management it may be possible to produce edible fodder/food crops in HM contaminated soils. There may certainly be scope for enhanced soil phytoextraction programmes utilizing metal hyperaccumulators, plants tolerant of very high levels of HM in tissue (Krämer, 2010), inoculated with appropriate HM tolerant AM fungal strains. The particularly high occurrence of hyperaccumulation in the Brassica family is excluded from enhancement by AM inoculation but Trotta *et al*. (2006) found that As hyperaccumulation in the roots of Chinese brake fern (*Pteris vittata*) was reduced and translocation to above-ground tissue increased when inoculated with *G. mosseae* and Buendia-González *et al*. (2010) reported hyperaccumulation of Cr and Cd in *Prosopis laevigata* (Fabaceae), which is known to be arbuscular mycorrhizal. Sarma (2011) states >500 plant species from 101 families have been documented as metal hyperaccumulators.

XVII. EFFECTS UPON AM FUNGI

A. Disturbance

Physical disturbance of the top 20–30 cm of soil drastically affects inoculum potential in the short term (Jasper *et al*., 1989) as the AM fungal mycelial web is fragmented. With the possible exception of fragile, low nutrient-available systems such as sand dunes and arid regions, the recovery period appears to be rapid. Hyphal repair, inoculum potential of both hyphal and root fragments, and re-connection of viable hyphal fragments *via* anastomosis may accelerate recovery. Arbuscular mycorrizal species diversity recovery response to restoration after fire was rapid where mycotrophic understorey herbaceous plants were re-planted (Korb *et al*., 2003). Winter freezing had little impact on the inoculum potential of AM fungal hyphae (Addy *et al*., 1997). Diversity also recovered rapidly where herbaceous plants re-established on newly created islands after flooding in a European alpine river (Harner *et al*., 2011). Recovery of diversity in agricultural soils in flood plains and deltas, for example annual floods in the Gangetic Plains of India, is also rapid, possibly due to the relatively large diversity of spores at 50–75 cm in agricultural soils (Oehl *et al*., 2005). Alluvial deposits are also a possible source of viable inoculum replenishment. Miller and Bever (1999), in their study of AM fungal species variation in a wetland grass species along a dry-to-wet gradient, found certain species in the drier regions only. There were no species found only in the wet regions. There are flooding effects reported that reduce AM colonization and spore numbers in rice paddy but sufficient inoculum survives to colonize (19–33%) subsequent non-flooded crops (Wangiyana *et al*., 2006).

In the long term, for example in agricultural practices of continuous tillage disturbance and in increasing land use intensity, AM fungal spore numbers and morphologically assessed species diversity were reported consistently reduced (Douds and Millner, 1999; Oehl *et al*., 2003). Continuous monoculture of maize and to a much less extent crop rotation also showed reduction in diversity. Soils left fallow or under sustainable or organic agricultural systems showed significantly greater diversity (Oehl *et al*., 2003; 2004). The greatest diversity was found in semi-natural grasslands. Hijri *et al*. (2006) reported similar results from molecular studies of the same sites as the Oehl *et al*. (2003) research. This evidence may suggest AM species diversity and abundance could be an 'indicator' of the fertility status of sustainable and organic agricultural soils. Where disturbance is severe, such as removal and stockpiling of topsoil, AM fungal propagule viability is considerably reduced after just three to four years of storage (Gould and Liberta, 1981).

B. Agrochemicals

Applications of agricultural chemical fertilizers, fungicides and pesticides have been shown to have both negative and positive effects upon AM fungal population characteristics. Increase in levels of plant available P by fertilizer application almost always promotes a negative feedback, reducing diversity and abundance in AM fungal community. Residual levels of P were found to inhibit AM fungal root colonization even after conversion to organic systems (Hijri *et al*., 2006). An interesting exception is described by Johnson (1984) where *G. intraradices* colonization of *Citrus aurantium* was unaffected after 26 weeks following weekly application of P, and more root cortex sporulation at the highest of concentrations.

The literature on the effects of N fertilizer applications gives a less clear picture. Early work at Rothamsted Experimental Station, Harpenden, UK suggested increasing levels of nitrates generally reduced AM colonization levels in lettuce (Owusu-Bennoah and Mosse, 1979), and in onion (Wang and Hayman, 1982), the latter also contrastingly reporting no effect of ammonium nitrate on AM colonization in *Trifolium repens*. Bååth and Spokes (1989), investigating various combinations of P and N application effects upon the growth response of *G. caledonium* in *Allium schoenoprasum* (chives), reported highest root colonization when N and P were at intermediate levels, no effect on the addition of N at low soil P levels nor at high P and low N, and lowest levels of colonization at high P and high N, where ammonium-N had a greater effect than nitrate-N. Douds and Schenck (1990) found sporulation in *Gi. margarita* colonizing *Paspalum notatum* (Poaceae) reduced, severely so in higher concentrations, by ammonium nitrate, yet root colonization was little affected. Johnson *et al.* (2003) concluded that granular ammonium nitrate effects on AM in grasslands in different biomes were N:P site-dependant, a general reduction in C allocation to AM structures in ample ambient P conditions, and an increase in P-deficient soils.

Fungicides captan and benomyl, the latter often applied in comparative field studies on AM fungi, were observed to decrease metabolic activity in AM fungal tissue as soon as three days after treatment (Kough *et al*., 1987). Schreiner and Bethlenfalvay (1996) investigated the effects of captan, benomyl,

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and PCNB on *G. etunicatum*, *G. mosseae* and *Gi. rosea* in pea plants. All three depressed percentage root colonization. They found *Gi. rosea* spore abundance significantly reduced in captan treated soils, *G. etunicatum* spore abundance increased in all three fungicide treated soils, and *G. mosseae* spore abundance increased only in captan-treated soils.

Herbicide applications can reduce or promote mycorrhiza formation. Ocampo and Barea (1985) found carbamate herbicides reduced soil fungal metabolism after 48 h but AM fungal root colonization levels had recovered by the end of the experiment. Dodd and Jeffries (1989) investigated the effects of four herbicides on three *Glomus* species in winter wheat, finding one had no effect on spore germination, another prevented spore germination, and the remaining two inhibited germination at low dosage but had a stimulatory effect at higher dosage. Glyphosate had no effect on *G. intraradices* colonizing genetically modified (GM) soybean (Powell *et al*., 2009). Simazine applications at concentrations above 1 mg kg^{-1} induced non-mycorrhizal *Chenopodium quinona* to form AM (Schwab *et al*., 1982).

Pesticides also have variable effect on AM fungi, generally decreasing colonization, sometimes significantly. Abd-Alla *et al*. (2000) found significant inhibition of AM fungal root colonization and spore production in an investigation of the effect of five different pesticides applied to three legume crops. Sreenivasa and Bagyaraj (1989), in their assessment of the effects of five insecticides on *G. fasciculatum* in pot culture found all were deleterious at recommended dosage but two applied at half that rate significantly increased root colonization and spore density.

C. Grazing

Grazing of AM fungal spores and mycelia has been observed. Feeding preferences of six species of mites and collembolans, among the latter *Folsomia candida*, were assessed in soils with AM- and conidial-fungal species populations. The grazers preferred conidial fungi, and when they did graze on AM fungi they showed clear preference for narrower hyphae (Klironomos and Kendrick, 1996). Klironomos *et al*. (1999) later found fecundity in AM fungi-grazing *F. candida* severely impaired, and in F_1 generation animals fed exclusively on AM fungi, inability to produce eggs.

Atul-Nayyar *et al*. (2008) investigated relationships between AM fungi, alfalfa, Russian wildrye and mycophagous nematodes at three levels of P fertilization (0, 20, 40 kg P_2O_5 ha^{-1}). Fungal colonization levels reduced with P fertilization with or without Russian wildrye. In the presence of wildrye, lower mycorrhizal colonization levels concurred with higher than monoculture nematode abundance, with an almost quadruple increase of omnivorous species. They attributed reduced yield observed in the dual crop at low P levels compared with alfalfa monoculture to enhanced nematode feeding on AM hyphae.

Faeces from seven of ten small rain-cloud forest mammals, and more than half of 94 samples examined, contained intact AM spores. Spore morphology analysis indicated the animals actively fed on AM fungi and showed preference for sporocarpic taxa. The authors propose the animals are AM propagule vectors not only in the terrestial habitat but also amongst high-canopy epiphytes (Mangan and Adler, 2000).

D. Parasitism: The Case for *Trichoderma harzianum* (Ascomycota)

Green *et al*. (1999), in a root-free soil experiment, concluded the biocontrol agent *Trichoderma harzianum* exploited the dead mycelium and not the living biomass of *G. intraradices*. There was no adverse effect upon hyphal growth or P uptake. Their evidence suggested *T. harzianum* was adversely affected by *G. intraradices*.

Martínez-Medina *et al*. (2011) inoculated melon seedlings with *G. intraradices*, *G. mosseae*, and *T. harzianum* singly and in combinations. Half of the plants were inoculated with *Fusarium oxysporum* after six weeks. *T. harzianum* alone increased shoot fresh wt. by 20%, neither AM fungal species increased shoot fresh wt. over controls, and co-inoculated treatments fresh wt. increase lay in-between, suggesting synergism as *T. harzianum* increased AM fungal root colonization compared with Glomales alone treatments. The greatest increase was observed in the combination with *G. intraradices*. *T. harzianum* was unaffected by either of the AM fungal species. *T. harzianum* alone reduced disease incidence by 50%, *G. mosseae* also by 50%, and *G. intraradices* by 25%. Disease incidence in *G. mosseae* - *T. harzianum* co-inoculation was no less than in individual treatments but *G. intraradices* - *T. harzianum* co-inoculation was significantly more effective than in individual treatments. The variations were correlated with decreased and increased IAA and ethylene levels, respectively, in stem tissue.

