



Tansley review

Resource stoichiometry elucidates the structure and function of arbuscular mycorrhizas across scales

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Summary

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Despite the fact that arbuscular mycorrhizal (AM) associations are among the most ancient, abundant and important symbioses in terrestrial ecosystems, there are currently few unifying theories that can be used to help understand the factors that control their structure and function. This review explores how a stoichiometric perspective facilitates integration of three complementary ecological and evolutionary models of mycorrhizal structure and function. AM symbiotic function should be governed by the relative availability of carbon, nitrogen and phosphorus (trade balance model) and allocation to plant and fungal structures should depend on the availabilities of these resources (functional equilibrium model). Moreover, in an evolutionary framework, communities of plants and AM fungi are predicted to adapt to each other and their local soil environment (co-adaptation model). Anthropogenic enrichment of essential resources in the environment is known to impact AM symbioses. A more predictive theory of AM structure and function will help us to better understand how these impacts may influence plant communities and ecosystem properties.

I. Introduction

Arbuscular mycorrhizal (AM) symbioses are inextricably linked with plant evolution and pedogenesis. Glomeromycota are believed to have evolved concurrently with terrestrial plants in the early Devonian 400 million yr ago (Pirozynski & Malloch, 1975; Brundrett, 2002). It is no exaggeration to state that 'arbuscular mycorrhizas are the mother of all plant root endosymbioses' (Parniske, 2008) because structures resembling AM fungi have been observed in fossil remains of the earliest land plants (Stubblefield *et al.*, 1987; Redecker *et al.*, 2000). Over hundreds of millions of years, Glomeromycotan symbioses have influenced the evolution of plant root morphology and physiology and, in turn, AM fungi evolved to be obligate biotrophs as their ecological and physiological requirements became more and more tightly intertwined with plant root functions. The mycelium of AM fungi constitutes a substantial proportion of the microbial biomass and organic carbon (C) of soils (Olsson *et al.*, 1999; Wilson *et al.*, 2009), and plays a major role in the formation of soil structure (Miller & Jastrow, 2000; Rillig & Mummey, 2006). Thus, concurrent evolution of land plants, Glomeromycotan fungi, and AM symbioses has been integral to soil formation.

Impacts of Glomeromycotan symbioses are initiated in microscopic arbuscules (Reinhardt, 2007) and manifested in ecosystem processes (Rillig, 2004). Arbuscular mycorrhizas influence the fitness of individual plants (e.g. Koide & Dickie, 2002), the composition of plant communities (e.g. Hartnett & Wilson, 2002) and the movement of matter and energy through ecosystems (e.g. Klironomos *et al.*, 2000; van der Heijden *et al.*, 2008), yet surprisingly little is known about the factors that control their structure and functioning. A conceptual framework that integrates mycorrhizal patterns across scales of organization is needed to advance our understanding about mycorrhizal symbioses to a predictive level (Miller & Kling, 2000; Graham, 2008). Sterner & Elser (2002) have shown that stoichiometric reasoning can correctly predict ecosystem phenomena from molecular principles and Allen *et al.* (2003) have suggested that this perspective may help advance mycorrhizal science.

Ecological stoichiometry provides an integrative conceptual framework by examining ecological interactions in the context of the law of conservation of matter and the law of definite proportions. Sterner & Elser (2002) define stoichiometry as the 'the quantitative relationship between constituents in a chemical substance', and their stoichiometric approach considers 'whole organisms as single abstract molecules'. Defining plants and Glomeromycotan fungi as chemical entities which must obey the laws of definite proportions and the conservation of mass and energy provides a common currency for many disparate models that may be used to understand the mechanisms of mycorrhizal structure and function. The purpose of this review is to explore

the usefulness of resource stoichiometry as a framework for understanding AM structure and function across ecological scales. The ultimate goal is to begin to develop a predictive theory to enable us to understand ecological and evolutionary constraints on AM symbioses. This may help predict how AM responses may either buffer or exacerbate global change (Bardgett *et al.*, 2008), and also guide agricultural and ecosystem management so that the beneficial effects of AM symbioses can be maximized (Abbott & Robson, 1991).

II. Overview of ecological and evolutionary models from a stoichiometric perspective

Models are abstractions of nature that help summarize and test our understanding of systems. Many different ecological and evolutionary models rely on the principles of resource stoichiometry. This review will explore how a stoichiometric perspective may be combined with these models to help explain empirical findings. One of the oldest and most fundamental models is the Sprengel–Liebig law of the minimum (Liebig, 1843; van der Ploeg *et al.*, 1999), which states that plant productivity may be controlled by a single essential resource that is in limited supply. Read (1991b) considered mycorrhizal associations to be '*nature's response to the law of the minimum*', and suggested that an 'ecologically sound approach to the question of mycorrhizal function would be to determine which nutrient or combination of nutrients most limits growth in a particular ecosystem and then to ask whether [mycorrhizal] infection can enhance access to that resource.' Indeed, a focus on limiting resources has often proved to be predictive of plant responses to their environment (Tilman, 1988).

1. Trade balance and functional equilibrium models

Biological market models use economic principles to explore the importance of resource stoichiometry in resource exchange between plants and their associated mycorrhizal fungi. The symbiotic dynamic of mycorrhizal trading partnerships is defined by two factors: resource requirements, and ability to acquire resources. These models build upon earlier cost–benefit models (Koide & Elliot, 1989; Fitter, 1991) and generally focus on the exchange of plant C for fungal phosphorus (P). Biological market models have been used to explicitly show the C and P availabilities at which mutualism will occur and, in this regard, they are useful for defining resource ratio thresholds and potential trade-offs for plants and fungi (Schwartz & Hoeksema, 1998; Hoeksema & Schwartz, 2003). The trade balance model adds further complexity by considering the interactive effects of C, nitrogen (N), and P on symbiotic outcomes.

The stoichiometry of essential resources in the environment has been a major selection pressure in the evolution of

plant roots and mycorrhizal symbioses, and tissue C:N:P ratios of plants and AM fungi are evolutionary outcomes of this selection. Optimal foraging theory predicts that, if organisms have limited access to essential resources (matter and energy), then, within populations, natural selection will favor individuals that are most effective at acquiring these resources (Pyke, 1984). This theory is the basis of the functional equilibrium model which states that plants should allocate biomass to structures that best garner essential resources that are most limiting (Brouwer, 1983; Bloom *et al.*, 1985; Ericsson, 1995). Chapin *et al.* (1987) suggested that optimal allocation occurs when plants are equally limited by all resources. For example, to adjust resource limitation imbalances when light or carbon dioxide (CO₂) is most limiting, plants should allocate more biomass to aboveground structures; but if belowground resources are more limiting then it is adaptive for plants to invest more biomass in roots and mycorrhizas than in shoots (Johnson *et al.*, 2003, 2008).

2. Competition, community feedback, and co-adaptation models

Populations of plants and AM fungi live within communities, and compete for limiting resources within and among species (intra- and inter-specific competition). Mycorrhizal symbioses affect both intra- and inter-specific competition among plants by influencing the supply rate of belowground resources (Allen & Allen, 1990; Schroeder & Janos, 2004; Li *et al.*, 2008). Furthermore, coexisting taxa of Glomeromycota compete for resources within host roots and in rhizosphere soil (Abbott & Robson, 1981; Maherali & Klironomos, 2007). Resource competition theory (Tilman, 1982, 1988) uses resource ratios (stoichiometry) to predict outcomes of competitive interactions. Coexistence of genotypes is predicted when they are most limited by different resources. The resource level at which the net rate of population change is zero is called R^* . When several genotypes are all limited by the same resource, the one with the lowest R^* is predicted to competitively exclude the other genotypes in a system at equilibrium (Tilman, 1982, 1988). Genotypes of plants and AM fungi vary in their resource requirements; consequently, the R^* concept may be very useful for predicting the success of various genotypes across soil fertility gradients. Mycorrhizal symbioses are expected to reduce plants' R^* for immobile soil minerals such as P and zinc (Zn). The efficiency of AM partnerships can be defined as the ability to increase the supply rate of the most limiting resource for both plants and fungi. In P-deficient soil, plant genotypes that form efficient AM symbioses should have a lower R^* and a competitive advantage over those that do not form efficient symbioses. Also, as with all symbiotic organisms, there is an underlying tension between the resource needs of host plants and those of their

associated AM fungi, and we can expect that they will compete for essential resources under certain environmental conditions (Smith & Holt, 1996). The R^* concept may help define the thresholds where beneficial resource trade gives way to detrimental resource competition.

Feedback models show how plant associations with AM fungi and other soil organisms may either stabilize or destabilize communities (van der Putten *et al.*, 1993; Bever, 2002; Reynolds *et al.*, 2003). Positive feedback occurs when the most beneficial community of soil organisms is cultivated in a plant rhizosphere; negative feedback occurs when the soil community is less beneficial for the plant species under which it develops compared with neighboring plant species. Positive feedbacks have a stabilizing effect and decrease the diversity of communities, while negative feedbacks increase community diversity by generating negative frequency dependence (Bever, 2002; Klironomos, 2002). For example, negative feedbacks between plants and soil organisms are predicted to be an important driving force in successional plant communities (Kardol *et al.*, 2006). Resource stoichiometry may be expected to influence the dynamics of community feedbacks over ecological and evolutionary time scales. Thrall *et al.* (2006) hypothesized that mutualistic associations are most likely to arise in nutrient-limited environments and parasitic associations are most likely in high-fertility environments.

Acquisition of soil resources is certain to be a strong selection pressure and is likely to structure the genetic composition of plant and AM fungal populations. The co-adaptation model states that plants and associated AM fungi exert reciprocal selective forces on one another such that symbiotic resource trade is optimized when soil fertility is conducive to beneficial exchange and the C cost of the symbiosis is minimized when high soil fertility precludes trade benefits. Empirical evidence supports the hypothesis that AM symbioses are an important mechanism for plant adaptation to local soil conditions (Schultz *et al.*, 2001) and that both plant genotypes and AM fungal communities are responding to this selection pressure (Johnson *et al.*, in press). There is increasing interest in linking heritable traits to community and ecosystem dynamics (Whitham *et al.*, 2006). More field-based research is needed to better understand how genotype-by-genotype interactions in plant–mycorrhizal symbioses are manifested in community and ecosystem patterns and processes. Such integration across scales, from genes to ecosystems (Whitham *et al.*, 2006), is likely to help advance mycorrhizal research to a predictive science.

3. Ecosystem patterns

Stoichiometry is at the heart of Read's model of the biogeography of mycorrhizas in the Northern Hemisphere (Read, 1991a,b; Read & Perez-Moreno, 2003) which links global

climate patterns, mineralization and pedogenic processes to the evolution of different forms of mycorrhizas. Across large latitudinal gradients there appears to be a strong relationship among litter quality, the humus that arises from it, and the predominant form of mycorrhizas that exploit soil resources (Read, 1991b). Ericoid mycorrhizas dominate cold and wet environments that contain high C:N litter, ectomycorrhizas dominate ecosystems containing litter with intermediate C:N ratios, and arbuscular mycorrhizas occur in warmer ecosystems containing lower C:N litter that is more easily mineralized. The catabolic abilities of the fungal endophytes involved in ericoid mycorrhizas, ectomycorrhizas, and arbuscular mycorrhizas are remarkably well adapted to ambient soil conditions. Read's conceptual model successfully integrates feedbacks among abiotic and biotic factors with ecosystem development. Albeit technically challenging, studying the role of AM symbioses in shaping ecosystem processes is most certainly the direction that must be taken to acquire a predictive understanding of mycorrhizal function at a global scale (Read, 2002).

