

Functioning of mycorrhizal associations along the mutualism–parasitism continuum*

BY N. C. JOHNSON¹†, J. H. GRAHAM² AND F. A. SMITH³

¹ Biological Sciences, Northern Arizona University, PO Box 5640, Flagstaff, Arizona 86011-5640, USA

² Citrus Research and Education Center, University of Florida, Lake Alfred, Florida 33850, USA

³ Department of Botany, University of Adelaide, SA 5005, Australia

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SUMMARY

A great diversity of plants and fungi engage in mycorrhizal associations. In natural habitats, and in an ecologically meaningful time span, these associations have evolved to improve the fitness of both plant and fungal symbionts. In systems managed by humans, mycorrhizal associations often improve plant productivity, but this is not always the case. Mycorrhizal fungi might be considered to be parasitic on plants when net cost of the symbiosis exceeds net benefits. Parasitism can be developmentally induced, environmentally induced, or possibly genotypically induced. Morphological, phenological, and physiological characteristics of the symbionts influence the functioning of mycorrhizas at an individual scale. Biotic and abiotic factors at the rhizosphere, community, and ecosystem scales further mediate mycorrhizal functioning. Despite the complexity of mycorrhizal associations, it might be possible to construct predictive models of mycorrhizal functioning. These models will need to incorporate variables and parameters that account for differences in plant responses to, and control of, mycorrhizal fungi, and differences in fungal effects on, and responses to, the plant. Developing and testing quantitative models of mycorrhizal functioning *in the real world* requires creative experimental manipulations and measurements. This work will be facilitated by recent advances in molecular and biochemical techniques. A greater understanding of how mycorrhizas function in complex natural systems is a prerequisite to managing them in agriculture, forestry, and restoration.

Key words: Mycorrhizal functioning, mutualism, parasitism, cost–benefit analysis, fitness.

INTRODUCTION

Relationships among species are often defined by the effect of the interaction on each of the species (Burkholder, 1952; Bronstein, 1994). There is a continuum of interactions ranging from mutually beneficial (+,+) to mutually detrimental (−,−) (Lewis, 1985; Fig. 1). Mutualisms are relationships that benefit both species. Commensalism occurs when one species benefits and the other is not affected. Parasitism, predation, herbivory, and fungivory are all consumer–resource relationships in

which one species (the consumer) benefits at the expense of the other species (the resource). Amensalism occurs when one species is inhibited and the other is not affected. Finally, competitive interactions are mutually detrimental because both species are inhibited by the relationship.

Mycorrhizas can be defined in structural terms as associations between symbiotic soil fungi and the absorbing organs of plants (Gerdemann, 1970). Mycorrhizas are often considered to be classical mutualisms: many experimental investigations have shown that both plant and fungal symbionts benefit from the reciprocal exchange of mineral and organic resources. However, this is not always the case and upon closer analysis, there appears to be a continuum of plant responses to mycorrhizal colonization ranging from positive to neutral to negative. Reports of neutral or negative plant growth responses are

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† To whom correspondence should be addressed.
E-mail: Nancy.Johnson@NAU.edu

			Competition (-, -)
-			
0		Neutralism (0, 0)	Amensalism (-, 0)
+	Mutualism (+, +)	Commensalism (0, +)	Parasitism (-, +)

Gradient of plant responses to mycorrhizal associations

Figure 1. Types of species interactions (modified from Burkholder, 1952 and Bronstein, 1994). This paper focuses on the continuum of plant responses to mycorrhizal formation illustrated by the shaded region.

remarkably common (e.g. Koide, 1985; Fitter, 1991; Modjo & Hendrix, 1986; Bouger, Grove & Malajczuk, 1990; see also references in Smith & Smith, 1996). Does this suggest that mycorrhizal fungi are sometimes parasitic on plants? The term *parasitic* is value-laden, and many mycorrhiza researchers resist using it to describe mycorrhizal interactions. However, technically it might be an accurate description of some mycorrhizal associations where the fungus is detrimental to the plant or vice versa (Leake, 1994; Smith & Smith, 1996).

One of the best ways to assess the value of a paradigm is to investigate and understand the conditions where it does not 'appear' to work. In the long run, we will have a much better understanding of mycorrhizal associations if we understand the conditions in which they appear to be neutral or even parasitic. The purpose of this paper is to explore the spectrum of plant responses to colonization by mycorrhizal fungi and develop a conceptual framework on which to construct testable hypotheses about mechanisms generating this diversity of responses. Although also important, the spectrum of fungal responses to associations with plants is not analysed in this paper. Because the majority of mycorrhizal fungi are obligate biotrophs with obvious benefits from the association, we will focus on the interactions illustrated by the shaded region on the bottom of Figure 1, in which the fungus always benefits from the interaction.