Purin and Rillig (2007) surmised there is little evidence of parasitism of AM fungi, suggesting glomalin may be a deterrent. They also questioned whether parasitism of AM fungi, by fungi, bacteria or viruses, has been conclusively demonstrated. The criteria they described fulfilling parasitic mode, particularly fitness parameter measurement in both populations, and confirmation of AM fungal loss of fitness in follow-up soil experiments, have not been met, they said, in any enquiry.

De Jaeger *et al*. (2010) observed invasion of *in vitro Glomus* species extraradical mycelia by *T. harzianum* and subsequent invasion into intraradical mycelia and root cells *via* AM intrahyphal growth. The mycoparasite caused protoplasm degradation. In further work, again in *Glomus* species *in vitro*, De Jaeger *et al*. (2011) demonstrated increased P uptake by the fungus but disruption of P transfer to host roots in the presence of *T. harzianum*.

E. Global Climate Change (GCC)

The considerable literature on the effects of current global climate change (GCC) on AM fungi is variable and in this review only briefly discussed. For more comprehensive reviews see Treseder and Allen (2000), and Treseder (2004).

Predicted global surface temperature rise affects AM fungi. Significant increase in AM fungal root colonization and 40%

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soil hyphal length increase in *Avena barbata* rhizosphere in a soil-warming field experiment was descibed by Rillig *et al*. (2002). Compant *et al*. (2010), in their review of 135 studies on the effects of GCC on beneficial soil organisms and interaction with host plants, found in the majority of investigations soil temperature increase had a positive impact on AM fungal root colonization and hyphal length.

Rising global atmospheric CO_2 levels are of concern. They too affect AM fungal diversity, abundance and function. Essentially increase in CO_2 enhances photosynthetic rates with more C directed to the soil pool and AM fungi, in turn a benefit to plant growth. Generally AM fungi increase in hyphal growth and colonization but species and species-host responses are variable. Colonization in obligate mycotroph C_4 grasses generally increases but not in facultative mycotroph C_3 grasses (Tang *et al*. 2009). Klironomos *et al*. (1998) reported two *Glomus* spp. colonizing *Artemisia tridentata* grown at 2× ambient CO_2 levels increased percentage arbuscular and hyphal colonization with significantly higher numbers of spores whereas an *Acaulospora* and a *Scutellospora* sp. developed significantly higher hyphal lengths only. Johnson *et al*. (2005) found CO_2 elevation frequently reduced AM benefits on plant growth in a laboratory experiment. They had investigated effects on 14 plant species including forbs, C_3 and C_4 grasses and five AM fungal communities, including mixtures of *Glomus* species and Gigasporaceae taxa. Rillig *et al*. (1999; 2001b) described an increase in hyphal length and consequent increase in soil concentrations of glomalin in response to rising CO_2 levels. There is also some indication increased soil microbial biomass and concomitant increase in respiration may itself contribute to climate change (Bardgett *et al*., 2008).

Anthropogenic nitrogen deposition reduces AM fungal diversity and abundance. Egerton-Warburton and Allen (2000) assessed AM fungal diversity in scrub vegetation along an N deposition gradient, compared with N-fertilized and unfertilized plots. They found anthropogenic deposition and N experimental plots to have similar downward trends in both abundance and diversity of AM fungal species, Gigasporaceae taxa displaced and proliferation of small-spored *Glomus* species. Egerton-Warburton *et al*. (2001) described an almost identical trend, here Acaulosporaceae also displaced, in archived woodland soil samples sequenced with air pollution records. In a later N fertilizer application experiment across five grasslands however (Egerton-Warburton *et al*., 2007), AM fungal productivity, species richness and diversity decreased in P rich soils (low N:P) but in P limited soils (high N:P) N fertilization had an opposite effect.

There is comparatively little literature describing the effects of elevated CO_2 and N deposition interaction on AM fungi. The above evidence suggests the two inputs have conflicting influences. Klironomos *et al*. (1997) and Rillig and Allen (1998) found AM fungal hyphal length increased with CO_2 in low-N but not in high-N treatments. Chung *et al*. (2007) reported increased CO_2 effects upon soil microbial and fungal biomass over a grass species diversity gradient (1, 4, 9 and 16). Phospholipid fatty acid (PLFA) analysis indicated that rates of soil C cycling, in which AM fungi play a significant role, were reduced relative to grasses diversity decrease.

F. AM - AM Competition

Competition amongst AM fungal species is difficult to assess. All species appear so variable in form and function that it seems impossible to draw consistent baselines from which to make comparisons. There is some evidence to suggest the first AM fungal taxon to colonize is frequently the most abundant within the root (Hart and Reader, 2002) and that the fastest colonizers, e.g. Glomaceae, develop greater intraradical biomass than later colonizers, e.g. Gigasporaceae, which develop greater extraradical biomass (Allen *et al*., 2003). Alkan *et al*. (2006) found *G. intraradices* and *G. mosseae*, as single isolates, colonized roots in both directions from the point of inoculation. Where *G. intraradices* colonization intensity was even, however, *G. mosseae* proliferated distally. In combination both showed unidirectional distal colonization. Bever *et al*. (2009) demonstrated preferential allocation of C to the more beneficial of two AM species in a wild onion split-root system, comparing allocation of labelled-C to roots in each of the two compartments. Adaptation to local environment gives advantage over exotic species.

Arbuscular mycorrhizal fungal community species richness increases with plant community diversity and is often correlated with increased nutrient content and productivity in host plants (van der Heijden *et al*., 1998). By inference it follows that diversity in AM fungal functional efficiency similarly increases. Where a species is able to exploit a niche few or no other can, traditionally a competitive edge would be ascribed, but where does the advantage lie? The nutrient exploited, unless there is direct link with the host, is transported into a common pool in the mycelial web and possibly distributed amongst several hosts. Reciprocity may be minimal.

Individual species tolerance of, and recovery from, the effects of fluctuation in environmental conditions might be described as 'efficiency of function' competition. During temporarily low soil-water status, for example, the species more efficient in water accumulation and transport to the host may increase in hyphal length and biomass at the expense of the momentarily defunct N transport (say) efficient species. However, reciprocal C gain should be converted to propagules, i.e., sporulation, for the species to have displayed a competitive advantage.

The argument may have support from the rapidity of AM fungal response to signaling (Drissner *et al*., 2007; Navazio *et al*., 2007) and cytoplasmic streaming (Smith and Gianinazzi-Pearson, 1988), and evidence of AM fungal spores temporal and spatial patchiness in soils (Friese and Koske, 1991; Carvalho *et al*., 2003). However, such a mechanism may perhaps be masked by variation in seasonal sporulation patterns (Pringle and Bever, 2002; Escudero and Mendoza, 2005) and host plant sporulation rates effects (Bever *et al*., 1996; Lugo and Cabello, 2002). Pringle and Bever (2002) suggested the

disparate temporal sporulation niches found in two common AM fungal species (*A. colossica* and *Gi. gigantea*) in the grassland they studied may facilitate co-existence.

Other effects are reported. Preliminary investigation of the effect of granitic rock-dust added to laterite iron-ore mine spoil conducted by Willis and Rodrigues (unpublished) suggested increase in AM fungal spore abundance. Biochar has positive effects on abundance of, and colonization by, AM fungi. Warnock *et al*. (2007) proposed four possible mechanisms, effects on soil physico-chemical properties; effects through influence on other soil microbes; interactions with plant-fungus signalling, including adsorption of labile and volatile toxins; and refuge from fungal grazers. Extraradical hyphal invasion of OM fraction in soil is often found to be extensive (Hodge *et al*., 2001) with significant positive influence on fungal biomass, colonization and sporulation. Several predicted scenarios of GCC outcome suggest significant increase in OM levels in soils. Where both roots and fungal hyphae occupy the same OM patch however, fungal biomass can be reduced (Hodge, 2003). A report by Mack and Rudgers (2008) described a strong reduction in AM fungal root colonization in the invasive grass species *Schedonorus phoenix* (tall fescue) simultaneously colonized by the symbiotic herbivore-deterring foliar endophyte *Neotyphodium coenophialum*. There was positive correlation between *Neotyphodium* hyphal density and plant biomass and negative correlation with AM fungal colonization. Mycorrhizal fungi treatments had no significant impact on the endophyte.

G. A Little P Goes a Long Way

Soil P scarcity is the most commonly reported effect of increase in AM fungal root colonization and spore abundance, a reflection on the phylums assistance in green plants gaining a foot-hold on dry land. Hostile, nutrient-deficient environments tend to carry diverse AM species even where the host plant diversity is low. Fungal species and functional diversities generally increase with plant community species diversity but even in low P monoculture fungal diversity is generally greater than in high P status multi-host soils (Hijri *et al*., 2006).

The control mechanism would seem to be direct positive feedback mediated by host plant increase in C supply. It is probable the hyphal web response is to increase in mass and length in order to forage further for soil nutrient, but to what extent is the more efficient, say, P donor AM fungal species advantaged? Is reciprocal exchange equal? Is P diverted away from the host plant species making the least demand, i.e., reduced C contribution, to the host plant species making the greatest demand, increased C contribution? If P supply is a direct feedback response, do plants with higher mycorrhizal dependancy allocate more C to the symbiont? What are the mechanisms which distribute nutrients throughout the web and control nutrient transport between plants in the community?

Such considerations assume Glomeromycota to be benign. Johnson *et al*. (1997), however, proposed AM fungi may operate along a mutualism–parasitism gradient, on the premise that the fungal symbiont is parasitic where it gains in nutrient exchange and mutualistic where net gains are equal. It is suggested here AM fungi may employ a rapid and dynamic mutualism-commensalism-parasitism gradient strategy whereby they continually alter mode of action in accommodation of even the smallest change in environmental influence. Cost : benefit ratio, to both plant and fungus, may constantly fluctuate.