III. Carbon, nitrogen and phosphorus in AM symbioses

Perhaps the reason that stoichiometry relates to such a variety of models of mycorrhizal function is that differences in the chemical composition and resource acquisition abilities of plants and fungi are key to the origin of mycorrhizas. To better understand the role of stoichiometry in the evolution and functioning of these symbioses, it is useful to consider the physical and chemical constraints faced by autotrophic plants and heterotrophic fungi. Photosynthetic plants harness solar energy to synthesize organic molecules from CO₂, water, and minerals. Mycorrhizal symbioses increase the fitness of plants living in mineral-deficient soils because fungi provide plants with access to limiting soil minerals with low mobility such as PO₄³⁻ (Marschner & Dell, 1994). By contrast, plants living in mineral-rich soil have less to gain from AM trading partnerships (but see Newsham *et al.*, 1995); consequently, most plant taxa are facultative mycotrophs and adjust their degree of dependence on mycorrhizas to complement ambient soil conditions (Graham & Eissenstat, 1994). Over the course of Glomeromycotan evolution, symbiosis became not only adaptive, but mandatory as these fungi lost their ability to acquire organic C without a partnership with living plants. Although some evidence suggests that Paraglomeraceae may have saprotrophic capability (Hildebrandt *et al.*, 2006; Hempel *et al.*, 2007), it is generally assumed that Glomeromycotan fungi are obligate biotrophs and have zero fitness in the absence of a host plant. In this regard, AM symbioses are asymmetrical; plants can usually survive at least for short periods without the fungus but the opposite is not true.

Plants and AM fungi symbiotically trade the commodity that they can most readily procure – plants trade carbohydrates and fungi trade mineral ions. For simplicity, this review will focus on the symbiotic exchange of C, N and P, but it is important to acknowledge that, in some environments, AM uptake of immobile micronutrients such as Zn may be more important to the symbiotic function of mycorrhizas (e.g. Thompson, 1990; George *et al.*, 1994). Furthermore, AM symbioses influence plant water relations and could therefore mediate mycorrhizal function in arid environments and droughty soil conditions (e.g. Allen & Boosalis, 1983; Hardie, 1985; Auge, 2001).

The dynamics of C, N and P cycling in mycorrhizal systems must be studied in a coordinated fashion because the availability of one of these elements influences the ability of plants and fungi to acquire the other elements (Miller *et al.*, 2002). This is particularly true for C and N because *c.* 75% of leaf N is invested in chloroplasts and hence in the procurement of C via photosynthesis (Chapin *et al.*, 1987). Consequently, there is generally a very tight relationship between leaf photosynthetic capacity and leaf N content. Although required in much smaller quantities, P is also critical for photosynthesis, plant growth and metabolism because P is a key ingredient in cell energetics through adenosine triphosphate (ATP) production. Furthermore, P also plays a key role in protein synthesis as a component of nucleic acids and lipid membranes.

Arbuscular mycorrhizal fungi may transport considerable amounts of N to their host plants and they can acquire N from both mineral and organic sources (George *et al.*, 1995; Tu *et al.*, 2006; Leigh *et al.*, 2008). Root-organ studies demonstrate that extraradical mycelia of AM fungi are able to acquire inorganic ¹⁵N (as either NO₃-N or NH₄-N), convert it to arginine, and transport it to intraradical fungal structures where the amino acid is broken down, transported to the plant, and assimilated into plant proteins (Govindarajulu *et al.*, 2005; Jin *et al.*, 2005). The N, but not the C, from the arginine is transferred from the fungus to the host across the host–fungus interface. This mechanism transports N in a nontoxic and concentrated form (four N atoms per molecule). Govindarajulu *et al.* (2005) showed that close to one-third of the N in root protein amino acids can be provided by symbiotic AM fungi. Furthermore, they suggest that N transport may be linked to polyphosphate transport, which is important because polyphosphate is the putative form of P translocated by the fungus (Smith & Read, 2008).

The importance of AM symbioses to plant P nutrition is well established and a rich literature shows that AM symbioses often improve plant growth through improved P nutrition (Smith & Read, 2008). The molecular mechanisms involved in symbiotic P exchange between fungus and plant

are increasingly being elucidated (Harrison, 2005; Bucher, 2007; Reinhardt, 2007; Parniske, 2008). Fitter (2006) proposed that the exchange of C-for-P in the apoplast surrounding arbuscules and intercellular hyphae regulates symbiotic trade between plant and fungal partners. He describes a mechanism where plants are stimulated to allocate photosynthates to areas of increased P supply in the vicinity of arbuscules where P ions are transported across the peri-arbuscular membrane. It appears that, although sucrose is the primary transport sugar in plants, hexose is the primary form in which C is transported from plant to fungus. The intraradical portion of AM fungi transforms these hexoses into triacylglycerides and trehaloses. Consequently, C transport from plants to AM fungi appears to be a one-way trip; once the plant-derived hexoses are assimilated into fungal tissues, the C will never be transferred back to plant hosts (Pfeffer *et al.*, 2004). Plant photosynthetic rates have been shown to be stimulated by the C sink exerted by AM fungi; and within legumes, this stimulation may represent an adaptive mechanism to optimize both AM and rhizobial symbioses (Kaschuk *et al.*, 2009). Smith *et al.* (2009) argue that high C drain to AM fungi does not adequately explain AM-induced plant growth depressions, particularly in natural environments in which plant competition is important (Li *et al.*, 2008). The factors controlling mycorrhizal function are clearly more complex than simply C costs and P benefits (e.g. Newsham *et al.*, 1995); however, C-for-P trade is certainly a key factor in predicting the outcome of AM symbioses.

Studies of the role of AM symbioses in plant N nutrition reveal a paradox. There is unequivocal evidence that the extraradical mycelia of AM fungi acquire N from the soil, and can transfer substantial quantities of N to host roots (Govindarajulu *et al.*, 2005; Jin *et al.*, 2005; Tu *et al.*, 2006; Leigh *et al.*, 2008); but studies that attempt to link mycorrhizal N uptake with plant benefit often find little or no evidence that AM fungi enhance plant biomass through improved N nutrition. For example, in a glasshouse study of five different prairie plant species colonized with four different AM fungal species, Reynolds *et al.* (2005) could find no evidence that AM symbioses promoted N acquisition or increased plant biomass. Plants in this experiment were grown in N-deficient soil with relatively high P availability and were exposed to five different N sources: ammonia, nitrate, glycine, urea and chitin. Across all 100 combinations of plants, fungi and N sources, there was not a single case in which the AM fungus increased either the biomass or the N content of the plant, although in several combinations the AM fungi acted as parasites and decreased total plant biomass and N content. Mycorrhizal uptake of P generally improves plant growth in P-limited soil (e.g. Mosse, 1973; Koide, 1991), so why is there so little evidence for mycorrhizal uptake of N improving plant growth in N-deficient soils?

IV. Trade balance and thresholds in the AM marketplace

A myco-centric perspective, combined with an understanding of the C:N:P stoichiometry of AM symbioses, provides a more predictive understanding of mycorrhizal responses to fertilization and helps resolve the 'nitrogen paradox'. Wallander (1995) hypothesized that fungal assimilation of plant C is the primary driver of ectomycorrhizal responses to N and P availability; and it appears likely that fungal C assimilation is also a key determinant of AM responses to N and P enrichment. Experimental N fertilization of P-rich systems frequently decreases AM fungal biomass and mycorrhizal benefits for plant growth (Johnson *et al.*, 2003; Blanke *et al.*, 2005), while N enrichment of P-limited soils often has the opposite effects: fungal biomass is increased along with plant growth benefits (Eom *et al.*, 1999; Johnson *et al.*, 2003; N. C. Johnson *et al.*, unpublished). This reversal is hypothesized to occur because N availability controls both plant C supply (plant photosynthesis) and fungal C demand (fungal assimilation) in mycorrhizal symbioses. Nitrogen fertilization will increase C supply and enhance mutualistic benefits in P-limited systems. But in P-rich systems, where symbiotic C-for-P trade is not advantageous, N enrichment will exacerbate fungal C demand (Wallander, 1995) and may generate plant growth depression (N. C. Johnson *et al.*, unpublished).

The trade balance model predicts that the function of AM symbioses depends on the stoichiometry of available N and P. Soils deficient in both N and P are predicted to support beneficial AM symbioses, but C-for-P trade will be reduced because of C limitation (Fig. 1, scenario I). Mutualistic benefits are predicted to be the greatest at high N and low P availability because a luxury supply rate of N increases the photosynthetic capacity of the host plant (Fig. 1, scenario II). Benefits of C-for-P trade will be eliminated in soil with a luxury supply rate of P, but if N availability is limited then plants and fungi are likely to compete for N and C and this will keep the fungal C sink in check because N limitation prevents proliferation of the AM fungus (Fig. 1, scenario III). By contrast, when neither N nor P is limited, fungal growth is only limited by C so the fungal C demand can increase to the point where it may depress plant growth and generate a parasitism (Fig. 1, scenario IV).

As mentioned above, the soil used in the Reynolds *et al.* (2005) experiment was relatively high in available P; consequently, experimental N enrichment probably generated parasitism as a result of fungal competition for plant C in the high-N, high-P environment. Future studies that quantify plant and fungal equilibrium resource levels (R^*) for C and N are likely to advance the predictive capability of the trade balance model. Low R^* for a resource indicates competitive superiority if mortality rate is constant (Tilman, 1982, 1988). Graham & Abbott (2000) provide evidence

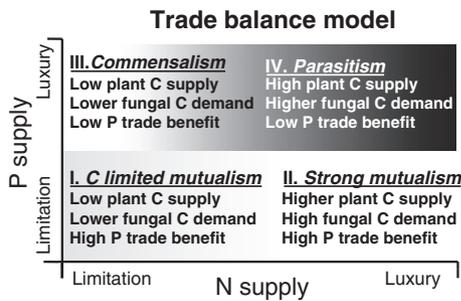


Fig. 1 The trade balance model predicts that arbuscular mycorrhizal (AM) function is determined by the interaction of nitrogen (N) and phosphorus (P) availability on carbon (C) supply and demand among plants and fungi. Four scenarios are predicted from the relative abundance of N and P. Scenario I: C-limited mutualism is predicted when both N and P are limited because, although C-for-P trade is favorable, N limitation restricts plant photosynthetic acquisition of C. Scenario II: strong mutualism is predicted when P is limited, making C-for-P trade favorable, and C supply is not limited by N deficiency. Scenario III: commensalism is predicted when P is not limited, so plants have nothing to gain from C-for-P trade, but C demand by AM fungi is kept in check because fungal growth is N-limited. Scenario IV: parasitism is predicted when neither N nor P is limited such that plants gain no benefit from C-for-P trade and fungal C demand is not limited by N deficiency.

that parasitic AM fungal species depress the sucrose and starch concentrations in wheat (*Triticum aestivum* cv. Kulin) roots more than mutualistic AM fungal species, which suggests that parasitic fungi have a lower R^* for sugars and consequently they are better competitors for apoplastic C compared with mutualistic fungi. Also, compared with mutualistic mycorrhizas and nonmycorrhizal controls, parasitic AM associations in the prairie grass *Andropogon gerardii* were shown to deplete rhizosphere soil N to lower levels (N. C. Johnson *et al.*, unpublished), suggesting that parasitic AM fungi have a lower R^* for N than their hosts and this may contribute to the parasitic outcome of the symbiosis (Smith & Holt, 1996).