PROBLEMS OF SCALE IN MYCORRHIZAL RESEARCH

Mycorrhizal associations are complex hierarchical systems (see O'Neill, O'Neill & Norby, 1991). At the core of every association is a fungus and a plant living symbiotically. The functioning of this symbiosis is mediated by direct and indirect effects of biotic and abiotic factors of the surrounding rhizosphere, community, and ecosystem (Fig. 2). It is important to recognize the complexity of mycorrhizal systems, and address the appropriate scale

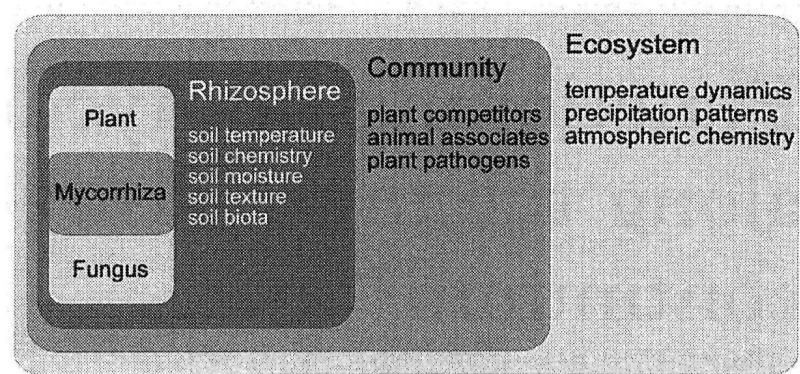


Figure 2. The functioning of mycorrhizal systems is mediated by a hierarchy of abiotic and biotic factors.

when assessing mycorrhizal function. The larger the scale of interest, the greater the potential for moderating mycorrhizal responses through indirect interactions. For example, a plant and associated fungus can be grown in sterile media in a growth chamber with very little mediation from biotic and abiotic factors in the environment. This study system is appropriate for many physiological questions, but it is not appropriate for many ecological questions because it is lacking properties that emerge from the actions and interactions between the plant–mycorrhiza–fungus and the milieu of biotic and abiotic factors in the rhizosphere, community, and ecosystem.

Some studies reporting 'parasitic effects' of mycorrhizal fungi were conducted in extremely simplified experimental systems, or were the result of a single season of research. It is possible that when systems are more thoroughly studied at larger spatial or temporal scales, interactions that originally appeared parasitic might become commensal or mutualistic. For example, a recent tillage study found maize grown under adequate soil phosphorus conditions in no-till fields to have higher levels of mycorrhizal colonization, and *lower yields*, compared with maize grown in fields tilled with a mouldboard plough (McGonigle & Miller, 1996). If only these two treatments are considered in the analysis one would conclude that mycorrhizal colonization is negatively correlated with crop performance. But if a third treatment is considered (ridge-till) that uncouples the effects of residues on soil temperature and the effects of soil disturbance on mycorrhizal inoculum, then colonization is positively correlated with early-season crop performance (McGonigle & Miller, 1993). It is important for investigators to study systems thoroughly in space and time so that confounding factors (such as soil temperature and soil disturbance in the example above) can be uncoupled from the functioning of mycorrhizas.

DEFINING COSTS AND BENEFITS IN MYCORRHIZAL SYSTEMS

At the most basic level, mycorrhizal associations are beneficial (mutualistic) to plants when net costs are less than net benefits, and detrimental (parasitic)