XVIII. CONCLUSIONS

Glomeromycota are complex ancient organisms, globally distributed and intrinsically involved in possibly all aspects of soil ecology, and directly or indirectly in many aspects of above-ground ecology. It is clear they have considerable impact upon their edaphic and biotic surroundings, above- and below-ground, spatially and temporally affecting every terrestrial niche across almost every biome. Wherever there are natural plant communities, there will be AM fungal influence. Mycorrhizodeposition of photosynthates plays a fundamental role in the carbon cycle, facilitating specific saprotrophic microbial community development which suggests a tripartite symbiosis in soils involving plant host, AM fungi and associative microbes is common. Infinite combinations of species could enhance plant growth and community development in almost all spatial and temporal complexities of soils heterogeneity.

The many functional roles of AM fungi and the spatial and temporal extent of those functions at the interface between abiotic and biotic elements suggest the phylum is a primary ecosystem facilitator, a 'keystone mutualist' (O'Neill *et al*., 1991), perhaps even a mediator in plant co-existance (Hart *et al*., 2003), co-operation, and self-maintaining strategies. Future research, particularly quantifying AM fungal impact or "*relative influence*" (Klironomos *et al*., 2011) will help clarify these concepts, even should, as the authors put it, "quantification raise(s) the spectre that the mycorrhizal symbiosis may not be a significant driver of plant community dynamics in some or many ecosystems." The higher plant/Glomeromycota symbiosis is, however, so entwined that it is probably implausible to study the ecology of either one in isolation.

REFERENCES

Abbott, L. K. and Robson, A. D. 1985. Formation of external hyphae in soil by four species of vesicular-arbuscular mycorrhizal fungi. *New Phytol*. **99**: 245–255.

Abd-Alla, M. H., Omar, S. A., and Karanxha, S. 2000. The impact of pesticides on arbuscular mycorrhizal and nitrogen fixing symbioses in legumes. *Appl. Soil Ecol.* **14**: 191–200.

Addy, H. D., Miller, M. H., and Peterson, R. L. 1997. Infectivity of the propagules associated with extraradical mycelia of two AM fungi following winter freezing. *New Phytol.* **135**: 745–753.

Alexander, T., Meier, R., Toth, R., and Weber, H. C. 1988. Dynamics of arbuscule development and degeneration in mycorrhizas of *Triticum aestivum* L. and *Avena sativa* L. with reference to *Zea mays* L. *New Phytol.* **110**: 363–370.

Alkan, N., Gadkar, V., Coburn, J., Yarden, O., and Kapulnik, Y. 1994. Quantification of the arbuscular mycorrhizal fungus *Glomus intraradices* in host tissue using real-time polymerase chain reaction. *New Phytol.* **161**: 877–885.

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Alkan, N., Gadkar, V., Yarden, O., and Kapulnik, Y. 2006. Analysis of quantitative interactions between two species of arbuscular mycorrhizal fungi, *Glomus mosseae* and *G. intraradices*, by Real-Time PCR. *Appl. Environ. Microbiol.* **72**: 4192–4199.

Allen, M. F. 2007. Mycorrhizal fungi: highways for water and nutrients in arid soils. *Vadose Zone J.* **6**: 291–297.

Allen, M. F. and Shachar-Hill, Y. 2009. Sulphur transfer through an arbuscular mycorrhiza. *Plant Physiol.* **149**: 549–560.

Allen, M. F., Smith, W. K., Moore, T. S. Jr., and Christensen, M. 1981. Comparative water relations and photosynthesis of mycorrhizal and non-mycorrhizal *Bouteloua gracilis* H.B.K. LAG EX STEUD. *New Phytol.* **88**: 683–693.

Allen, M. F., Swenson, W., Querejeta, J. I., Egerton-Warburton, L. M., and Treseder, K. K. 2003. Ecology of Mycorrhizae: A conceptual framework for complex interactions among plants and fungi. *Annu. Rev. Phytopathol.* **42**: 271–303.

Anderson, R. C., Anderson, M. R., Bauer, J. T., Slater, M., Herold, J., Baumhardt, P., and Borowicz, V. 2010. Effect of removal of garlic mustard (*Alliaria petiolata*, Brassicaceae) on arbuscular mycorrhizal fungi inoculum potential in forest soils. *Open Ecol. J.* **3**: 41–47.

Antunes, P. M., Koch, A. M., Morton, J. B., Rillig, M. C., and Klironomos, J. N. 2011. Evidence for functional divergence in arbuscular mycorrhizal fungi from contrasting climatic origins. *New Phytol.* **189**: 507–514.

Aristizábal, C., Rivera, E. L., and Janos, D. P. 2004. Arbuscular mycorrhizal fungi colonize decomposing leaves of *Myrica parvifoliar*, *M. pubescens* and *Paepalanthus sp*. *Mycorrhiza* **14**: 221–228.

Artursson, V., Finlay, R. D., and Jansson, J. K. 2006. Interactions between arbuscular mycorrhizal fungi and bacteria and their potential for stimulating plant growth. *Environ. Microbiol.* **8**: 1–10.

Atul-Nayyar, Hamel, C., Forge, T., Selles, F., Jefferson, P. G., Hanson, K., and Germida, J. 2008. Arbuscular mycorrhizal fungi and nematodes are involved in negative feedback on a dual culture of alfalfa and Russian wildrye. *Appl. Soil Ecol.* **40**: 30–36.

Augé, R. M. 2001. Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis. *Mycorrhiza* **11**: 3–42.

Azcón-Aguilar, C., Bago, B., and Barea, J. M. 1999. Saprophytic growth of arbuscular mycorrhiza. **In:** *Mycorrhiza: Structure, Function, Molecular Biology and Biotechnology*. Varma, A. and Hock, B., Eds., Springer-Verlag, Berlin.

Bååth, E. and Spokes, J. 1989. The effect of added nitrogen and phosphorus on mycorrhizal growth response and infection in *Allium schoenoprasum*. *Can. J. Bot.* **67**: 3227–3232.

Bago, B., Pfeffer, P. E., Abubaker, J., Jun, J., Allen, J. W., Brouilette, J., Douds, D. D., Lammers, P. J., and Shachar-Hill, Y. 2003. Carbon export from arbuscular mycorrhizal roots involves the translocation of carbohydrate as well as lipid. *Plant Physiol.* **131**: 1496–1507.

Bago, B., Pfeffer, P. E., and Shachar-Hill, Y. 2000. Carbon metabolism and transport in arbuscular mycorrhizas. *Plant Physiol.* **124**: 949–958.

Bago, B., Pfeffer, P. E., Zipfel, W., Lammers, P., and Shachar-Hill, Y. 2002a. Tracking metabolism and imaging transport in arbuscular mycorrhizal fungi. *Plant Soil* **244**: 189–197.

Bago, B., Zipfel, W., Williams, R. M., Jeonwong, J., Arreola, R., Lammers, P. J., Pfeffer, P. E., and Shachar-Hill, Y. 2002b. Translocation and utilization of fungal storage lipid in the arbuscular mycorrhizal symbiosis. *Plant Physiol.* **128**: 108–124.

Bardgett, R. D., Freeman, C., and Ostle, N. J. 2008. Microbial contribution to climate change through carbon cycle feedbacks. *ISME J.* **2**: 805–814.

Barto, K., Friese, C., and Cipollini, D. 2010. Arbuscular mycorrhizal fungi protect a native plant from allelopathic effects of an invader. *J. Chem. Ecol.* **36**: 351–360.

Bennett, A. E., Bever, J. D., and Bowers, M. D. 2009. Arbuscular mycorrhizal fungal species suppress inducible plant responses and alter defensive strategies following herbivory. *Oecologia* **160**: 771–779.

Bever, J. D., Morton, J. B., Antonovics, J., and Schultz, P. A. 1996. Host-dependant sporulation and species diversity of arbuscular mycorrhizal fungi in a mown grassland. *J. Ecol.* **84**: 71–82.

Bever, J. D., Richardson, S. C., Lawrence, B. M., Holmes, J., and Watson, M. 2009. Preferential allocation to beneficial symbiont with spatial structure maintains mycorrhizal mutualism. *Ecol. Lett.* **12**: 13–21.

Bever, J. D., Scholtz, P. A., Pringle, A., and Morton, J. B. 2001. Arbuscular mycorrhizal fungi: More diverse than meets the eye, and the ecological tale of why. *Bioscience* **51**: 923–932.

Blanke, V., Renker, C., Wagner, M., Füllner, K., Held, M., Kuhn, A. J., and Buscot, F. 2005. Nitrogen supply affects arbuscular mycorrhizal colonization of *Artimisia vulgaris* in a phosphate-polluted field site. *New Phytol.* **166**: 981–992.

Bohrer, K., Friese, C., and Amon, J. 2004. Seasonal dynamics of arbuscular mycorrhizal fungi in differing wetland habitats. *Mycorrhiza* **14**: 329–337.

Bolan, N. S. 1991. A critical review on the role of mycorrhizal fungi in the uptake of phosphorus by plants. *Plant Soil* **134**: 189–207.

Brundrett, M. C. 2002. Coevolution of roots and mycorrhizas of land plants. *New Phytol.* **154**: 275–304.

Buendia-González, L., Orozco-Villefuerte, J., Cruz-Sosa, F., Barrera-Diáz, C. E., and Vernon-Carter, E. J. 2010. *Prosopis laevigata* a potential chromium (VI) and cadmium (II) hyperaccumulator desert plant. *Bioresource Technol.* **101**: 5862–5867.

Burke, D. J. 2008. Effects of *Alliaria petiolata* (garlic mustard, Brassicaceae) on mycorrhizal colonization and community structure in three herbaceous plants in a mixed deciduous forest. *Am. J. Bot.* **95**: 1416–1425.