Many studies show that the relative amounts of both N and P determine mycorrhizal function and support the predictions of the trade balance model (e.g. Bååth & Spokes, 1989; Sylvia & Neal, 1990; Valentine *et al.*, 2001; Azcón *et al.*, 2003; Blanke *et al.*, 2005). This phenomenon can be illustrated by calculating an index for the mycorrhizal growth response (MGR) as: $\ln(AM/NM)$, where AM is the total dry weight of a mycorrhizal plant and NM is the total dry weight of a matched nonmycorrhizal plant. For example, Valentine *et al.*, 2001; (Fig. 2a) found that the MGR of cucumbers (*Cucumis sativus* L.) was negative (Fig. 1, scenario IV) when plants were watered with regular Long Aston nutrient solution; but reducing the P content by an order of magnitude (low-P Long Ashton solution) generated a strongly positive MGR (Fig. 1, scenario II). It is important to stress that the N:P ratio of the nutrient solutions applied to the plants is not a sufficient predictor of

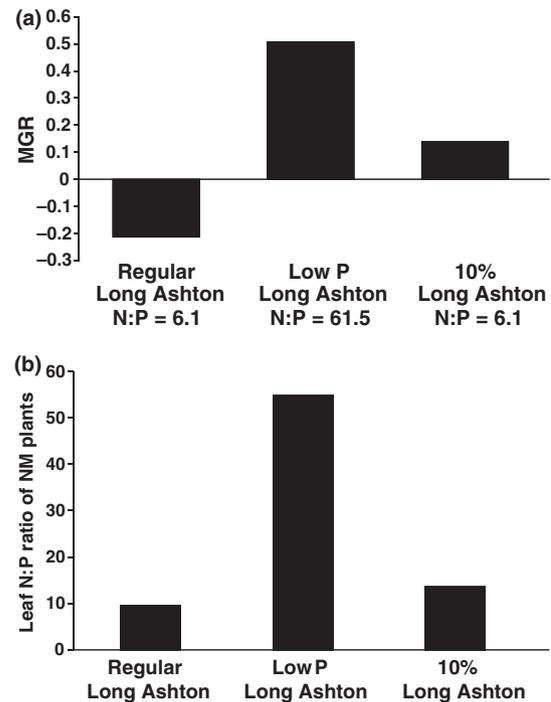


Fig. 2 Cucurbit plants were grown in Long Ashton solution that was full-strength (1.3 mM phosphorus (P)), low P (0.13 mM P + high concentrations of all other nutrients), or a 10% dilution of Long Ashton solution. (a) Mycorrhizal growth response (MGR) measured as $\log_e(AM/NM)$, where AM is the total dry mass of mycorrhizal plants and NM is the total dry mass of plants grown in similar conditions except without mycorrhizas. (b) Leaf nitrogen (N):P ratio of nonmycorrhizal (NM) cucumbers. Data are from Valentine *et al.* (2001).

AM responses. The Valentine *et al.* (2001) study (Fig. 2a) showed that MGR increased when Long Ashton's nutrient solution was uniformly diluted to 10%; although this maintained a constant N:P ratio (6.1), it generated N limitation for both the plant and the fungus which probably kept the fungal C demand in check so that the trade balance was moved to the realm of scenario III instead of IV in Fig. 1.

Although the N:P ratio of the nutrient solution is not a satisfactory predictor of MGR, the tissue N:P ratio of plants grown without AM fungi could be predictive of mycorrhizal function because this ratio often indicates plant nutrient status in the ambient soil and light environment, which may ultimately determine the potential costs and benefits of symbiotic trade between plants and AM fungi. Koerselman & Meuleman (1996) found that, among mesic grassland plants, tissue N:P < 14 generally indicates N limitation and N:P > 16 indicates P limitation. The leaf N:P ratios of nonmycorrhizal cucumbers in the Valentine *et al.* (2001) study (Fig. 2b) indicate that MGR was mutualistic when plants were P-limited (N:P = 54.9), negative when they were N-limited (N:P = 9.7), and intermediate when they were equally limited by N and P (N:P = 13.7). The value of

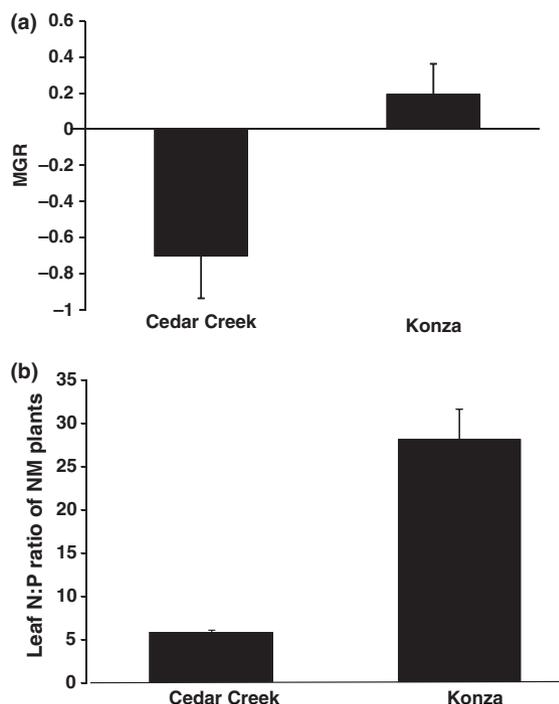


Fig. 3 *Andropogon gerardii* was grown in high-phosphorus (P), low-nitrogen (N) soil from Cedar Creek or low-P soil from Konza Prairie. (a) Mycorrhizal growth response (MGR) measured as $\log_e(\text{AM}/\text{NM})$, where AM is the total dry mass of mycorrhizal plants and NM is the total dry mass of plants grown in similar conditions except without mycorrhizas. (b) Leaf N:P ratio of nonmycorrhizal (NM) *A. gerardii*. Data are from N. C. Johnson & A. E. Redman (unpublished data).

tissue N:P thresholds for predicting mycorrhizal function is further illustrated by the positive MGR of *A. gerardii* grown in P-limited Konza Prairie soil and the negative MGR in P-rich, N-limited Cedar Creek soil (Fig. 3a). The leaf N:P of *A. gerardii* grown without mycorrhizas (Fig. 3b) showed that plants grown in Konza soil were strongly P-limited (N:P = 28.2) and those grown in Cedar Creek soil were strongly N-limited (N:P = 5.8).

The trade balance model accounts for the reversal in mycorrhizal responses to N enrichment in P-rich versus P-limited systems; but it does not explain why AM fungi often do not improve plant N nutrition and biomass gain in N-deficient soil in the same way that they improve P nutrition and biomass gain in P-deficient soil. Certainly the greater capacity for plant roots to acquire N compared with P is part of the answer (Mengel & Kirkby, 1982). But also, a more in-depth stoichiometric analysis of plants and AM fungi may help solve this puzzle. The C:N ratio of plant tissues varies tremendously with genotype, age, and structure. For example, the C:N ratio of an apple tree (*Malus* sp.) ranges from 45 : 1 in leaves and young roots to 400 : 1 in the woody stem (Sterners & Elser, 2002). By contrast, the C:N ratio of AM fungal tissues is *c.* 10 : 1 (Garraway & Evans, 1984). Clearly, a gram of fungal tissue contains

much more N than a gram of plant tissue. It has long been recognized that the disparity between the C:N ratios of litter and microbial decomposers is a critical determinant of decomposition dynamics. When the C:N ratio of detritus is greater than 25 : 1 (by mass), detritivore microorganisms are predicted to immobilize N (i.e. consume and retain N), but microbial detritivores are predicted to mineralize detritus with lower C:N ratios because ambient N availability is sufficient for construction of microbial biomass so that organic N is decomposed and NH_4 is released (Waksman & Tenney, 1927; Hodge *et al.*, 2000). The law of the minimum explains this phenomenon because, if microbial growth is most limited by N, then the detritivores acquire and recycle this element in their own living biomass. The same principle can help us understand N dynamics in AM symbioses. When soil N is so rare that it limits growth of both plants and fungi, then one can expect that each organism will provision itself and not release any N to its partner. Because fungi require more N in their tissues than plants, they will continue to sequester N until their own needs are met, and, given the disparity between plant and fungal C:N ratios, this is likely to be at a level that exceeds the minimum requirement of their host plant. The reason why AM fungi deliver P to their host plants, despite the fact that they have higher tissue P concentrations than plants, is probably because their superiority in acquiring P allows them to readily satisfy their own needs and create a surplus that can be used in C-for-P trade. Phosphate ions are often tightly bound to soil particles and have low mobility; consequently, the enhanced surface area provided by a symbiotic AM mycelium is a great advantage for P uptake. By contrast, it is likely that plants and AM fungi are more evenly matched in their abilities to acquire N from the soil. Nitrogen is more readily accessible to plants in the soil water because nitrate has a relatively high solubility. This highlights the importance of considering both (1) resource requirements and (2) the ability to procure resources in biological market and trade balance models.

Sterners & Elser (2002) define threshold element ratios as the stoichiometric ratio where control of growth shifts from one element to another. Further research is necessary to determine whether or not critical tissue N:P and C:N ratios can be identified for mycorrhizal function that are as useful as the C:N threshold of 25 : 1 is for predicting decomposition dynamics. It might be difficult or even impossible to determine absolute values for the critical thresholds where P limitation makes C-for-P trade advantageous, or the threshold where N limitation prevents run-away C demand by AM fungi, because so many factors influence these values. Plant age, temperature, light, and water availability are likely to be extremely important, as is the biotic neighborhood in which a plant is living, particularly in relation to the proximity of plant competitors, pathogens, or other mutualists. Perhaps the best we can hope for is the knowl-

edge that a key factor in determining the outcome of N or P enrichment for mycorrhizal function may be whether or not AM hosts are limited by these resources. A general rule of thumb might be that, if plants are not limited by P, then AM fungi are less likely to provide plant growth benefits, and, if plants are not limited by either P or N, then AM fungi are more likely to cause growth depressions.

V. Optimal foraging and functional equilibrium in AM symbioses

The trade balance model helps to explain how the relative abundance of C, N and P controls mycorrhizal function; while the functional equilibrium model helps to predict how plant and fungal morphology should respond to resource availability. Optimal foraging theory acknowledges that plants face an unavoidable trade-off between biomass allocations to aboveground and belowground structures. The functional equilibrium model predicts that, in a balanced mycorrhizal trading partnership, plants should allocate sufficient photosynthates to roots and mycorrhizas so that they are equally limited by soil resources and by light or CO₂ (Fig. 4a). Fertilization reduces nutrient limitation and makes aboveground resources more limited so that plants should produce more shoots and leaves and fewer

roots and mycorrhizal symbioses (Fig. 4b). As discussed in the previous section, this can potentially generate a competitive relationship between plants and AM fungi and cause plant growth depression as well as reduce fungal biomass; however, the relative availability of N and P is a critical factor in determining the outcome (Fig. 1). The trade balance model predicts that N enrichment of P-limited soil will increase the value of P acquisition by mycorrhizal symbioses so plants should allocate more biomass to roots and mycorrhizas (Fig. 4c); however, N enrichment of P-rich soil is predicted to cause plants to reduce allocation belowground to roots and AM fungal structures and reduce plant MGR (Fig. 4b).