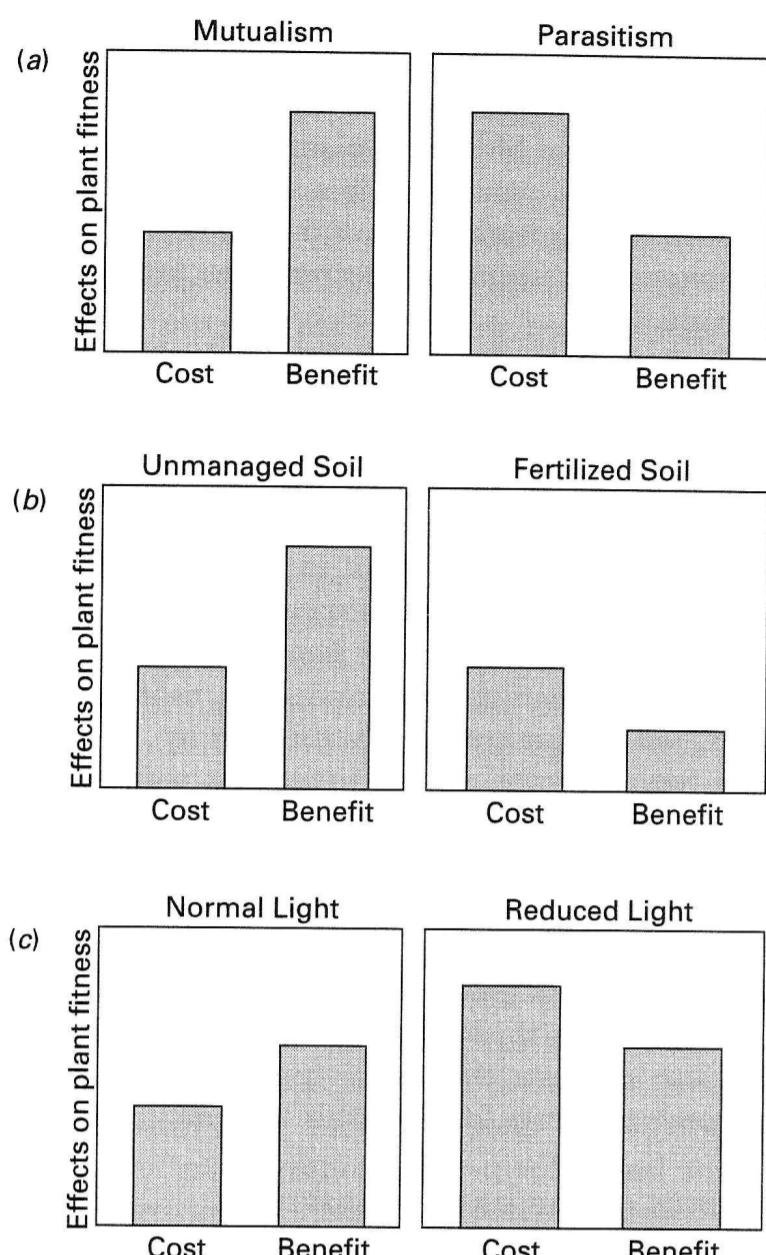


Figure 3. Mycorrhizal associations are mutualistic to plants when benefits exceed costs and parasitic when costs exceed benefits (a). Fertilization diminishes benefits and can generate parasitic associations (b). Factors that limit production of photosynthate, such as reduced irradiance, can generate parasitic associations by increasing relative costs (c).

when costs exceed benefits (Fig. 3a). Potential fitness is often the currency used in ecological cost:benefit analysis (Cushman & Beattie, 1991). In natural systems, plant fitness is typically measured by survival and fecundity, and biomass changes might or might not be a good indicator of reproductive success. By contrast, biomass is usually a good variable to measure in many agricultural systems where seed or biomass yields are the currency of agricultural success. Fitness is measured at the scale of an individual. But in the real world, individuals are not isolated in experimental pots. Interactions at the scale of populations, communities, and ecosystems, mediate the actual fitness of individuals. The challenge in analysing plant responses to formation of mycorrhizas is measuring costs and benefits at scales that are appropriate for the question of interest.

From a plant perspective, costs of mycorrhizas are traditionally expressed in terms of photosynthate allocated to the fungus and the supporting root tissue

(e.g. Koide & Elliot, 1989; Fitter, 1991; Peng *et al.*, 1993). Estimates of the amount of carbon allocated to fungal associates can be substantial, ranging from 4 to 20 % of a plant's total C budget (Peng *et al.*, 1993; Rygiewicz & Andersen, 1994; Tinker, Durall & Jones, 1994; Watkins *et al.*, 1996). Mycorrhizas of heterotrophic (achlorophyllous) plants (i.e. orchid and monotropoid mycorrhizas) are major exceptions to this pattern, because in these associations, C flow is reversed so that the fungus supplies the plant heterotrophically acquired C for all or part of the plant's life cycle (Alexander & Hadley, 1985; Leake, 1994). In these cases, the plant appears to be parasitic on the fungus—what benefits the latter derives from the association are unclear (Leake, 1994).