Bürkert, B. and Robson, A. 1994. ^{65}Zn uptake in subterranean clover (*Trifolium subterranium* L.) by three vesicular-arbuscular mycorrhizal fungi in a root-free sandy soil. *Soil Biol. Biochem.* **26**: 1117–1124.

Callaway, R. M., Cipollini, D., Barto, K., Thelen, G. C., Hallett, S. G., Prati, D., Stinson, K., and Klironomos, J. 2008. Novel weapons: invasive plant suppresses fungal mutualists in America but not in its native Europe. *Ecology* **89**: 1043–1055.

Callaway, R. M., Mahall, B. E., Wicks, C., Pankey, J., and Zabinski, C. 2003. Soil fungi and the effects of an invasive forb on grasses: neighbor identity matters. *Ecology* **84**: 129–135.

Caris, C., Hördt, W., Hawkins, H-J., Römheld, V., and George, E. 1998. Studies of iron transport by arbuscular mycorrhizal hyphae to peanut and sorghum plants. *Mycorrhiza* **8**: 35–39.

Carvalho, L. M., Correia, P. M., Ryel, R. J., and Martins-Loucão, M. A. 2003. Spatial variability of arbuscular mycorrhizal fungal spores in two natural plant communities. *Plant Soil* **251**: 227–236.

Chen, X., Wu, C., Tang, J., and Hu, S. 2005. Arbuscular mycorrhizae enhance metal lead uptake and growth of host plants under a sand culture experiment. *Chemosphere* **60**: 665–671.

Cheng, X. and Baumgartner, K. 2004. Arbuscular mycorrhizal fungi-mediated nitrogen transfer from vineyard cover crops to grapevines. *Biol. Fertil. Soils* **40**: 406–412.

Chung, H., Zak, D. R., Reich, P. B., and Ellsworth, D. S. 2007. Plant species richness, elevated CO_2, and atmospheric nitrogen deposition alter soil microbial community composition and function. *Glob. Change Biol.* **13**: 980–989.

Clark, R. B. 1996. Growth and root colonization of mycorrhizal maize grown on acid and alkaline soil. *Soil Biol. Biochem.* **28**: 1505–1511.

Clark, R. B. and Zeto, S. K. 2000. Mineral acquisition by arbuscular mycorrhizal plants. *J. Plant Nutr.* **23**: 867–902.

Compant, S., van der Heijden, M. G.A., and Sessitsch, A. 2010. Climate change effects on beneficial plant-microorganism interactions. *FEMS Microbiol. Ecol.* **73**: 197–214.

Cornelissen, J. H.C., Aerts, R., Cerabolini, B., Werger, M. J.A., and van der Heijden, M. G.A. 2001. Carbon cycling traits of plant species are linked with mycorrhizal strategy. *Oecologia* **129**: 611–619.

Cox, G., Moran, K. J., Sanders, F., Nockolds, C., and Tinker, P. B. 1980. Translocation and transfer of nutrients in vesicular-arbuscular mycorrhizas. III. Polyphosphate granules and phosphorus translocation. *New Phytol.* **84**: 649–659.

Croll, D., Wille, L., Gamper, H. A., Mathimaran, N., Lammers, P. J., Corradi, N., and Sanders I. R. 2008. Genetic diversity and host plant preferences revealed by simple sequence repeat and mitochondrial markers in a population of

the arbuscular mycorrhizal fungus *Glomus intraradices*. *New Phytol.* **178**: 672–687.

Dauber, J., Niechoj, R., Baltruschat, H., and Wolters, V. 2008. Soil engineering ants increase grass root arbuscular mycorrhizal colonization. *Biol. Fert. Soils* **44**: 791–796.

De Jaeger, N., de la Providencia, I. E., Dupré de Boulois, H., and Declerck, S. 2011. *Trichoderma harzianum* might impact phosphorus transport by arbuscular mycorrhizal fungi. *FEMS Microbiol. Ecol.* **77**: 558–567.

De Jaeger, N., Declerck, S., and De La Providencia, I. E. 2010. Mycoparasitism of arbuscular mycorrhizal fungi: a pathway for the entry of saprotrophic fungi into roots. *FEMS Microbiol. Ecol.* **73**: 312–322.

de la Providencia, I., de Souza, F. A., Fernandez, F., Sejalon-Delmas, N., and Declerck, S. 2005. Arbuscular mycorrhizal fungi reveal distinct pattern of anastomoses formation and hyphal healing mechanism between different phylogenetic groups. *New Phytol.* **165**: 261–271.

Dhillion, S. S. 1993. Vesicular-arbuscular mycorrhizas of *Equisetum* species in Norway and the U.S.A.: occurrence and mycotrophy. *Mycol. Res.* **97**: 656–660.

Dickson, S. 2004. The *Arum-Paris* continuum of mycorrhizal symbioses. *New Phytol.* **163**: 187–200.

Dodd, J. C. and Jeffries, P. 1989. Effects of herbicides on three vesicular-arbuscular fungi associated with winter wheat (*Triticum aestivum* L.). *Biol. Fert. Soils* **7**: 113–119.

Douds Jr., D. D. and Millner, P. D. 1999. Biodiversity of arbuscular mycorrhizal fungi in agroecosystems. *Agr. Ecosyst. Environ.* **74**: 77–93.

Douds Jr., D. D. and Schenk, N. C. 1990. Increased sporulation of arbuscular-mycorrhizal fungi by manipulation of nutrient regimens. *Appl. Environs. Microbiol.* **56**: 413–418.

Drissner, D., Kunze, G., Calleweart, N., Gehrig, P., Tamasloukht, M'B., Boller, T., Felix, G., Amrhein, N., and Bucher, M. 2007. Lyso-Phosphatidylcholine is a signal in the arbuscular mycorrhizal symbiosis. *Science* **318**: 265–268.

Duckett, J. G., Carafa, A., and Ligrone, R. 2006. A highly differentiated glomeromycotean association with the mucilage-secreting, primitive antipodean liverwort *Treubia* (Treubiaceae): clues to the origins of mycorrhizas. *Am. J. Bot.* **93**: 797–813.

Egerton-Warburton, L. M. and Allen E. B. 2000. Shifts in arbuscular mycorrhizal communities along an anthropogenic nitrogen deposition gradient. *Ecol. Appl.* **10**: 484–496.

Egerton-Warburton, L. M., Graham, R. C., Allen, E. B., and Allen, M. F. 2001. Reconstruction of the historical changes in mycorrhizal fungal communities under anthropogenic nitrogen deposition. *P. Roy. Soc. Lond. B Bio.* **268**: 2479–2484.

Egerton-Warburton, L. M., Johnson, N. C., and Allen, E. B. 2007. Mycorrhizal community dynamics following nitrogen fertilization: a cross-site test in five grasslands. *Ecol. Monogr.* **77**: 527–544.

Emiliani, G., Fondi, M., Fani, R., and Gribaldo, S 2009. A horizontal gene transfer at the origin of phenylpropanoid metabolism: a key adaptation of plants to land. *Biol. Dir.* **4**: 7.

Escudero, V. and Mendoza, R. 2005. Seasonal variation of arbuscular mycorrhizal fungi in temperate grasslands along a wide hydrologic gradient. *Mycorrhiza* **15**: 291–299.

Fitter, A. H. 1985. Functioning of vesicular-arbuscular mycorrhizas under field conditions. *New Phytol.* **99**: 257–265.

Fracchia, S., Mujica, M. T., García-Romera, I., García-Garrido, J. M., Martín, J., Ocampo, J. A., and Godeas, A. 1998. Interactions between *Glomus mosseae* and arbuscular mycorrhizal sporocarp-associated saprophytic fungi. *Plant Soil* **200**: 131–137.

Friese, C. F. and Allen M. F. 1991. The spread of VA mycorrhizal fungal hyphae in the soil: inoculum types and external hyphal architecture. *Mycologia* **83**: 409–418.

Friese, C. F. and Koske, R. E. 1991. The spatial dispersion of spores of vesicular-arbuscular mycorrhizal fungi in a sand dune; microscale patterns associated with the root architecture of American beachgrass. *Mycol. Res.* **95**: 952–957.

Gange, A. and Smith, A. K. 2005. Arbuscular mycorrhizal fungi influence visitation rates of pollinating insects. *Ecol. Entomol.* **30**: 600–606.

Gange, A. C., Brown, V. K., and Aplin, D. M. 2005. Ecological specificity of arbuscular mycorrhizae: evidence from foliar- and seed-feeding insects. *Ecology* **86**: 603–611.

Genre, A., Chabaud, M., Timmers, T., Bonfante, P., and Barker, D. G. 2005. Arbuscular mycorrhizal fungi elicit a novel intracellular apparatus in *Medicago truncatula* root epidermal cells before infection. *Plant Cell* **17**: 3489–3499.

Gerdeman, J. W. 1965. Vesicular-arbuscular mycorrhizas formed on maize and tulip tree by *Endogone fasciculata*. *Mycologia* **57**: 562–575.

Giovannetti, M., Avio, L., Fortuna, P., Pellegrino, E., Sbrana, C., and Strani, P. 2006. At the root of the wood wide web. *Plant Signal. Behav.* **1**: 1–5.

Giovannetti, M., Azzolini, D., and Citernesi, A. S. 1999. Anastomosis formation and nuclear and protoplasmic exchange in arbuscular mycorrhizal fungi. *Appl. Environ. Microbiol.* **65**: 5571–5575.

Giovannetti, M. and Hepper, C. M. 1985. Vesicular-arbuscular infection in *Hedysarum coronarium* and *Onobrychis viciifolia*: host-endophyte specificity. *Soil Biol. Biochem.* **17**: 899–900.

Giovannetti, M., Sbrana, C., Avio, L, Cisternesi, and Logi, C. 1993. Differential hyphal morphogenesis in arbuscular mycorrhizal fungi during pre-infection stages. *New Phytol*. **125**: 587–593.