Mycotrophy is only one of many possible strategies that plants may use to overcome nutrient deficiency: root hairs, enzymatic exudates and cluster roots are some of the alternative adaptations that plants have evolved to facilitate growth in P-deficient soil (Miller, 2005; Lambers *et al.*, 2008). If mycotrophy is an evolutionarily stable strategy, then optimal foraging theory predicts that, over time, natural selection will favor plant genotypes that are most successful in maximizing AM growth benefits when mycorrhizas are advantageous and minimizing growth depressions when mycorrhizas are not cost effective. Hetrick (1991) linked C and P stoichiometry with the evolution of

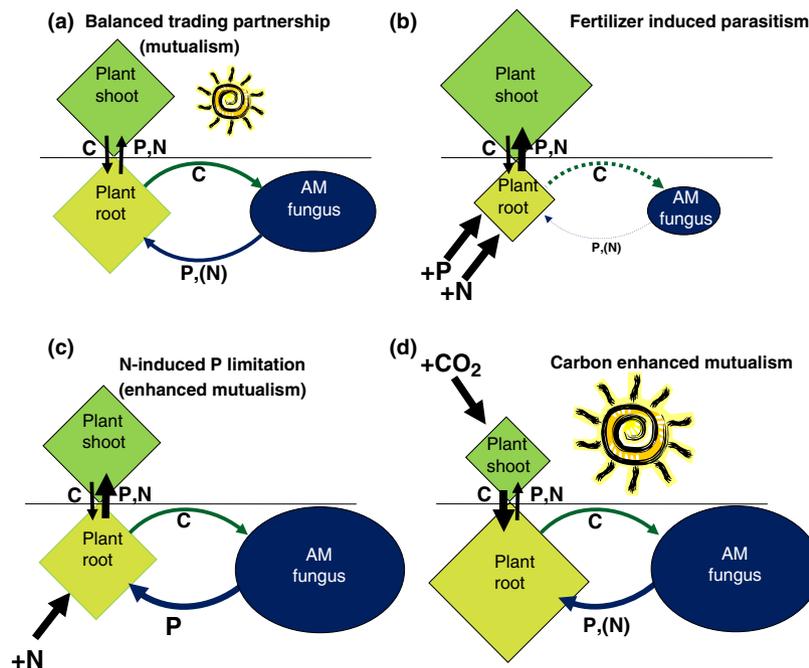


Fig. 4 The functional equilibrium model predicts that enrichment of above- and belowground resources will generate different arbuscular mycorrhizal (AM) dynamics. (a) A mutualistic AM symbiosis occurs when there is a balanced trading partnership between plant and fungus. The plant delivers carbon compounds to the fungus in return for mineral nutrients, most notably phosphorus, and in some circumstances nitrogen. (b) Nitrogen enrichment of a phosphorus-rich system generates a parasitic AM symbiosis because plants will reduce allocation to roots and mycorrhizas in favor of aboveground structures when no belowground resources are limited. (c) Nitrogen enrichment of a phosphorus-limited system generates a mutualistic AM symbiosis because nitrogen-enriched plants require additional phosphorus to synthesize biomass and this increases the value of AM trading partnerships. (d) Increased light intensity or CO₂ enrichment of plants growing in nutrient-limited soils will increase plant demand for belowground resources and increase the value of AM trading partnerships.

mycotrophy and noted that plant species and genotypes with a high degree of dependence on AM symbioses (*sensu* Janos, 2007) have less plasticity in their root:shoot ratio and, in nutrient-limited soils, these species change their root architecture to become coarser – which is more conducive to dependence on AM fungi and less conducive to ‘solo resource acquisition’. Hetrick (1991) also acknowledged that resource competition among plants and soil microorganisms could be an important driver of mycorrhizal benefits in nutrient-limited systems. Mycotrophy may provide plants with a competitive advantage against rhizosphere microbes because the external mycelium of AM fungi may help to conserve essential limiting nutrients within the fungus–plant network; and perhaps more importantly, mycorrhizas can reduce the concentration of soluble carbohydrates in root exudates (Graham *et al.*, 1981), and this will reduce substrate for saprotrophic microbes in the rhizosphere that may compete for nutrients with plants (Kaye & Hart, 1997; Hodge *et al.*, 2000).

It has long been recognized that AM fungi are capable of absorbing nutrients that are inaccessible to roots because their minute hyphae extend beyond the nutrient depletion zones surrounding roots. Root morphology varies predictably with plant mycotrophy (Baylis, 1975; Schweiger *et al.*, 1995), and plant taxa vary in their abilities to exclude AM fungi when they are not necessary for nutrient acquisition. This is clearly seen among citrus cultivars (Graham *et al.*, 1991), wheat varieties (Azcón & Ocampo, 1981; Hetrick *et al.*, 1993), and prairie grasses (Schultz *et al.*, 2001; Johnson *et al.*, 2008). Plant ecotypes that have evolved in low-fertility soils are often highly mycotrophic with coarse roots and little ability to reduce AM fungal colonization if soils are fertilized and mycorrhizas are no longer a cost-effective investment. By contrast, plants that are adapted to fertile soils often have fibrous roots and more plasticity in their ability to restrict AM fungal colonization when nutrients are plentiful (Graham *et al.*, 1991; Graham & Eissenstat, 1994).

There is strong empirical evidence that mycorrhizas may substitute for root surface area, and that highly mycotrophic plant taxa allocate less biomass to the construction of roots compared with less mycotrophic taxa. An excellent example is Azcón & Ocampo's (1981) comparison of 13 different wheat cultivars, which shows an inverse relationship between root:shoot ratios and plant growth response to *Glomus mosseae* (Fig. 5a). This study also supports the trade balance model prediction that mutualism is strongest when P is more limiting than N by showing a positive relationship between the tissue N:P ratio of nonmycorrhizal wheat plants and the MGR of that cultivar (Fig. 5b).

The functional equilibrium model predicts that enrichment of light or CO₂ should cause plants to allocate more biomass to roots (Brouwer, 1983; Ericsson, 1995) and mycorrhizas (Fig. 4d). This is strongly supported in the lit-

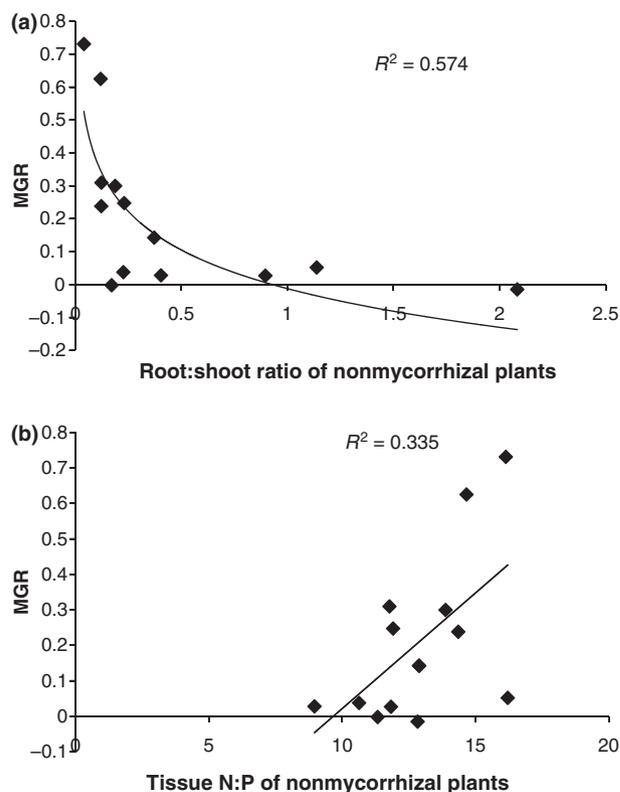


Fig. 5 Mycorrhizal growth response (MGR, measured as $\log_e(\text{AM}/\text{NM})$, where AM is the total dry mass of mycorrhizal plants and NM is the total dry mass of plants grown in similar conditions except without mycorrhizas) of 13 wheat cultivars versus (a) root:shoot ratio and (b) tissue nitrogen:phosphorus ratio of nonmycorrhizal plants. Data are from Azcón & Ocampo (1981).

erature; many studies have shown that AM fungal colonization of roots decreases with decreasing light intensity (e.g. Hayman, 1974; Daft & El-Giahmi, 1978; Gehring, 2003). For example, Graham *et al.* (1982) showed that shading reduces the MGR of *Sorghum vulgare* (Fig. 6), presumably because shading increases C limitation relative to below-ground resources. Furthermore, Graham *et al.* (1982) found that this reduction in MGR is exacerbated by P fertilization, which reinforces the idea that AM parasitism may be generated by increased C cost as well as reduced P benefit (Johnson *et al.*, 1997).

Results of CO₂ enrichment experiments also generally corroborate the functional equilibrium model. Plants often increase biomass allocation to roots in response to elevated CO₂ (Rogers *et al.*, 1996); and a meta-analysis of 14 mycorrhizal studies (seven with AM symbioses) showed that CO₂ enrichment consistently increases AM colonization (Treseder, 2004). However, most of these studies compared AM and nonmycorrhizal plants at a single point in time, and, because plants typically grow more rapidly at elevated CO₂, the increase in AM fungal biomass can often be accounted for by the increase in plant size in the enriched CO₂ treatment, suggesting that CO₂ enrichment does not

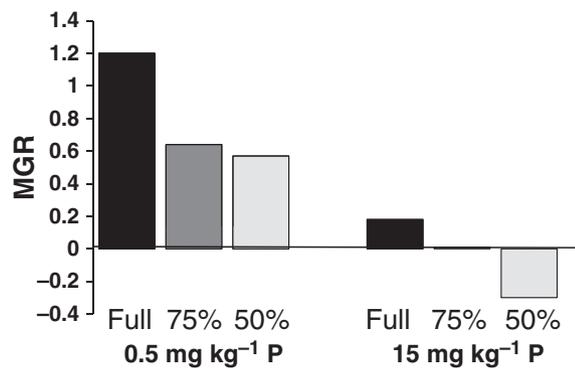


Fig. 6 Mycorrhizal growth response (MGR, measured as $\log_e(\text{AM}/\text{NM})$, where AM is the total dry mass of mycorrhizal plants and NM is the total dry mass of plants grown in similar conditions except without mycorrhizas) of *Sorghum vulgare* grown at full, 75% and 50% glasshouse light intensity and with low or high levels of phosphorus (P). Data are from Graham *et al.* (1982).

necessarily change the proportion of root length colonized by AM fungi (Staddon & Fitter, 1998). Nevertheless, several studies have found that elevated CO_2 increases allocation to external AM hyphae in the soil (Sanders *et al.*, 1998) and results in more rapid C cycling in the rhizosphere (Allen *et al.*, 2005).

Plant taxa vary greatly in their dependence on AM symbioses and this influences their responses to enrichment of aboveground and belowground resources. For example, a study of 14 plant species colonized by five different types of fungal inocula showed that the influence of CO_2 availability on MGR varies tremendously with plant and AM fungal taxa (Johnson *et al.*, 2005). Jifon *et al.* (2002) compared the responses of two citrus genotypes to CO_2 enrichment: sour orange (*Citrus aurantium* L.) has a high AM dependence, and sweet orange (*C. sinensis* L.) has a low dependence. The results of this study showed that (1) the highly AM-dependent sour orange suffered from mycorrhizal-induced growth depression at luxury P supply rates while the sweet orange showed no growth depression and was largely unresponsive to AM colonization; and (2) elevated CO_2 compensated for mycorrhizal growth depression in sour orange. These results stress that it is not possible to extrapolate across all genotypes within a single plant species, much less across all species! Mycorrhizal responses vary among and within plant taxa; some genotypes utilize AM symbioses for nutrient acquisition and others do not; the trade balance and functional equilibrium models are likely to successfully predict mycorrhizal function in mycotrophic genotypes but not in genotypes that are unresponsive to mycorrhizas.