Where mycorrhizal plants are linked by a hyphal network, the issue of costs and benefits, and hence of parasitism, can become blurred if C flows from a 'donor' to a 'receiver' plant (Francis & Read, 1984). Transfer of C has been primarily demonstrated with ^{14}C and this has mostly given no indication of the amount of C transferred, its form, or even whether there is in fact always net transfer. For example, complex cycling of organic C (and of organic N) will be associated with synthesis of amino acids and amides in a mycorrhizal fungus that connects two plants: see Smith & Smith (1996) for a critical discussion of this issue. Recent work with stable C isotopes has overcome many of the problems and has demonstrated significant plant to plant transfer of organic C through a common hyphal network (Watkins *et al.*, 1996). Furthermore, recent ^{13}C -labelling experiments with *Festuca* turves indicate that C exported to neighboring plants does not enter the root tissues of the receiver, but remains in the arbuscular mycorrhizal (AM) fungus (J. D. Graves *et al.*, unpublished). Consequently, the ecological and evolutionary significance of mycorrhizal links between autotrophic plants is still unclear (Janos, 1987, Smith & Smith, 1996).

Benefits from mycorrhizas are traditionally recognized as improved access to limiting soil resources, most notably immobile nutrients (e.g. P, Cu, Zn, and ammonium), but also organic C in the case of orchids and monotropoids. The nutritional benefits of mycorrhizas can be significant. For example, Marschner & Dell (1994) estimated that external hyphae of AM fungi can deliver up to 80 % of a plant's P requirements and 25 % of a plant's nitrogen requirements. Nutritional benefits are even greater in most ectomycorrhizal associations. For example, ectomycorrhizal pine roots can supply up to 3·2 times more P and 1·8 times more N than a nonmycorrhizal root system (Bowen, 1973). Resource limitation is a key component of cost:benefit analysis of mycorrhizal effects on plant fitness (see Eissenstat *et al.*, 1993). *Carbon allocated to a fungus is only a cost if it could otherwise have been allocated to increase plant fitness, and resources gained through the*

activities of a fungal symbiont are only beneficial if those resources are in limiting supply.

Although reciprocal exchange of limiting resources is the most obvious (and traditional) choice for cost:benefit analysis, in many natural systems, other (often subtle) mycorrhiza-induced changes might ultimately be more important to plant fitness. For example, plant morphology, allometry, phenology, and chemistry are affected by the presence of mycorrhizal fungi (e.g. Allen, Moore & Christensen, 1980; Miller, Jarstfer & Pillai, 1986; Pacovsky, Bethlenfalvay & Paul, 1986; Hetrick, Wilson & Leslie, 1991; Bethlenfalvay, Mihara & Schreiner, 1994; Lu & Koide, 1994). Some of these changes will complicate the cost:benefit analysis. Thus, if formation of a mycorrhiza results in reduction of root growth compared with that in an equivalent non-mycorrhizal plant, then the cost to the plant in terms of loss of C to the fungus might be less than the cost resulting from 'additional' root formation in the non-mycorrhizal plant.

Put into a community or ecosystem context, mycorrhizal symbioses can substantially impact plant fitness both directly and indirectly through altered relationships with other components of the system (e.g. Marx 1972; Grime *et al.*, 1987; Linderman, 1988; Malajczuk, 1988; Miller & Jastrow, 1990). These relationships might be difficult to disentangle. For example, in a winter annual grass system, Newsham, Fitter & Watkinson (1994) found that colonization by AM fungi was not directly related to plant fecundity, but mycorrhizal interference with asymptomatic root pathogens was positively correlated with fecundity. Consequently, mycorrhizas contributed to plant fitness by protecting plants from pathogens. Depending upon the system of interest, mycorrhizal effects on plant-pathogen interactions can be either a benefit (as shown in the previous example), or a cost to plant fitness. Although mycorrhizas frequently reduce the incidence of soil-borne diseases (Graham, 1988) they might indirectly enhance the incidence of other diseases, like viruses, that are stimulated by improved plant nutrition, growth, and other physiological factors (Dehne, 1982).