Göhre, V. and Paszkowski, U. 2006. Contribution of arbuscular mycorrhizal symbiosis to heavy metal phytoremediation. *Planta* **223**: 1115–1122.

González-Chávez, M. C., Carillo-González, R., Wright, S. F., and Nichols, K. A. 2004. The role of glomalin, a protein produced by arbuscular mycorrhizal fungi, in sequestering potentially toxic elements. *Environ. Pollut.* **130**: 317–323.

Gould, A. B. and Liberta, A. E. 1981. Effects of topsoil storage during surface mining on the viability of vesicular-arbuscular mycorrhiza. *Mycologia* **73**: 914–922.

Govindarajulu, M., Pfeffer, P. E., Jin, H., Abubaker, J., Douds, D. D., Allen, J. W., Bücking, H., Lammers, P. J., and Shachar-Hill, Y 2005. Nitrogen transfer in the mycorrhizal symbiosis. *Nature* **435**: 819–823.

Green, H., Larsen, J., Olsson, P. A., Jensen, D. F., and Jakobsen, I. 1999. Suppression of the biocontrol agent *Trichoderma harzianum* by mycelium of the arbuscular mycorrhizal fungus *Glomus intraradices* in root-free soil. *Appl. Environ. Microbiol.* **65**: 1428–1434.

Guether, M., Volpe, V., Balestrini, R., Requena, N., Wipf, D., and Bonfante, P. 2011. LjLHT1.2 – a mycorrhiza-inducible plant amino acid transporter from *Lotus japonicus*. *Biol. Fertil. Soils* **47**: 924–936.

Hall, J. L. 2002. Cellular mechanisms for heavy metal detoxification and tolerance. *J. Exp. Bot.* **53**: 1–11.

Harley, J. L. and Smith, S. E. 1983. *Mycorrhizal Symbiosis*. Academic Press, London.

Harner, M. J., Opitz, N., Geluso, K., Tockner, K, and Rillig, M. C. 2011. Arbuscular mycorrhizal fungi on developing islands within a dynamic river floodplain: an investigation across successional gradients and soil depth. *Aquat. Sci.* **73**: 35–42.

Harper, J. L. 1977. *Population Biology of Plants.* Academic Press, London.

Hart, M. M. and Reader, R. J. 2002. Taxanomic basis for variation in the colonization strategy of arbuscular mycorrhizal fungi. *New Phytol.* **153**: 335–344.

Hart, M. M., Reader, R. J., and Klironomos, J. N. 2003. Plant coexistance mediated by by arbuscular mycorrhizal fungi. *Trends Ecol. Evol.* **18**: 418–423.

Hart, M. M., Reader, R. J., and Klironomos, J. N. 2001. Life-history strategies of arbuscular mycorrhizal fungi in relation to their successional dynamics. *Mycologia* **93**: 1186–1194.

Helgason, T. and Fitter, A. 2005. The ecology and evolution of the arbuscular mycorrhizal fungi. *Mycologist* **19**: 96–101.

Hempel, S., Stein, C., Unsicker, S. B., Renker, C., Auge, H., Weisser, W. W., and Buscot, F. 2009. Specific bottom-up effects of arbuscular mycorrhizal fungi across a plant-herbivore-parasitoid system. *Oecologia* **160**: 267–277.

Hijri, M. and Sanders, I. R. 2005. Low gene copy number shows that arbuscular mycorrhizal fungi inherit genetically different nuclei. *Nature* **433**: 160–163.

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Hijri, M., Sýkorová, Z., Oehl, F., Ineichen, K., Mäder, P., Wiemken, A., and Redecker, D. 2006. Communities of arbuscular mycorrhizal fungi in arable soils are not necessarily low in diversity. *Mol. Ecol.* **15**: 2277–2289.

Hodge, A. 2003. Plant nitrogen capture from organic matter as affected by spatial dispersion, interspecific competition and mycorhizal colonization. *New Phytol.* **157**: 303–314.

Hodge, A. and Fitter, A. H. 2010. Substantial nitrogen acquisition by arbuscular mycorrhizal fungi from organic material has implication for N cycling. *Proc. Natl. Acad. Sci. USA* **107**: 13754–13759.

Hodge, A., Campbell, C. D., and Fitter, A. H. 2001. An arbuscular mycorrhizal fungus accelerates decomposition and acquires nitrogen directly from organic material. *Nature* **413**: 297–299.

Hoffmann, D., Vierheilig, H., and Schausberger, P. 2010. Mycorrhiza–induced trophic cascade enhances fitness and population growth of an acarine predator. *Oecologia* **166**: 141–149.

Husband, R., Herre, E. A., Turner, S. L., Gallery, R., and Young, J. P.W. 2002. Molecular diversity of arbuscular mycorrhizal fungi and patterns of host association over time and space in a tropical forest. *Mol. Ecol.* **11**: 2669–2678.

Janos, D. P. 1987. VA mycorrhizas in humid tropical ecosystems. **In:** *Ecophysiology of VA Mycorrhizal Plants.* Safir, G. R., Ed., CRC Press, Boca Raton, Florida.

Jansa, J., Smith F. A., and Smith S. E. 2008. Are there benefits of simultaneous root colonization by different arbuscular mycorrhizal fungi? *New Phytol.* **177**: 779–789.

Jasper, D. A., Abbott, L. K., and Robson, A. D. 1989. Soil disturbance reduces the infectivity of external hyphae of arbuscular mycorrhizal fungi. *New Phytol.* **112**: 93–99.

Jia, Y., Gray, V. M., and Straker, C. J. 2004. The influence of *Rhizobium* and arbuscular mycorrhizal fungi on nitrogen and phosphorus accumulation by *Vicia faba*. *Ann.Bot.* **94**: 251–258.

Johnson, C. R. 1984. Phosphorus nutrition on mycorrhizal colonization, photosynthesis, growth and nutrient composition of *Citrus aurantium*. *Plant Soil* **80**: 35–42.

Johnson, N. C. and Pfleger, F. L. 1992. Vesicular-arbuscular mycorrhizae and cultural stress. **In:** *VA Mycorrhizae in Sustainable Agriculture.* pp. 71–99. Bethlenfalvay, G. et al., Eds., ASA/SSSA Special publication No. 54. American Society of Agronomy, Madison.

Johnson, N. C., Graham, J. H., and Smith, F. A. 1997. Functioning of mycorrhizal associations along the mutualism-parasitism continuum. *New Phytol.* **135**: 575–585.

Johnson, N. C., Rowland, D. L., Corkidi, L., Egerton-Warburton, L. M., and Allen, E. B. 2003. Nitrogen enrichment alters mycorrhizal allocation at five mesic to semiarid grasslands. *Ecology* **84**: 1895–1908.

Johnson, N. C., Wilson, G. W.T., Bowker, M. A., Wilson, J. A., and Miller, R. M. 2010. Resource limitation is a driver of local adaptation in mycorrhizal symbioses. *P. Natl. Acad. Sci. USA* **107**: 2093–2098.

Johnson, N. C., Wolf, J., Reyes, M. A., Panter, A., Koch, G. W., and Redman, A. 2005. Species of plants and associated arbuscular mycorrhizal fungi mediate mycorrhizal responses to CO_2 enrichment. *Glob. Change Biol.* **11**: 1156–1166.

Joner, E. J., Briones, R., and Leyval, C. 2000. Metal-binding capacity of arbuscular mycorrhizal mycelium. *Plant Soil* **226**: 227–234.

Joner, E. J., van Aarle, I. M., and Vosatka, M. 2000. Phosphatase activity of extra-radical arbuscular mycorrhizal hyphae: a review. *Plant Soil* **226**: 199–210.

Jones, D. L., Nguyen, C., and Finlay, R. D. 2009. Carbon flow in the rhizosphere: carbon trading at the soil-root interface. *Plant Soil* **321**: 5–33.

Jurkiewicz, A., Ryszka, P., Anielska, T., Waligórski, P., Bialońska, D., Góralska, K., Tsimilli-Michael, M., and Turnau, K. 2010. Optimization of culture conditions of *Arnica montana* L.: effects of mycorrhizal fungi and competing plants. *Mycorrhiza* **20**: 293–306.

Karandashov, V. and Bucher, M. 2005. Symbiotic phosphate transport in arbuscular mycorrhizas. *Trends Plant Sci.* **10**: 22–29.

Kinden, D. A. and Brown, M. F. 1975. Electron microscopy of vesicular-arbuscular mycorrhizae of yellow poplar. II. Intracellular hyphae and vesicles. *Can. J. Microbiol.* **21**: 1768–1780.

Klironomos, J. N. 2003. Variation in plant response to native and exotic arbuscular mycorrhizal fungi. *Ecology* **84**: 2292–2301.

Klironomos, J. N. and Kendrick, W. B. 1996. Palatability of microfungi to soil arthropods in relation to the functioning of arbuscular mycorrhizae. *Biol. Fert. Soils* **21**: 43–52.

Klironomos, J. N., Bednarczuk, E. M., and Neville, J. 1999. Reproductive significance of feeding on saprobic and arbuscular mycorrhizal fungi by the collembolan, *Falsomia candida*. *Funct. Ecol.* **13**: 756–761.

Klironomos, J. N., Rillig, M. C., Allen, M. F., Zak, D. R., Kubiske, M., and Pregitzer, K. S. 1997. Soil fungal-arthropod responses to *Populus tremuloides* grown under enriched atmospheric CO_2 under field conditions. *Glob. Change Biol.* **3**: 473–478.

Klironomos, J. N., Ursic, M., Rillig, M., and Allen, M. F. 1998. Interspecific differences in the response of arbuscular mycorrhizal fungi to *Artemisia tridentata* grown under elevated atmospheric CO_2. *New Phytol.* **138**: 599–605.