VI. Fungal life histories and resource utilization

A major barrier to progress in the field of AM ecology is the lack of basic life history information about Glomeromycotan fungi. Outside of controlled pot experiments, it is very

difficult to define an individual AM fungal clone. Little is known about the population sizes and generation times of AM fungi in natural ecosystems, although studies suggest that individual clones can be extremely large and very ancient (Rosendahl, 2008). It has often been assumed that Glomeromycota is depauperate of species, but this is probably not the case, as it appears that the vast majority of AM fungal species are undescribed (Bever *et al.*, 2001; Rosendahl, 2008; Öpik *et al.*, 2009). More importantly, there is a great deal of hidden genetic diversity within AM fungal populations of the same morphospecies (Bever *et al.*, 2001; Sanders, 2002), and this diversity affects their symbiotic function. It is not uncommon to find functional differences among isolates of the same apparent AM fungal 'species' that are as great as differences among different species (e.g. Hart & Reader, 2002; Munkvold *et al.*, 2004; Koch *et al.*, 2006). Thus, for ecological studies, geographic isolates may be a more meaningful taxonomic unit than species. However, the practicality of using geographic ecotypes is unclear because functional differences among AM fungal isolates may occur at very small scales. For example, genetically distinct isolates of *Glomus intraradices* collected from a single agricultural field in Switzerland affected plant root growth differently (Koch *et al.*, 2006). If isolates of the same fungal species from the same location vary in their effects on plants, then what taxonomic unit is ecologically meaningful for studies of mycorrhizal function (Sanders, 2004)?

Despite the difficulties in defining individual clones of AM fungi and understanding their population genetics, it is obvious that taxa of AM fungi vary tremendously in their resource requirements and abilities to acquire resources; and these differences most certainly influence their impacts on communities and ecosystems. Descriptive studies of Glomeromycotan occurrences show that the species composition of AM fungal communities is affected by disturbances which influence the availability of aboveground and belowground resources. For example, the composition of AM fungal communities is affected by agricultural management (e.g. Schenck & Kinloch, 1980; Helgason *et al.*, 1998; Jansa *et al.*, 2003), N enrichment (e.g. Egerton-Warburton & Allen, 2000; Egerton-Warburton *et al.*, 2007; Porras-Alfaro *et al.*, 2007), and CO_2 enrichment (e.g. Klironomos *et al.*, 1998; Treseder *et al.*, 2003; Wolf *et al.*, 2003). Patterns in these descriptive studies may help to elucidate the resource requirements of various AM fungal taxa. Hart & Reader (2002) showed that there is family-level variation in the life history strategies of AM fungi. Ecological models using a stoichiometric perspective may help to define functional groups of AM fungi to provide a framework for understanding the general life history characteristics of Glomeromycotan families.

One of the most obvious patterns in spore community responses to experimental perturbations is the loss or gain of the extremely large spores (200 to 600 μm in diameter),

Table 1 Abundance of Gigasporaceae may either increase (↑) or decrease (↓) in response to experimental manipulation of resource availability

Experimental treatment	Gigasporaceae response	Study
N enrichment of P-rich grassland	↓ spores ↓ spores and hyphae	Johnson (1993) Egerton-Warburton <i>et al.</i> (2007)
N enrichment of P-limited grassland	↑ spores ↑ spores and hyphae	Eom <i>et al.</i> (1999) Egerton-Warburton <i>et al.</i> (2007)
P enrichment	↓ spores	Douds & Schenck (1990)
Shade	↓ spores	Bowker, Johnson & Wilson, unpublished data
CO ₂ enrichment	↑ hyphae ↑ spores and hyphae ↓ hyphae ¹ ↓ coarse orange hyphae	Klironomos <i>et al.</i> (1998) Treseder <i>et al.</i> (2003) Klironomos <i>et al.</i> (2005) Antoninka <i>et al.</i> (2009)

¹Gigasporaceae hyphae decreased when CO₂ concentration increased abruptly in one generation, but not when it increased gradually over 21 generations.

N, nitrogen; P, phosphorus.

produced by fungi within the family Gigasporaceae. Several field studies have shown that the abundance of Gigasporaceae spores and hyphae decreases in response to N fertilization of P-rich grasslands but increases in response to N fertilization of P-limited grasslands (Table 1). The trade balance model may account for this reversal if Gigasporaceae have a high C requirement, and N enrichment increases belowground C allocation in P-limited soil but decreases it in P-rich soil. In such a case, Gigasporaceae appear to favor environments where C-for-P trade is favorable for plants because N availability is not limiting photosynthesis. This hypothesis is supported by glasshouse studies showing that *Gigaspora* spp. produce more spores when plant tissue N:P ratios are imbalanced toward N (Douds & Schenck (1990), and fewer spores when their host plants are light-limited (M. A. Bowker *et al.*, unpublished; Table 1).

The abundance of Gigasporaceae spores and hyphae is frequently reported to respond to CO₂ enrichment, but the direction of the responses varies among experiments (Table 1). Variability of responses to CO₂ enrichment is probably related to differences in the soils and plant species used among the studies. Plant species differ in their effects on the sporulation of various AM fungal taxa (e.g. Johnson *et al.*, 1992b; Sanders & Fitter, 1992; Eom *et al.*, 2000), so plant community response to CO₂ enrichment is a confounding factor in measuring AM fungal responses; mycorrhizal function could be changing because of either altered fungal behavior or composition shifts in the plant community.

The functional equilibrium model may help to explain the ecological strategies of AM fungi. In the same way that plants face a trade-off between aboveground and belowground biomass allocations, AM fungi face a trade-off between allocations to structures inside and outside plant roots. Hart & Reader (2002) showed that, compared with Acaulosporaceae and Glomaceae, the Gigasporaceae form much more extensive extraradical mycelium and have less

intraradical colonization. Relative allocation to structures that are involved in resource trade, such as arbuscules and extraradical hyphae, has been shown to decrease in response to long-term N fertilization (Johnson *et al.*, 2003). Testing hypotheses about the functional significance of these and other differences in the allocation to fungal structures deserves serious consideration in future research (van der Heijden & Scheublin, 2007). Conducting such studies in realistic field conditions has been hindered by the difficulty of identifying AM fungi within roots and soil; however, recent developments in DNA-based methods (Krüger *et al.*, 2009; Öpik *et al.*, 2009) are certain to help advance this work.

VII. Community feedbacks, co-adaptation and ecosystem consequences

There appears to be reciprocity between the species compositions of plant and AM fungal communities and a surprising level of integration among AM symbioses and their biotic and abiotic environment. Most plants are simultaneously colonized by multiple species of AM fungi, and there is evidence that plants may optimize belowground foraging through active cultivation of a phylogenetically diverse assemblage of fungi within their roots (Maherali & Klironomos, 2007). Control of the species of AM fungi within root systems seems to be a highly dynamic process which occurs at the cellular scale in response to the spatial structure of resources in the soil environment (Reinhardt, 2007; Parniske, 2008). There is evidence that, when clones of AM fungi are spatially separated, plants preferentially allocate C to the fungal taxa that are most beneficial to their growth (Bever *et al.*, 2009). In this way, AM symbioses may be an important driver of plant community structure through the generation of either positive or negative feedbacks (Bever, 2002; Reynolds *et al.*, 2003).

Successional development of communities may, in part, be driven by these feedbacks (van der Putten *et al.*, 2001).

Plant genotypes that are competitively dominant and best able to resist pathogens are expected to increase in number over time. Accordingly, populations of AM fungi that best reduce host plant R^* for the most limiting resources and best protect plants from ambient pathogens are expected to track the abundance of host plants. The outcome of soil feedbacks has been shown to vary among plant species. Klironomos (2002) found that dominant (invasive) plant species experience positive feedbacks with their local (home) soil organisms while rare plant species experience negative feedbacks with home soil organisms. Kardol *et al.* (2006) found negative soil feedbacks to be common in early successional plants and positive soil feedbacks to be common in late successional plants.

Both evolutionary and ecological mechanisms can account for the propensity of negative feedbacks in rare plant species and recently disturbed ecosystems and positive feedbacks in dominant plant species and mature ecosystems. The co-adaptation model states that, over time, suites of plants, AM fungi, and other soil organisms will be selected that are best able to coexist with local communities under ambient soil conditions. Mutually beneficial AM symbioses will stabilize community composition if they have the potential to increase the competitive dominance of host plants. In this way, nutritional mutualisms are most likely to be favored in resource-deficient environments (Thrall *et al.*, 2006). By contrast, parasitic symbioses are likely to arise when plants have unlimited access to resources such that AM trading partnerships are superfluous.

There is experimental evidence that both evolutionary and ecological mechanisms drive plant–soil feedbacks through co-adaptation of plants with AM fungi and other soil organisms. A reciprocal inoculation experiment using home and away combinations of *A. gerardii* ecotypes, AM fungal communities and soils from a P-rich and two P-limited grasslands showed that significantly more arbuscules were formed in home combinations of plants, fungi and soils compared with away combinations. Furthermore, all-home combinations were more mutualistic in the two P-limited soils and less parasitic in the P-rich soil (Johnson *et al.*, in press). This study is important because it suggests that plant ecotypes are co-adapted with their local AM fungal communities and that soil fertility mediates AM function in mature grasslands. The interaction between resource availability and AM function was also demonstrated in constructed mesocosm communities (Collins & Foster, 2009). This study showed that AM symbioses influenced plant productivity and community structure when P was limiting, but not when P was available at luxury supply rates, presumably because AM symbioses have little influence on plant fitness in the P-enriched mesocosms. This finding highlights the point that mycorrhizas are most likely to impact communities and ecosystems that are limited by P or some other mycorrhizal commodity and much less likely

to influence ecosystems that are not limited by resources that can be acquired through AM symbioses.

If Glomeromycotan fungi are truly obligate biotrophs, and have no option for life outside of AM symbioses, then they should have evolved strategies to gain C from living plants regardless of trade reciprocity. This appears to be the case; some fungal taxa appear to be better than others at acquiring photosynthate that is not allocated to them, and populations of these fungi are likely to increase in abundance in highly fertilized systems and generate plant growth depressions (Modjo *et al.*, 1987; Hendrix *et al.*, 1992; Johnson, 1993). Negative feedback between crops and AM fungal communities may be partially responsible for the growth declines that are often observed in continuous crop monocultures (Johnson *et al.*, 1992a). Farmers looking to harness AM symbioses as ‘biological fertilizers’ may want to generate conditions that encourage positive feedbacks between crop plants and soil organisms. The trade balance model suggests that the best way to accomplish this goal is to manage inputs so that plants are P-limited but not N-limited. Development of management systems that encourage effective mycorrhizal function will also require the planting of mycotrophic crop cultivars that are more likely to be co-adapted with the indigenous AM fungal communities (Hetrick *et al.*, 1993).

Changing the stoichiometry of essential resources in the environment, either slowly through ecosystem succession or rapidly through anthropogenic perturbations, may set in motion a cascade of community changes that have long-lasting effects on ecosystem properties. Heathlands are extremely N-limited ecosystems that are dominated by ericaceous plants that depend upon ericoid mycorrhizas for uptake of organic forms of N (Read, 1991a,b). Anthropogenic N deposition is often accompanied by invasion of these heathland communities by AM grasses and the loss of dominance by ericaceous plants (Berendse *et al.*, 1993). Aerts (2002) hypothesized that this plant community shift is mediated by mycorrhizas. Ericoid mycorrhizas reduce the R^* for N in ericaceous plants, and AM symbioses reduce the R^* for P in grasses. As pollution makes N less limiting, P becomes relatively more limiting so that AM grasses can competitively exclude the ericoid hosts. Thus, once a threshold in mineral N availability is reached where the costs of ericoid mycorrhizas may outweigh their benefits, the plant community becomes dominated by grasses with AM symbioses that facilitate P uptake.