Klironomos, J. N., Zobel, N., Tibbett, M., Stock, W. D., Rillig, M. C., Parrent, J. L., Moora, M., Koch, A. M., Facelli, J. M., Facelli, E., Dickie, I. A., and Bever, J. D. 2011. Forces that structure plant communities: quantifying the importance of the mycorrhizal symbiosis. *New Phytol.* **189**: 366–370.

Kobae, Y. and Hata, S. 2010. Dynamics of periarbuscular membranes visualized with a fluorescent phosphate transporter in arbucular mycorrhizal roots of rice. *Plant Cell Physiol.* **51**: 341–353.

Koide, R. T. and Kabir, Z. 2000. Extraradical hyphae of the mycorrhizal fungus *Glomus intraradices* can hydrolyze organic phosphate. *New Phytol.* **148**: 511–517.

König, S., Wubet, T., Dormann, C. F., Hempel, S., Renker, C., and Buscot, F. 2010. TaqMan real-time PCR assays to assess arbuscular mycorrhizal responses to field manipulation of grassland biodiversity: effects of soil characteristics, plant species richness, and functional traits. *Appl. Environ. Microbiol.* **76**: 3765–3775.

Korb, J. E., Johnson, N. C., and Covington, W. W. 2003. Arbuscular mycorrhizal propagule densities respond rapidly to ponderosa pine restoration treatments. *J. Appl. Ecol.* **40**: 101–110.

Kough, J. L., Gianinazzi-Pearson, V., and Gianinazzi, S. 1987. Depressed metabolic activity of vesicular-arbuscular mycorrhizal fungi after fungicide applications. *New Phytol.* **106**: 707–715.

Krämer, U. 2010. Metal hyperaccumulation in plants. *Ann. Rev. Plant Biol.* **61**: 517–534.

Kubota, M., McGonigle, T. P., and Hyakumachi, M. 2005. Co-occurance of *Arum*- and *Paris*-type morphologies of arbuscular mycorrhizae in cucumber and tomato. *Mycorrhiza* **15**: 73–77.

Lacey, J. R., Marlow, C. B., and Lane, J. R. 1989. Influence of spotted Knapweed (*Centaurea maculosa*) on surface runoff and sediment yield. *Weed Technol.* **3**: 627–631.

Leigh, J., Hodge, A., and Fitter, A. H. 2008. Arbuscular mycorrhizal fungi can transfer substantial amounts of nitrogen to the host plant from organic material. *New Phytol.* **181**: 199–207.

Li, X-L., Marschner, H., and George, E. 2006. Acquisition of phosphorus and copper by VA-mycorrhizal hyphae and root-to-shoot transport in white clover. *Plant Soil* **136**: 49–57.

Lücking, R., Huhndorf, S., Pfister, D. H., Plata, E. R., and Lumbsch, H. T. 2009. Fungi evolved right on track. *Mycologia* **101**: 810–822.

Lugo, M. A. and Cabello, M. N. 2002. Native arbuscular mycorrhizal fungi (AMF) from mountain grassland (Córdoba, Argentina) I. Seasonal variation of fungal spore diversity. *Mycologia* **94**: 579–586.

Mack, K. M.L. and Rudgers, J. A. (2008. Balancing multiple mutualists: asymmetric interactions among plants, arbuscular mycorrhizal fungi, and fungal endophytes. *Oikos* **117**: 310–320.

Mangan, S. A. and Adler, G. H. 2000. Consumption of arbuscular mycorrhizal fungi by terrestial and arboreal small mammals in a Panamanian cloud forest. *J. Mammal.* **81**: 563–570.

Marler, M. J., Zabinski, C. A., and Callaway, R. M. 1999. Mycorrhizae indirectly enhance competitive effects of an invasive forb on a native bunchgrass. *Ecology* **80**: 1180–1186.

Marschner, H. and Dell, B. 2006. Nutrient uptake in mycorrhizal symbiosis. *Plant Soil* **159**: 89–102.

Martínez-Medina, A., Roldán, A., Albacete, A., and Pascual, J. A. 2011. The interaction with arbuscular mycorrhizal fungi or *Trichoderma harzianum* alters the shoot hormonal profile in melon plants. *Phytochemistry* **72**: 223–229.

Miller, R. M., Reinhardt, D. R., and Jastrow, J. D. 1995. External hyphal production of vesicular-arbuscular mycorrhizal fungi in pasture and tallgrass prairie communities. *Oecologia* **103**:17–23.

Miller, S. P. and Bever, J. D. 1999. Distribution of arbuscular mycorrhizal fungi in stands of the wetland grass *Panicum hemitomon* along a wide hydrologic gradient. *Oecologia* **119**: 586–592.

Mosse, B. and Hepper, C. 1975. Vesicular-arbuscular mycorrhizal infections in root organ cultures. *Physiol. Plant Pathol.* **5**: 215–223.

Motosugi, H. and Terashima, S. 2006. Nitrogen transport by hyphae of arbuscular mycorrhizal fungi between grapevine and cover crop (*Vulpia myuros*). *Acta Hortic.* **767**: 361–368.

Mummey, D. L. and Rillig, M. C. 2006. The invasive plant species *Centaurea maculosa* alters arbuscular mycorrhizal fungal communities in the field. *Plant Soil* **288**: 81–90.

Munkvold, L., Kjøller, R., Vestberg, M., Rosendahl, S., and Jakobsen, I. 2004. High functional diversity within species of arbuscular mycorrhizal fungi. *New Phytol.* **164**: 357–364.

Muthukumar, T. and Udaiyan, K. 2002. Arbuscular mycorrhizas in cycads of southern India. *Mycorrhiza* **12**: 213–217.

Muthukumar, T. and Udaiyan, K. 2000. Influence of organic manures on arbuscular mycorrhizal fungi associated with *Vigna unguiculata* (L.) Walp. in relation to tissue nutrients and soluble carbohydrate in roots under field conditions. *Biol. Fert. Soils* **31**: 114–120.

Muthukumar, T., Radhika, K. P., Vaingankar, J., D'Souza, J., Dessai, S., and Rodrigues, B. F. 2009. Taxonomy of AM Fungi—An Update. **In:** *Arbuscular Mycorrhizae of Goa—A Manual of Identification Protocols*. Rodrigues, B. F. and Muthukumar, T., Eds., Goa University, Goa.

Navazio, L., Moscatiello, R., Genre, A., Novero, M., Baldan, B., Bonfante, P., and Mariani, P. 2007. A diffusable signal from arbuscular mycorrhizal fungi elicits a transient cytosolic calcium elevation in host plant cells. *Plant Physiol.* **144**: 673–681.

Newsham, K. K., Fitter, A. H., and Watkinson, A. R. 1995. Arbuscular mycorrhiza protect an annual grass from root pathogenic fungi in the field. *J. Ecol.* **83**: 991–1000.

Nicolson, T. H. 1975. Evolution of vesicular-arbuscular mycorrhizas. **In:** *Endomycorrhizas*. pp 25–34. Sanders F .E., Mosse B., and Tinker, P. B., Eds., Academic Press, London.

Ocampo, J. A. and Barea, J. M. 1985. Effect of carbamate herbicides on VA mycorrhizal infection and plant growth. *Plant Soil* **85**: 375–383.

Oehl, F., Sieverding, E., Ineichen, K., Mäder, P., Boller, T., and Wiemken, A. 2003. Impact of land use intensity on the species diversity of arbuscular mycorrhizal fungi in agroecosystems of Central Europe. *Appl. Environ. Microbiol.* **69**: 2816–2824.

Oehl, F., Sieverding, E., Ineichen, K., Ris, E., Boller, T., and Wiemken, A. 2005. Community structure of arbuscular mycorrhizal fungi at different soil depths in extensively and intensively managed agroecosystems. *New Phytol.* **165**: 273–283.

Oehl, F., Sieverding, E., Mäder, P., Dubois, D., Ineichen, K., Boller, T., and Wiemken, A. 2004. Impact of long-term conventional and organic farming on the diversity of arbuscular mycorrhizal fungi. *Oecologia* **138**: 574–583.

O'Neill, E. G., O'Neill, R. V., and Norby, R. J. 1991. Hierarchy theory as a guide to mycorrhizal research on large-scale problems. *Environ. Pollut.* **73**: 271–284.

Öpik, M., Vanatoa, A., Vanatoa, E., Moora, M., Davison, J., Kalwij, J. M., Reier, Ü., and Zobel, M. 2010. The online datadase Maarj*AM* reveals global and ecosystemic distribution patterns in arbuscular mycorrhizal fungi (Glomeromycota). *New Phytol.* **188**: 223–241.

Ortega-Larrocea, M. P. 2001. Arbuscular mycorrhizal fungi (AMF) spore abundance is affected by wastewater pollution in soils of Mezquital Valley in Central Mexico. **In:** *Sustaining the Global Farm*, pp. 676–681. Stott, D. E., Mohtar, R. H., and Steinhardt, G. C., Eds., USDA-ARS National Soil Erosion Laboratory, West Lafayette.

Owusu-Bennoah, E. and Mosse, B. 1979. Development of VA mycorrhiza (Eg and YV) in plants fed with nutrient solution in sand and nutrient film, culture. *Annual Report of Rothamsted Experimental Station for 1978, Part I*, p. 235.

Pawlowska, T. E. 2005. Genetic processes in arbuscular mycorrhizal fungi. *FEMS Microbiol. Lett.* **251**: 185–192.

Pellegrino, E., Ramasamy, C. K., Sbrana, C., Barberi, P., and Giovennetti, M. 2010. Selection of infective arbuscular mycorrhiza fungal isolates for field inoculation. *Ital. J. Agron.* **5**: 225–232.

Pirozynski, K. A. and Malloch, D. W. 1975. The origin of land plants: a matter of mycotrophism. *Biosystems* **6**: 153–164.

Pongrac, O., Vogel-Mikuš, K., Kump, P., Nečemer, M., Tolrà, R., Poschenrieder, C., Barceló, J., and Regvar, M. 2007. Changes in elemental uptake and arbuscular mycorrhizal colonization during the life cycle of *Thlaspi praecox* Wulfen. *Chemosphere* **69**: 1602–1609.

Posada, R. H., Franco, L. A., Ramos, C., Plazas, L. S., Suárez, J. C., and Álvarez, F. 2007. Effect of physical chemical and environmental characteristics on arbuscular mycorrhizal fungi in *Brachiaria decumbens* (stapf) pastures. *J. Appl. Microbiol.* **104**: 132–140.

Powell, J. R., Campbell, R. G., Dunfield, K. E., Gulden, R. H., Hart, M. M., Levy-Booth, D. J., Klironomos, J. N., Pauls, K. P., Swanton, C. J., Trevors, J. T., and Antunes, P. M. 2009. Effect of glyphosate on the tripartite symbiosis formed by *Glomus intraradices*, *Bradyrhizobium japonicum*, and genetically modified soybean. *Appl. Soil Ecol.* **41**: 128–136.

Pringle, A. and Bever, J. D. 2002. Divergent phenologies may facilitate the coexistence of arbuscular mycorrhizal fungi in a North Carolina grassland. *Am. J. Bot.* **89**: 1439–1446.

Pringle, A., Bever, J. D., Gardes, M., Parrent, J. L., Rillig, M.C., and Klironomos, J. N. 2009. Mycorrhizal symbioses and plant invasions. *Annu. Rev. Ecol. Evol. S.* **40**: 699–715.

Purin, S. and Rillig M. C. 2007. Parasitism of arbuscular mycorrhizal fungi: reviewing the evidence. *FEMS Microbiol. Lett.* **279**: 8–14.

Radhika, K. P. (2008) Studies of arbuscular mycorrhizal (AM) fungi in some commonly occurring medicinal plants of Goa. Unpublished PhD thesis, Botany Department, Goa University, Goa, India.

Radhika, K. P. and Rodrigues, B. F. 2007. Arbuscular mycorrhizae in association with aquatic and marshy plant species in Goa, India. *Aquat. Bot.* **86**: 291–294.

Redecker, D., Morton, J. B., and Bruns, T. D. 2000. Molecular phylogeny of the arbuscular mycorrhizal fungi *Glomus sinuosum* and *Sclerocystis coremioides*. *Mycologia* **92**: 282–285.

Redecker, D. and Raab, P. 2006. Phylogeny of the Glomeromycota (arbuscular mycorrhizal fungi): recent developments and new gene markers. *Mycologia* **98**: 885–895.

Remy, W., Taylor, T. N., Haas, H., and Kerp, H. 1994. Four hundred-million-year-old vesicular-arbuscular mycorrhizae. *P. Natl. Acad. Sci.* **91**: 11841–11843.

Reynolds, H. L., Hartley, A. E., Vogelsang, K. M., Bever, J. D., and Schultz, P. A. 2005. Arbuscular mycorrhizal fungi do not enhance nitrogen acquisition and growth of old-field perennials under low nitrogen supply in glasshouse culture. *New Phytol.* **167**: 869–880.

Rillig, M. C. 2004. Arbuscular mycorrhizae and terrestial ecosystem processes. *Ecol. Lett.* **7**: 740–754.

Rillig, M. C. and Allen, M. F. 1998. Arbuscular mycorrhizae of *Gutierrezia sarothrae* and elevated carbon dioxide: evidence for shifts in C allocation to within the mycobiont. *Soil Biol. Biochem.* **30**: 2001–2008.

Rillig, M. C., Lutgen, E. R., Ramsey, P. W., Klironomos, J. N., and Gannon, J. E. 2005. Microbiota accompanying different arbuscular mycorrhizal fungal isolates influence soil aggregation. *Pedobiologia* **49**: 251–259.

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Rillig, M. C. and Mummey, D. L. 2006. Mycorrhizas and soil structure. *New Phytol.* **171**: 41–53.

Rillig, M. C., Mummey, D. L., Ramsey, P. W., Klironomos, J. N., and Gannon, J. E. 2006. Phylogeny of arbuscular mycorrhizal fungi predicts community composition of symbiosis-associated bacteria. *FEMS Microbiol. Ecol.* **57**: 389–395.

Rillig, M. C., Wright, S. F., Allen, M. F., and Field, C. B. 1999. Rise in carbon dioxide changes soil structure. *Nature* **400**: 628.

Rillig, M. C., Wright, S. F., Kimball, B. A., Pinter, P. J., Wall, G. W., Ottman, M. J., and Leavitt, S. W. 2001a. Elevated carbon dioxide and irrigation effects on water stable aggregates in a *Sorghum* field: a possible role for arbuscular mycorrhizal fungi. *Glob. Change Biol.* **7**: 333–337.

Rillig, M. C., Wright, S. F., Nichols, K. A., Schmidt, W. F., and Torn, M. F. 2001b. Large contribution of arbuscular mycorrhizal fungi to soil carbon pools in tropical forest soils. *Plant Soil* **233**: 167–177.

Rillig, M. C., Wright, S. F., Shaw, M. R., and Field, C. B. 2002. Artificial climate warming positively affects arbuscular mycorrhizae but decreases soil aggregate water stability in an annual grass. *Oikos* **97**: 52–58.

Robinson-Boyer, L., Grzyb, I., and Jeffries, P. 2009. Shifting the balance from qualitative to quantitative analysis of arbuscular mycorrhizal communities in field soils. *Fungal Ecol.* **2**: 1–9.

Sakai, A. K., Allendorf, F. W., Holt, J. S. *et al.* 2001. The population biology of invasive species. *Annu. Rev. Ecol. Syst.* **32**: 305–332.

Sarma, H. 2011. Metal hyperaccumulation in plants: a review focusing on phytoremediation technology. *J. Environ. Sci. Technol.* **4**: 118–138.

Sbrana, C. M. and Giovannetti, M. 2005. Chemotropism in the arbuscular mycorrhizal fungus *Glomus mosseae*. *Mycorrhiza* **15**: 539–545.

Schreiner, R. P. and Bethlenfalvay, G. J. 1996. Mycorrhizae, biocides, and biocontrol. 4. Response of a mixed culture of arbuscular mycorrhizal fungi and host plant to three fungicides. *Biol. Fert. Soils* **23**: 189–195.

Schreiner, R. P., Tarara, J. M., and Smithyman, R. P. 2007. Deficit irrigation promotes arbuscular colonization of fine roots by mycorrhizal fungi in grapevines (*Vitis vinifera* L.) in an arid climate. *Mycorrhiza* **17**: 551–562.

Schüßler, A. 2000. *Glomus claroideum* forms an arbuscular mycorrhiza-like symbiosis with the hornwort *Anthoceros punctatus*. *Mycorrhiza* **10**: 15–21.

Schwab, S. M., Johnson, E. L.V., and Menge, J. A. 1982. Influence of simazine on formation of vesicular-arbuscular mycorrhizae in *Chenopodium quinona* Wild. *Plant Soil* **64**: 283–287.

Selosse, M-A., Richard, F., He, X., and Simard, S. W. 2006. Mycorrhizal networks: *des liaisons dangereuses*? *Tr. Ecol. Evol.* **21**: 621–628.

Shen H., Christie, P., and Li, X. 2006. Uptake of zinc, cadmium and phosphorus by arbuscular mycorrhizal maize (*Zea mays* L.) from a low available phosphorus calcareous soil spiked with zinc and cadmium. *Environ. Geochem. Hlth.* **28**: 111–119.

Simard, S. W., Perry, D. A., Jones, M. D., Myrold, D. D., Durall, D. M., and Molina, R. 1997. Net transfer of carbon between ectomycorrhizal tree species in the field. *Nature* **388**: 579–582.

Simon, L., Lalonde, M., and Bruns, T. D. 1992. Specific amplification of 18S fungal ribosomal genes from vesicular-arbuscular endomycorrhizal fungi colonizing roots. *Appl. Environ. Microbiol.* **58**: 291–295.

Sjöberg, J., Persson, P., Mårtensson, A., Mattsson, L., Adholeya, A., and Alström, S. 2004. Occurrence of *Glomeromycota* spores and some arbuscular mycorrhizal species in arable fields in Sweden. *Acta Agric. Scand., Section B-Soil and Plant Sci.* **54**: 202–212.

Smith, F. A. and Smith, S. E. 1997. Structural diversity in (vesicular)-arbuscular mycorrhizal symbioses. *New Phytol.* **137**: 373–388.

Smith, F. A., Jakobsen, I., and Smith, S. E. 2000. Spatial differences in acquisition of soil phosphate between two arbuscular mycorrhizal fungi in symbiosis with *Medicago truncatula*. *New Phytol.* **147**: 357–366.

Smith, S. E. and Gianinazzi-Pearson, V. 1988. Physiological interactions between symbionts in vesicular-arbuscular mycorrhizal plants. *Annu. Rev. Plant Phys.* **39**: 221–244.

Smith, S. E., Facelli, E., Pope, S., and Smith, F. A. 2010. Plant performance in stressful environments: interpreting new and established knowledge of the roles of arbuscular mycorrhizas. *Plant Soil* **326**: 3–20.

Smith, S. E. and Read, D. J. 2008. *Mycorrhizal Symbiosis.* 3rd Ed., Academic Press, London.

Smith, S. E., Smith, F. A., and Jakobsen, I. 2004. Functional diversity in arbuscular mycorrhizal (AM) symbioses: the contribution of the mycorrhizal P uptake pathway is not correlated with mycorrhizal responses in growth or total P uptake. *New Phytol.* **162**: 511–524.