Grasslands are not immune to the effects of anthropogenic N deposition. Indeed, N eutrophication of grasslands frequently reduces plant species richness as a few species become competitively dominant (Tilman, 1988; Bobbink, 1991). As predicted by the functional equilibrium model, in two separate grassland locations, the grass species that gained biomass in response to long-term N enrichment allocated less biomass to roots and mycorrhizas, and had a neutral or

negative MGR compared with grass species that lost biomass in response to eutrophication (Johnson *et al.*, 2008).

Ecosystem responses to resource enrichment often result from complex indirect interactions that are mediated through community-scale interactions (Antoninka *et al.*, 2009). A better understanding of the species composition of AM fungal communities may help to predict ecosystem responses to global change, because taxa of AM fungi differ in their functional traits. For example, AM fungi differ in their effects on soil aggregation (Piotrowski *et al.*, 2004). Anthropogenic changes that cause a reduction in below-ground allocation may have long-term effects on soil organic matter because both roots and AM mycelia contribute to belowground C storage (Rillig, 2004; Wilson *et al.*, 2009).

VIII. The scaling-up challenge

The importance of AM symbioses to community structure and ecosystem function is increasingly recognized, yet designing research methods to elucidate large-scale effects remains a challenging frontier in mycorrhizal biology (Graham, 2008). Although the precision of traditional reductionist experiments is appealing, results from these studies are often too narrow to be extrapolated to the complex world that we live in (Read, 2002). The outcome of interactions among plants and soil communities varies with spatial scale (De Deyn & van der Putten, 2005) and spatial structure (Bever *et al.*, 2009). Temporal scale is also a critical consideration (Bardgett *et al.*, 2005), especially if evolutionary processes alter the outcomes of species interactions (Klironomos *et al.*, 2005). The complexity of communities and ecosystems is daunting and no single approach can satisfactorily describe, much less predict, this complexity. However, testing ecological and evolutionary models using suites of reductionist experiments in conjunction with holistic models is a promising approach for developing a more predictive science (Johnson *et al.*, 2006). General models of mycorrhizal community distribution can be developed using geographic information systems (Lilleskov & Parrent, 2007). Structural equation models are also useful for conceptualizing (Chaudhary *et al.*, 2008) and testing complex, multivariate hypotheses without disassembly of biological systems (Antoninka *et al.*, 2009; Chaudhary *et al.*, 2009). Heritability models combined with community phenotypes are being used to integrate patterns and processes from genes to ecosystems (Whitham *et al.*, 2006). A stoichiometric perspective may help inform these and other types of ecological and evolutionary models so that they can integrate across spatial and temporal scales.

Successful integration of reductionist precision with holistic realism requires that the mechanisms controlling C, N and P fluxes among the soil, AM fungi and host plants (Shachar-Hill, 2007) are studied in ecologically realistic combinations of plant and fungal genotypes grown in their

local soil (Read, 2002). Comparisons of mycorrhizal structure and function across natural resource gradients will help to test the predictions of the trade balance and functional equilibrium models and to identify resource thresholds where mycorrhizal function may switch from mutualistic and desirable to parasitic and undesirable. This information may be used to design agricultural and ecosystem management systems that generate stabilizing feedbacks between aboveground and belowground communities. Truly integrative studies require collaborations among a variety of experts with fluency in a variety of approaches, including ecosystem modelers, community ecologists and mycorrhizal physiologists, among others. Cross-discipline studies can be challenging because of disparities among research fields in the scales at which measurements are made. A stoichiometric perspective of C, N and P fluxes through mycorrhizas may provide a 'common currency' to facilitate cross-scale communication among a diversity of scientists interested in understanding AM symbioses from genes to ecosystems.

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References

- Abbott LK, Robson AD. 1981. Infectivity and effectiveness of five endomycorrhizal fungi: competition with indigenous fungi in field soils. *Australian Journal of Agricultural Research* 32: 621–630.
- Abbott LK, Robson AD. 1991. Field management of VA mycorrhizal fungi. In: Keister DL, Cregan PB, eds. *The rhizosphere and plant growth*. Amsterdam, The Netherlands: Kluwer Academic Publishers, 355–362.
- Aerts R. 2002. The role of various types of mycorrhizal fungi in nutrient cycling and plant competition. In: van der Heijden MGA, Sanders I, eds. *Mycorrhizal ecology*. Berlin Heidelberg, Germany: Springer-Verlag, 117–133.
- Allen EB, Allen MF. 1990. The mediation of competition by mycorrhizae in successional and patchy environments. In: Grace JB, Tilman D, eds. *Perspectives on plant competition*. San Diego, CA, USA: Academic Press, 367–385.
- Allen MF, Boosalis MG. 1983. Effects of two species of vesicular arbuscular fungi on drought tolerance of winter wheat. *New Phytologist* 93: 67–76.
- Allen MF, Swenson W, Querejeta JI, Egerton-Warburton LM, Treseder KK. 2003. Ecology of mycorrhizae: a conceptual framework for complex interactions among plants and fungi. *Annual Review of Phytopathology* 41: 271–303.
- Allen MF, Klironomos JN, Treseder KK, Oechel WC. 2005. Responses of soil biota to elevated CO₂ in a chaparral ecosystem. *Ecological Applications* 15: 1701–1711.
- Antoninka A, Wolf J, Bowker MA, Classen AT, Johnson NC. 2009. Linking above- and belowground responses to global change at community and ecosystem scales. *Global Change Biology* 15: 914–929.

- Auge RM. 2001. Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis. *Mycorrhiza* 11: 3–42.
- Azcón R, Ocampo JA. 1981. Factors affecting the vesicular-arbuscular infection and mycorrhizal dependency of thirteen wheat cultivars. *New Phytologist* 87: 677–685.
- Azcón R, Ambrosano E, Charest C. 2003. Nutrient acquisition in mycorrhizal lettuce plants under different phosphorus and nitrogen concentration. *Plant Science* 165: 1137–1145.
- Bååth E, Spokes J. 1989. The effect of added nitrogen and phosphorus on mycorrhizal growth response and infection in *Allium schoenoprasum*. *Canadian Journal of Botany* 67: 3227–3232.
- Bardgett RD, Bowman WD, Kaufman R, Schmidt SK. 2005. A temporal approach to linking aboveground and belowground ecology. *Trends in Ecology & Evolution* 20: 634–641.
- Bardgett RD, Freeman C, Ostle NJ. 2008. Microbial contributions to climate change through carbon cycle feedbacks. *International Society for Microbial Ecology Journal* 2: 805–814.
- Baylis GTS. 1975. The magnolioid mycorrhiza and mycotrophy in root systems derived from it. In: Sanders F, Mosse B, Tinker P, eds. *Endomycorrhizas*. London, UK: Academic Press, 373–389.
- Berendse F, Aerts R, Bobbink R. 1993. Atmospheric nitrogen deposition and its impact on terrestrial ecosystems. In: Vos CC, Opdam P, eds. *Landscape ecology of a stressed environment*. London, UK: Chapman and Hall, 104–121.
- Bever JD. 2002. Soil community feedback and the coexistence of competitors: conceptual frameworks and empirical tests. *New Phytologist* 157: 465–473.
- Bever JD, Schultz PA, Pringle A, Morton JB. 2001. Arbuscular mycorrhizal fungi: more diverse than meets the eye, and the ecological tale of why. *BioScience* 51: 923–931.
- Bever JD, Richardson SC, Lawrence BM, Holmes J, Watson M. 2009. Preferential allocation to a beneficial symbiont with spatial structure maintains mycorrhizal mutualism. *Ecology Letters* 12: 13–21.
- Blanke V, Renker C, Wagner M, Fullner K, Held M, Kuhn AJ, Buscot F. 2005. Nitrogen supply affects arbuscular mycorrhizal colonization of *Artemisia vulgaris* in a phosphate-polluted field site. *New Phytologist* 166: 981–992.
- Bloom AJ, Chapin FS III, Mooney HA. 1985. Resource limitation in plants: an economic analogy. *Annual Review of Ecology and Systematics* 16: 363–393.
- Bobbink R. 1991. Effects of nutrient enrichment in dutch chalk grassland. *Journal of Applied Ecology* 28: 28–41.
- Brouwer R. 1983. Functional equilibrium: sense or nonsense? *Netherlands Journal of Agricultural Science* 31: 335–348.
- Brundrett MC. 2002. Coevolution of roots and mycorrhizas of land plants. *New Phytologist* 154: 275–304.
- Bucher M. 2007. Functional biology of plant phosphate uptake at root and mycorrhiza interfaces. *New Phytologist* 173: 11–26.
- Chapin FSI, Bloom AJ, Field CB, Waring RH. 1987. Plant responses to multiple environmental factors. *BioScience* 37: 49–57.
- Chaudhary VB, Lau MK, Johnson NC. 2008. Macroecology of microbes – biogeography of the Glomeromycota. In: Vama A, ed. *Mycorrhiza*. Berlin, Heidelberg, Germany: Springer-Verlag, 529–564.
- Chaudhary VB, Bowker MA, O'Dell TE, Grace JB, Redman AE, Rillig MC, Johnson NC. 2009. Untangling the biological contributions to soil stability in semiarid shrublands. *Ecological Applications* 19: 110–122.
- Collins CD, Foster BL. 2009. Community-level consequences of mycorrhizae depend on phosphorus availability. *Ecology* 90: 2567–2576.
- Daft MJ, El-Giahmi AA. 1978. Effect of arbuscular mycorrhiza on plant growth. VIII. Effects of defoliation and light on selected hosts. *New Phytologist* 80: 365–372.
- De Deyn GB, Van der Putten WH. 2005. Linking aboveground and belowground diversity. *Trends in Ecology & Evolution* 20: 625–633.
- Douds DD, Schenck NC. 1990. Relationship of colonization and sporulation by VA mycorrhizal fungi to plant nutrient and carbohydrate contents. *New Phytologist* 116: 621–627.
- Egerton-Warburton LM, Allen EB. 2000. Shifts in arbuscular mycorrhizal communities along an anthropogenic nitrogen deposition gradient. *Ecological Applications* 10: 484–496.
- Egerton-Warburton L, Johnson NC, Allen EB. 2007. Mycorrhizal community dynamics following nitrogen fertilization: a cross-site test in five grasslands. *Ecological Monographs* 77: 527–577.
- Eom A-H, Harnett DC, Wilson GWT, Figge DAH. 1999. The effect of fire, mowing and fertilizer amendment on arbuscular mycorrhizas in tall grass prairie. *American Midland Naturalist* 142: 55–70.
- Eom AH, Hartnett DC, Wilson GWT. 2000. Host plant species effects on arbuscular mycorrhizal fungal communities in tallgrass prairie. *Oecologia* 122: 435–444.
- Ericsson T. 1995. Growth and shoot:root ratio of seedlings in relation to nutrient availability. *Plant and Soil* 168–169: 205–214.
- Fitter AH. 1991. Costs and benefits of mycorrhizas: implications for functioning under natural conditions. *Experientia* 47: 350–355.
- Fitter AH. 2006. What is the link between carbon and phosphorus fluxes in arbuscular mycorrhizas? A null hypothesis for symbiotic function. *New Phytologist* 172: 3–6.
- Garraway MO, Evans RC. 1984. *Fungal nutrition and physiology*. New York, NY, USA: Wiley & Sons, 401.
- Gehring CA. 2003. Growth responses to arbuscular mycorrhizae by rain forest seedlings vary with light intensity and tree species. *Plant Ecology* 167: 127–139.
- George E, Romheld V, Marschner H. 1994. Contribution of mycorrhizal fungi to micronutrient uptake by plants. In: Manthey JA, Crowley DE, Luster DG, eds. *Biochemistry of metal micronutrients in the rhizosphere*. Boca Raton, FL, USA: Lewis Publishers, 93–109.
- George E, Marschner H, Jakobsen I. 1995. Role of arbuscular mycorrhizal fungi in uptake of phosphorus and nitrogen from soil. *Critical Reviews in Biotechnology* 15: 257–270.
- Govindarajulu M, Pfeffer PE, Jin H, Abudaker J, Douds DD, Allen JA, Bucking H, Lammers PJ, Shachar-Hill Y. 2005. Nitrogen transfer in the arbuscular mycorrhizal symbiosis. *Nature* 435: 819–823.
- Graham JM. 2008. Scaling-up evaluation of field functioning of arbuscular mycorrhizal fungi. *New Phytologist* 180: 1–2.
- Graham JH, Abbott LK. 2000. Wheat responses to aggressive and non-aggressive arbuscular mycorrhizal fungi. *Plant and Soil* 220: 207–218.
- Graham JH, Eissenstat DM. 1994. Host genotype and the formation and function of VA mycorrhizae. *Plant and Soil* 159: 179–185.
- Graham JH, Leonard RT, Menge JA. 1981. Membrane mediated decrease in root exudation responsible for phosphorus inhibition of vesicular-arbuscular mycorrhizae formation. *Plant Physiology* 68: 548–552.
- Graham JH, Leonard RT, Menge JA. 1982. Interaction of light intensity and soil temperature with phosphorus inhibition of vesicular-arbuscular mycorrhizae formation. *New Phytologist* 91: 683–690.
- Graham JH, Eissenstat DM, Drouillard DL. 1991. On the relationship between a plant's mycorrhizal dependency and rate of vesicular-arbuscular mycorrhizal colonization. *Functional Ecology* 5: 773–779.
- Hardie K. 1985. The effect of removal of extraradical hyphae on water uptake by vesicular-arbuscular mycorrhizal plants. *New Phytologist* 101: 677–684.
- Harrison MJ. 2005. Signaling in the arbuscular mycorrhizal symbiosis. *Annual Review of Microbiology* 59: 19–42.
- Hart MM, Reader RJ. 2002. Taxonomic basis for variation in the colonization strategy of arbuscular mycorrhizal fungi. *New Phytologist* 153: 335–344.
- Hartnett DC, Wilson GWT. 2002. The role of mycorrhizas in plant community structure and dynamics: Lessons from grasslands. *Plant and Soil* 244: 319–331.

- Hayman DS. 1974. Plant growth responses to *va* mycorrhiza *vi*. Effect of light and temperature. *New Phytologist* 73: 71–80.
- van der Heijden MGA, Scheublin TR. 2007. Functional traits in mycorrhizal ecology: their use for predicting the impact of arbuscular mycorrhizal fungal communities on plant growth and ecosystem functioning. *New Phytologist* 174: 244–250.
- van der Heijden MGA, Bardgett RD, van Straalen NM. 2008. The unseen majority: Soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecology Letters* 11: 296–310.
- Helgason T, Daniell TJ, Husband R, Fitter AH, Young JPW. 1998. Ploughing up the wood-wide web? *Nature* 394: 431.
- Hempel S, Renker C, Buscot F. 2007. Differences in the species composition of arbuscular mycorrhizal fungi in spore, root and soil communities in a grassland ecosystem. *Environmental Microbiology* 9: 1930–1938.
- Hendrix JW, Jones KJ, Nesmith WC. 1992. Control of pathogenic mycorrhizal fungi in maintenance of soil productivity by crop rotation. *Journal Production Agriculture* 5: 383–386.
- Hetrick BAD. 1991. Mycorrhizas and root architecture. *Experientia* 47: 355–362.
- Hetrick BAD, Wilson GWT, Cox TS. 1993. Mycorrhizal dependence of modern wheat cultivars and ancestors: a synthesis. *Canadian Journal of Botany* 71: 512–518.
- Hoeksema JD, Ouziad F, Marner F-J, Bothe H. 2006. The bacterium *Paenibacillus validus* stimulates growth of the arbuscular mycorrhizal fungus *Glomus intraradices* up to the formation of fertile spores. *FEMS Microbiology Letters* 254: 258–267.
- Hodge A, Robinson D, Fitter A. 2000. Are microorganisms more effective than plants at competing for nitrogen? *Trends in Plant Science* 5: 304–308.
- Hoeksema JD, Schwartz MW. 2003. Expanding comparative-advantage biological market models: contingency of mutualism on partners' resource requirements and acquisition trade-offs. *Proceedings of the Royal Society of London B* 270: 913–919.
- Janos DP. 2007. Plant responsiveness to mycorrhizas differs from dependence upon mycorrhizas. *Mycorrhiza* 17: 75–91.
- Jansa J, Mozafar A, Kuhn G, Ruh R, Sanders IR, Frossard E. 2003. Soil tillage affects the community structure of mycorrhizal fungi in maize roots. *Ecological Applications* 13: 1164–1176.
- Jifon JL, Graham JH, Drouillard DL, Syvertsen JP. 2002. Growth depression of mycorrhizal citrus seedlings grown at high phosphorus supply is mitigated by elevated CO₂. *New Phytologist* 153: 133–142.
- Jin H, Pfeffer PE, Douds DD, Pitotrowski E, Lammers PJ, Shachar-Hill Y. 2005. The uptake, metabolism, transport and transfer of nitrogen in an arbuscular mycorrhizal symbiosis. *New Phytologist* 168: 687–696.
- Johnson NC. 1993. Can fertilization of soil select less mutualistic mycorrhizae? *Ecological Applications* 3: 749–757.
- Johnson NC, Copeland PJ, Crookston RK, Pflieger FL. 1992a. Mycorrhizae: Possible explanation for yield decline with continuous corn and soybean. *Agronomy Journal* 84: 387–390.
- Johnson NC, Tilman D, Wedin D. 1992b. Plant and soil controls on mycorrhizal fungal communities. *Ecology* 73: 2034–2042.
- Johnson NC, Graham JH, Smith FA. 1997. Functioning of mycorrhizal associations along the mutualism-parasitism continuum. *New Phytologist* 135: 575–585.
- Johnson NC, Rowland DL, Corkidi L, Egerton-Warburton L, Allen EB. 2003. Nitrogen enrichment alters mycorrhizal allocation at five mesic to semiarid grasslands. *Ecology* 84: 1895–1908.
- Johnson NC, Wolf J, Reyes MA, Panter A, Koch GW, Redman A. 2005. Species of plants and associated arbuscular mycorrhizal fungi mediate mycorrhizal responses to CO₂ enrichment. *Global Change Biology* 11: 1156–1166.
- Johnson NC, Hoeksema JD, Bever JD, Chaudhary VB, Gehring CA, Klironomos JN, Koide R, Miller RM, Moore J, Moutoglou P *et al.* 2006. From Lilliput to Brobdingnag: Extending models of mycorrhizal function across scales. *BioScience* 56: 889–900.
- Johnson NC, Rowland DL, Corkidi L, Allen EB. 2008. Characteristics of plant winners and losers in grassland eutrophication – importance of allocation plasticity and mycorrhiza function. *Ecology* 89: 2868–2878.
- Johnson NC, Wilson GWT, Bowker MA, Wilson J, Miller RM. (in press). Mycorrhizal mutualisms are enhanced when plant and fungal partners are in home soil. *Proceedings of the National Academy of Sciences, USA*.
- Kardol P, Bezemer TM, Van der Putten WH. 2006. Temporal variation in plant-soil feedback controls succession. *Ecology Letters* 9: 1080–1088.
- Kaschuk G, Kuypers TW, Leffelaar PA, Hungria M, Giller KE. 2009. Are the rates of photosynthesis stimulated by the carbon sink strength of rhizobial and arbuscular mycorrhizal symbioses? *Soil Biology and Biochemistry* 41: 1233–1244.
- Kaye JP, Hart SC. 1997. Competition for nitrogen between plants and soil microorganisms. *Trends in Ecology & Evolution* 12: 139–143.
- Klironomos JN. 2002. Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature* 417: 67–70.
- Klironomos J, Ursic M, Rillig M, Allen M. 1998. Inter-specific differences in the response of arbuscular mycorrhizal fungi to *Artemisia tridentata* grown under elevated atmospheric CO₂. *New Phytologist* 138: 599–605.
- Klironomos JN, McCune J, Hart M, Neville J. 2000. The influence of arbuscular mycorrhizae on the relationship between plant diversity and productivity. *Ecology Letters* 3: 137–141.
- Klironomos JN, Allen MF, Rillig MC, Piotrowski JS, Makvandi-Nejad S, Wolfe BE, Powell JR. 2005. Abrupt rise in atmospheric CO₂ overestimates community response in a model plant-soil system. *Nature* 433: 21–624.
- Koch AM, Croll D, Sanders IR. 2006. Genetic variability in a population of arbuscular mycorrhizal fungi causes variation in plant growth. *Ecology Letters* 9: 103–110.
- Koerselman W, Meuleman AFM. 1996. The vegetation N:P ratio: A new tool to detect the nature of nutrient limitation. *Journal of Applied Ecology* 33: 1441–1450.
- Koide RT. 1991. Nutrient supply, nutrient demand and plant response to mycorrhizal infection. *New Phytologist* 117: 365–386.
- Koide RT, Dickie IA. 2002. Effects of mycorrhizal fungi on plant populations. *Plant and Soil* 244: 307–317.
- Koide R, Elliot G. 1989. Cost, benefit and efficiency of the vesicular-arbuscular mycorrhizal symbiosis. *Functional Ecology* 3: 252–255.
- Krüger M, Stockinger H, Krüger C, Schussler A. 2009. DNA-based species level detection of glomeromycota: One PCR primer set for all arbuscular mycorrhizal fungi. *New Phytologist* 183: 212–223.
- Lambers H, Raven JA, Shaver GR, Smith SE. 2008. Plant nutrient-acquisition strategies change with soil age. *Trends in Ecology & Evolution* 23: 95–103.
- Leigh J, Hodge A, Fitter AH. 2008. Arbuscular mycorrhizal fungi can transfer substantial amounts of nitrogen to their host plant from organic material. *New Phytologist* 181: 199–207.
- Li H, Smith FA, Dickson S, Holloway RE, Smith SE. 2008. Plant growth depressions in arbuscular mycorrhizal symbioses: Not just caused by carbon drain? *New Phytologist* 178: 852–862.
- Liebig J. 1843. *Chemistry in its application to agriculture and physiology*. London, UK: Taylor and Walton.
- Lilleskov EA, Parrent JL. 2007. Can we develop general predictive models of mycorrhizal fungal community – environment relationships? *New Phytologist* 174: 250–256.
- Maherali H, Klironomos JN. 2007. Influence of phylogeny on fungal community assembly and ecosystem functioning. *Science* 316: 1746–1748.
- Marschner H, Dell B. 1994. Nutrient uptake in mycorrhizal symbiosis. *Plant and Soil* 159: 89–102.