Solaiman, M. Z., Ezawa, T., Kojima, T., and Saito, M. 1999. Polyphosphates in intraradical and extraradical hyphae of an arbuscular mycorrhizal fungus, *Gigaspora margarita*. *Appl. Environ. Microbiol.* **65**: 5604–5606.

Sreenivasa, M. N. and Bagyaraj, D. J. 1989. Use of pesticides for mass production of vesicular-arbuscular mycorrhizal inoculum. *Plant Soil* **119**: 127–132.

Srivastava, D. and Mukerji, K. G. 1995. Field response of mycorrhizal and nonmycorrhizal *Medicago sativa* var. local in the F1 generation. *Mycorrhiza* **5**: 219–221.

Stinson, K. A., Campbell, S. A., Powell, J. R., Wolfe, B. E., Callaway, R. M., *et al.* 2006. Invasive plant suppresses the growth of native tree seedlings by disrupting belowground mutualisms. *PLoS Biol.* **4**: 0727–0731.

Strullu-Derrien, C. and Strullu, D-G. 2007. Mycorrhization of fossil and living plants. *CR Palevol* **6**: 483–494.

Stubblefield, S. P., Taylor, T. N., and Trappe, J. M. 1987. Fossil mycorrhizae: a case for symbiosis. *Science* **237**: 59–60.

Suzuki, H., Kumagai, H., Oohashi, K., Sakamoto, K., Inubushi, K., and Enomoyo, S. 2001. Transport of trace elements through the hyphae of an arbuscular mycorrhizal fungus into marigold determined by the multitracer technique. *Soil Sci. Plant Nutr.* **47**: 131–137.

Sylvia, D. M. 1992. Quantification of external hyphae of vesicular-arbuscular mycorrhizal fungi. *Method Microbiol.* **24**: 53–65.

Tamasloukht, M. B., Séjalon-Delmas, N., Kluever, A., Jauneau, A., Roux, C., Bécard, G., and Franken, P. 2003. Root factors induce mitochondrial-related gene expression and fungal respiration during the developmental switch from asymbiosis to presymbiosis in the arbuscular mycorrhizal fungus *Gigaspora rosea*. *Plant Physiol.* **131**: 1468–1478.

Tang, J., Xu, L., Chen, X., and Hu, S. 2009. Interaction between C_4 barnyard grass and C_3 upland rice under elevated CO_2: impact of mycorrhizae. *Acta Ecol.* **35**: 227–235.

Thao, H. T.B., George, T., Yamakawa, T., and Widowati, L. R. 2008. Effects of soil aggregate size on phosphorus extractability and uptake by rice (*Oryza sativa* L.) and corn (*Zea mays* L.) in two Ultisols from the Philippines. *Soil Sci. Plant Nutr.* **54**: 148–158.

Tobar, R., Azcón, R. and Barea, J. M. 1994 Improved nitrogen uptake and transport from ^{15}N-labelled nitrate by external hyphae of arbuscular mycorrhiza under water-stressed conditions. *New Phytol.* **126**: 119–122.

Toljander, J. F., Lindahl, B. D., Paul, L. R., Elfstrand, M., and Finlay, R. 2007. Influence of arbuscular mycorrhizal exudates on soil bacterial growth and community structure. *FEMS Microbiol. Ecol.* **61**: 295–304.

Treseder, K. K. 2004. A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO_2 in field studies. *New Phytol.* **164**: 347–355.

Treseder, K. K. and Allen, M. F. 2000. Mycorrhizal fungi have a potential role in soil carbon storage under elevated CO_2 and nitrogen deposition. *New Phytol.* **147**: 189–200.

Treseder, K. K. and Cross, A. 2006. Global distributions of arbuscular mycorrhizal fungi. *Ecosystems* **9**: 305–316.

Trotta, A., Falaschi, P., Cornara, L., Minganti V., Fusconi, A., Drava, G., and Berta, G. 2006. Arbuscular mycorrhiza increase the arsenic translocation factor in the As hyperaccumulating fern *Pteris vittata* L. *Chemosphere* **65**: 74–81.

Tullio, M., Pierandrei, F., Salerno, A., and Rea, E. 2003. Tolerance to cadmium of vesicular mycorrhizal spores isolated from a cadmium polluted and unpolluted soil. *Biol. Fert. Soils* **37**: 211–214.

Ultra, V., Tanaka, S., Sakurai, K., and Iwasaki, K. 2007. Effects of arbuscular mycorrhiza and phosphorus application on arsenic toxicity in sunflower

(*Helianthus annuus* L.) and on the transformation of arsenic in the rhizosphere. *Plant Soil* **290**: 29–41.

Van Aarle, I. M., Cavagnaro, T. R., Smith, S. E., Smith, F. A., and Dickson, S. 2005. Metabolic activity of *Glomus intraradices* in *Arum*- and *Paris*-type arbuscular mycorrhizal colonization. *New Phytol.* **166**: 611–618.

Vandenkoornhuyse, P., Ridgway, K. P., Watson, I. J., Fitter, A. H., and Young, J. P.W. 2003. Co-existing grass species have distinctive arbuscular mycorrhizal communities. *Mol. Ecol.* **12**: 3085–3095.

Vandenkoornhuyse, P., Husband, R., Daniell, D. J., Watson, I. J., Duck, J. M., Fitter, A. H., and Young, J. P.W. 2002. Arbuscular mycorrhizal community composition associated with two plant species in a grassland ecosystem. *Mol. Ecol.* **11**: 1555–1564.

van der Heijden, M. G. A., Bardgett, R. D., and van Straalen, N. M. 2008. The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestial ecosystems. *Ecol. Lett.* **11**: 296–310.

van der Heijden, M. G. A., Klironomos, J. N., Ursic, M., Moutoglis, P., Streitwolf-Engel, R., Boller, T., Wiemken, A., and Sanders, I. R. 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* **396**: 69–72.

Walker, C. and Schüßler, A. 2002. online <http://invam.caf.wvu.edu/index.html> [21.6.2011]

Walling, S. Z. and Zabinski, C. A. 2004. Host plant differences in arbuscular mycorrhizae: Extra radical hyphae differences between an invasive forb and a native bunchgrass. *Plant Soil* **265**: 335–344.

Wang, B., and Qui, Y-L. 2006. Phylogenetic distribution and evolution of mycorrhizae in land plants. *Mycorrhiza* **16**: 299–363.

Wang, B., Yeun, L. H., Xue, J-Y., Liu, Y., Ané, J-M., and Qiu, Y-L. 2010. Presence of three mycorrhizal genes in the common ancestor of land plants suggests a key role of mycorrhizas in the colonization of land by plants. *New Phytol.* **186**: 514–525.

Wang, B., Yost, R. S., and Linquist, B. A. 2001. Soil aggregate size affects phosphorus desorption from highly weathered soils and plant growth. *Soil Sci. Soc. Am. J.* **65**: 139–146.

Wang, S. and Hayman, D. S. 1982. Effect of nitrogen on mycorrhizal infection. *Annual Report of RothamstedExperimental Station for 1981, Part 1*, p. 211.

Wangiyana, W., Cornish, P. S., and Morris, E. C. 2006. Arbuscular mycorrhizal fungi dynamics in contrasting cropping systems on vertisol and regosol soils of Lombok, Indonesia. *Exp. Agr.* **42**: 427–439.

Warnock, D. D., Lehmann, J., Kuyper, T. W., and Rillig, M. C. 2007. Mycorrhizal responses to biochar in soils—concepts and mechanisms. *Plant Soil* **300**: 9–20.

Weissenhorn, I., Leyval, C., Belgy, G., and Berthelin, J. 1995. Arbuscular mycorrhizal contribution to heavy metal uptake by maize (*Zea mays* L.) in pot culture with contaminated soils. *Mycorrhiza* **5**: 245–251.

Westall, F., de Wit, M. J., Dann, J., van der Gaast, S., de Ronde, C. E.J., and Gerneke, D. 2001. Early Archean fossil bacteria and biofilms in the hydrothermally influenced sediments from the Barberton greenstone belt, South Africa. *Precambrian Res.* **106**: 93–116.

Whittingham, J. and Read, D. J. 1982. Vesicular-arbuscular mycorrhiza in natural vegetation systems. III. Nutrient transfer between plants with mycorrhizal interconnections. *New Phytol*. **90**: 277–284.

Wilson, G. W.T., Hartnett, D. C., and Rice, C. W. 2006. Mycorrhizal-mediated phosphorus transfer between tallgrass prairie plants Sorghastrum nutans and Artimisia ludoviciana. *Funct. Ecol.* **20**: 427–435.

Wilson, J. M. 1984. Competition for infection between vesicular-arbuscular mycorrhizal fungi. *New Phytol.* **97**: 427–435.

Winther, J. L. and Friedman, W. E. 2008. Arbuscular mycorrhizal associations in Lycopodiaceae. *New Phytol.* **177**: 790–801.

Wright, S. F. and Upadhyaya, A. 1998. A survey of soils for aggregate stability and glomalin, a glycoprotein produced by hyphae of arbuscular mycorrhizal fungi. *Plant Soil* **198**: 97–107.

Zabinski, C. A., Quinn, L., and Callaway, R. M. 2002. Phosphorus uptake, not carbon transfer, explains arbuscular mycorrhizal enhancement of *Centaurea maculosa* in the presence of native grassland species. *Funct. Ecol.* **16**: 758–765.

Zhang, Y. and Guo, L-D. 2007. Arbuscular mycorrhizal structure and function associated with mosses. *Mycorrhiza* **17**: 319–325.

Zhu, Y. G. and Miller, R. M. 2003. Carbon cycling by arbuscular mycorrhizal fungi in soil-plant systems. *Trends Plant Sci.* **8**: 407–409.

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