- Mengel K, Kirkby EA. 1982. *Principles of plant nutrition*. Warblaufen-Bern, Switzerland: International Potash Institute.
- Miller RM. 2005. The nonmycorrhizal root – a strategy for survival in nutrient-impovertised soil. *New Phytologist* 165: 655–658.
- Miller RM, Jastrow JD. 2000. Mycorrhizal fungi influence soil structure. In: Kapulnik Y, Douds DD Jr, eds. *Arbuscular mycorrhizas: physiology and function*. Dordrecht, The Netherlands: Kluwer Academic Publishers, 3–18.
- Miller RM, Kling M. 2000. The importance of integration and scale in the arbuscular mycorrhizal symbiosis. *Plant and Soil* 226: 295–309.
- Miller RM, Miller SP, Jastrow JD, Rivetta CB. 2002. Mycorrhizal mediated feedback influence net carbon gain and nutrient uptake in *Andropogon gerardii*. *New Phytologist* 155: 149–162.
- Modjo HS, Hendrix JW, Nesmith WC. 1987. Mycorrhizal fungi in relation to control of tobacco stunt disease with soil fumigants. *Soil Biology and Biochemistry* 19: 289–295.
- Mosse B. 1973. Plant growth responses to vesicular-arbuscular mycorrhizas. IV. In soil given additional phosphorus. *New Phytologist* 72: 127–136.
- Munkvold L, Kjoller R, Vestberg M, Rosendahl S, Jakobsen I. 2004. High functional diversity within species of arbuscular mycorrhizal fungi. *New Phytologist* 164: 357–364.
- Newsham K, Fitter A, Watkinson A. 1995. Multi-functionality and bio-diversity in arbuscular mycorrhizas. *Trends in Ecology & Evolution* 10: 407–411.
- Olsson PA, Thingstrup I, Jakobsen I, Baath E. 1999. Estimation of the biomass of arbuscular mycorrhizal fungi in a linseed field. *Soil Biology and Biochemistry* 31: 1879–1887.
- Öpik M, Metsis M, Daniell TJ, Moora M. 2009. Large-scale parallel 454 sequencing reveals host ecological group specificity of arbuscular mycorrhizal fungi in a borenomoral forest. *New Phytologist* 184: 424–437.
- Parniske M. 2008. Arbuscular mycorrhiza: The mother of plant root endosymbioses. *Nature Reviews Microbiology* 6: 763–775.
- Pfeffer PE, Douds DD, Bucking H, Schwartz DP, Shachar-Hill Y. 2004. The fungus does not transfer carbon to or between roots in an arbuscular mycorrhizal symbiosis. *New Phytologist* 163: 617–627.
- Piotrowski JS, Denich T, Klironomos JN, Graham JM, Rillig MC. 2004. The effects of arbuscular mycorrhizas on soil aggregation depend on the interaction between plant and fungal species. *New Phytologist* 164: 365–373.
- Pirozynski KA, Malloch DW. 1975. The origin of land plants: a matter of mycotrophism. *Biosystems* 6: 153–164.
- van der Ploeg RR, Böhm W, Kirkham MB. 1999. On the origin of the theory of mineral nutrition of plants and the law of the minimum. *Soil Science Society of America Journal* 63: 1055–1062.
- Porras-Alfaro A, Herrera J, Natvig DO, Sinsabaugh RL. 2007. Effect of long-term nitrogen fertilization on mycorrhizal fungi associated with a dominant grass in a semiarid grassland. *Plant and Soil* 296: 65–75.
- van der Putten WH, Van Dijk c, Peters BAM. 1993. Plant-specific soil-borne diseases contribute to succession in foredune vegetation. *Nature* 362: 53–56.
- van der Putten WH, Vet LEM, Harvey JA, Wackers FL. 2001. Linking above- and belowground multitrophic interactions of plants, herbivores, pathogens, and their antagonists. *Trends in Ecology & Evolution* 16: 547–554.
- Pyke GH. 1984. Optimal foraging theory: a critical review. *Annual Review of Ecology and Systematics* 15: 523–575.
- Read DJ. 1991a. Mycorrhizas in ecosystems. *Experientia* 47: 376–391.
- Read DJ. 1991b. Mycorrhizas in ecosystems – nature’s response to the “law of the minimum”. In: Hawksworth DL, ed. *Frontiers in mycology*. Kew Surrey, UK: CAB International, 101–130.
- Read DJ. 2002. Towards ecological relevance – progress and pitfalls in the path towards an understanding of mycorrhizal functions in nature. In: van der Heijden MGA, Sanders IR, eds. *Mycorrhizal ecology*. Berlin, Heidelberg, Germany: Springer-Verlag, 3–29.
- Read DJ, Perez-Moreno J. 2003. Mycorrhizas and nutrient cycling in ecosystems – a journey towards relevance? *New Phytologist* 157: 475–492.
- Redecker D, Kodner R, Graham LE. 2000. Glomalean fungi from the ordovician. *Science* 289: 1920–1921.
- Reinhardt D. 2007. Programming good relations – development of the arbuscular mycorrhizal symbiosis. *Current Opinions in Plant Biology* 10: 98–105.
- Reynolds HL, Packer A, Bever A, Clay K. 2003. Grassroots ecology: Plant-microbe-soil interactions as drivers of plant community structure and dynamics. *Ecology* 84: 2281–2291.
- Reynolds HL, Hartley AE, Vogelsang KM, Bever JD, Schultz PA. 2005. Arbuscular mycorrhizal fungi do not enhance nitrogen acquisition and growth of old-field perennials under low nitrogen supply in glasshouse culture. *New Phytologist* 167: 869–880.
- Rillig MC. 2004. Arbuscular mycorrhize and terrestrial ecosystem processes. *Ecology Letters* 7: 740–754.
- Rillig MC, Mummey DL. 2006. Mycorrhizas and soil structure. *New Phytologist* 171: 41–53.
- Rogers HH, Prior SA, Runion GB, Mitchell RJ. 1996. Root to shoot ratio of crops as influenced by CO₂. *Plant and Soil* 187: 229–248.
- Rosendahl S. 2008. Communities, populations and individuals of arbuscular mycorrhizal fungi. *New Phytologist* 178: 253–266.
- Sanders IR. 2002. Ecology and evolution of multigenomic arbuscular mycorrhizal fungi. *American Naturalist Supplement* 160: s128–s141.
- Sanders IR. 2004. Plant and arbuscular mycorrhizal fungal diversity – are we looking at the relevant levels of diversity and are we using the right techniques? *New Phytologist* 164: 415–418.
- Sanders IR, Fitter A. 1992. Evidence for differential responses between host-fungus combinations of vesicular-arbuscular mycorrhizas from a grassland. *Mycological Research* 96: 415–419.
- Sanders IR, Streitwolf-Engel R, van der Heijden MGA, Boller T, Wiemken A. 1998. Increased allocation to external hyphae of arbuscular mycorrhiza fungi under CO₂ enrichment. *Oecologia* 117: 496–503.
- Schenck NC, Kinloch RA. 1980. Incidence of mycorrhizal fungi on six field crops in monoculture on a newly cleared woodland site. *Mycologia* 72: 445–456.
- Schroeder MS, Janos DP. 2004. Phosphorus and intraspecific density alter plant responses to arbuscular mycorrhizas. *Plant and Soil* 264: 335–348.
- Schultz PA, Miller RM, Jastrow JD, Rivetta CV, Bever JD. 2001. Evidence of a mycorrhizal mechanism for the adaptation of *Andropogon gerardii* (poaceae) to high- and low-nutrient prairies. *American Journal of Botany* 88: 1650–1656.
- Schwartz M, Hoeksema J. 1998. Specialization and resource trade: Biological markets as a model of mutualisms. *Ecology* 79: 1029–1038.
- Schweiger P, Robson AD, Barrow NJ. 1995. Root hair length determines beneficial effect of a *Glomus* species on shoot growth of some pasture species. *New Phytologist* 131: 247–254.
- Shachar-Hill Y. 2007. Quantifying flows through metabolic networks and the prospects for fluxomic studies of mycorrhizas. *New Phytologist* 174: 235–240.
- Smith VH, Holt RD. 1996. Resource competition and within-host disease dynamics. *Trends in Ecology & Evolution* 11: 386–389.
- Smith SE, Read DJ. 2008. *Mycorrhizal symbiosis*. New York, NY, USA: Academic Press.
- Smith FA, Grace EJ, Smith SE. 2009. More than a carbon economy: nutrient trade and ecological sustainability in facultative arbuscular mycorrhizal symbioses. *New Phytologist* 182: 347–358.
- Staddon P, Fitter A. 1998. Does elevated atmospheric carbon dioxide affect arbuscular mycorrhizas? *Trends in Ecology & Evolution* 13: 455–458.
- Sterner RW, Elser JJ. 2002. *Ecological stoichiometry: the biology of elements from molecules to the biosphere*. Princeton, NJ, USA: Princeton University Press.

- Stubblefield SP, Taylor TN, Trappe JM. 1987. Fossil mycorrhizae: a case for symbiosis. *Science* 237: 59–60.
- Sylvia DM, Neal LH. 1990. Nitrogen affects the phosphorus response of va mycorrhiza. *New Phytologist* 115: 303–310.
- Thompson JP. 1990. Soil sterilization methods to show VA-mycorrhizae aid P and Zn nutrition of wheat in vertisols. *Soil Biology and Biochemistry* 22: 229–240.
- Thrall PH, Hochbert ME, Burdon JJ, Bever JD. 2006. Coevolution of symbiotic mutualists and parasites in a community context. *Trends in Ecology & Evolution* 22: 120–126.
- Tilman D. 1982. *Resource competition and community structure*. Princeton, NJ, USA: Princeton University Press.
- Tilman D. 1988. *Plant strategies and the dynamics and structure of plant communities*. Princeton, NJ, USA: Princeton University Press.
- Treseder KK. 2004. A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO₂ in field studies. *New Phytologist* 164: 347–355.
- Treseder KK, Egerton-Warburton LM, Allen MF, Chen Y, Oechel W. 2003. Alteration of soil carbon pools and communities of mycorrhizal fungi in chaparral exposed to elevated CO₂. *Ecosystems* 6: 786–796.
- Tu C, Booker FL, Watson DM, Chen X, Rufty TW, Shi W, Hu S. 2006. Mycorrhizal mediation of plant N acquisition and residue edecomposition: Impact of mineral N inputs. *Global Change Biology* 12: 793–803.
- Valentine AJ, Osborne BA, Mitchell DT. 2001. Interactions between phosphorus supply and total nutrient availability on mycorrhizal colonization, growth and photosynthesis of cucumber. *Scientia Horticulturae* 88: 177–189.
- Waksman SA, Tenney FG. 1927. The composition of natural organic materials and their decomposition in the soil II: Influence of age of plant upon the rapidity and nature of its decomposition – rye plant. *Soil Science* 24: 317–333.
- Wallander H. 1995. A new hypothesis to explain allocation of dry matter between mycorrhizal fungi and pine seedlings in relation to nutrient supply. *Plant and Soil* 168–169: 243–248.
- Whitham TG, Bailey JK, Schweitzer JA, Shuster SM, Bangert RK, LeRoy CJ, Lonsdorf EV, Allan GJ, DiFazio SP, Potts BM *et al.* 2006. A framework for community and ecosystem genetics: From genes to ecosystems. *Nature Reviews Genetics* 7: 511–523.
- Wilson GWT, Rice CW, Rillig MC, Springer A, Hertnett DC. 2009. Soil aggregation and carbon sequestration are tightly correlated with the abundance of arbuscular mycorrhizal fungi: Results from long-term field experiments. *Ecology Letters* 12: 452–461.
- Wolf J, Johnson NC, Rowland DL, Reich PB. 2003. Elevated carbon dioxide and plant species richness impact arbuscular mycorrhizal fungal spore communities. *New Phytologist* 157: 579–588.



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