Complexity at community and ecosystem scales means that mycorrhiza-induced changes in plant allocation patterns might have unpredictable effects on plant fitness. Streitwolf-Engel *et al.* (1997) showed that colonization by different isolates of AM fungi differentially affected reproductive allocation by two *Prunella* species. Some isolates stimulated clonal propagation through stolons, while other isolates stimulated sexual reproduction through flowering. Whether these fungal isolates increase or decrease plant fitness is a function of the criteria used to measure fitness and the scale of observation. If fitness is measured only as annual seed set, then the flower-inducing fungal isolates would normally be

considered more beneficial than the stolon-inducing isolates. However, if the system of interest is expanded to include hypothetical herbivores that selectively graze blooming plants, then the flower-inducing fungi would be less beneficial than the stolon-inducing fungi because they indirectly attract herbivores that ultimately decrease the fitness of the individual.

The hypothetical example linking the functioning of *Prunella* mycorrhizas with its herbivores is not unreasonable. In one of the relatively few analyses of mycorrhizal functioning at the ecosystem level, Gehring & Whitham (1994; 1995) linked the incidence of ectomycorrhizas in pinyon pine with environmental stress and herbivory. Trees growing in low-fertility cinder-soils had more mycorrhizal colonization than trees growing in nearby sandy loam soil. Furthermore, herbivory by stem and cone-boring moths caused significant reductions of mycorrhizal colonization in the stressful cinder soil, but similar levels of herbivory on trees growing in less stressful sandy loam soil did not reduce mycorrhizal colonization. These results suggest that pine trees growing in stressful conditions were more C limited than those growing in more fertile soils, and also suggests that herbivores can out compete mycorrhizal fungi for C in this system.

FORMULAS FOR PARASITISM

Given the complexity of mycorrhizal functioning in the real world, is there any hope of understanding these systems well enough to manage them consistently and over long periods of time in restoration, forestry, and agriculture? A starting place might be to assume mutualism as the normal state of mycorrhizal functioning and try to understand causes of 'parasitic' exceptions to this norm. Situations in which net costs of a mycorrhizal association are expected to exceed net benefits should be identified. These hypothesized *formulas for parasitism* can be experimentally tested, modified, re-tested, and eventually used to help design management practices that avoid parasitism by mycorrhizal fungi. Based on the mycorrhizal system illustrated in Figure 2, fungal parasitism of a host plant can be hypothesized to result from (1) developmental factors (temporal relationships of the plant-mycorrhiza-fungus), (2) environmental factors (outside the plant-mycorrhiza-fungus), or (3) genotypic factors (inside the plant-mycorrhiza-fungus).

(1) Developmental factors

Parasitic mycorrhizal associations can occur at particular stages in the development of the association. For example, formation of arbuscular mycorrhizas can depress seedling growth in the first few weeks following germination. At this time benefits are low because necessary resources are

obtained internally from seed reserves, and costs are high because C allocated to the developing fungus decreases allocation to photosynthetic or defense structures or compounds that would increase a seedling's chances for survival. Many reports show growth depressions in AM plants during the first several weeks of seedling development which disappear as internal seed reserves become depleted (e.g. Bethlenfalvay, Brown & Pacovsky, 1982; Koide, 1985). In other words, short-term losses are often compensated by long-term gains. In contrast to early-stage net C drain in arbuscular mycorrhizas, some orchid mycorrhizas might potentially generate late-stage C drain as the endophyte shifts from being a C source to a C sink (Leake, 1994). The balance between net costs and net benefits is remarkably dynamic through the development of a mycorrhizal association and it is dependent on interactions with the environment.

(2) Environmental factors

Parasitic mycorrhizal associations can occur when the chemical, physical, or biotic environment of mycorrhizal systems cause net costs to exceed net benefits. Nutrient status of soil is the best studied, and probably the most relevant environmental mediator of plant responses to mycorrhizal associations. Fertilizing a system can potentially eliminate resource limitations so that mycorrhizas become superfluous for facultatively mycotrophic plants (e.g. Mosse, 1973; Bethlenfalvay, Bayne & Pacovsky, 1983; Kiernan, Hendrix, & Maronek, 1983; Koide, 1985; Johnson, 1993; Graham, Drouillard & Hodge, 1996). If colonization does not decrease with fertilization, then net costs will remain intact (Fig. 3b) but where colonization and hence total fungal biomass decreases the net costs to the plant will also decrease. Effects of increased soil P on colonization vary, in some cases a large decrease in colonization occurs and in others there is little if any effect until levels of added P become very high. Generally speaking, increasing the availability of a limiting soil resource can convert balanced mutualistic relationships into less balanced ones, some of which are clearly parasitic (Fig. 3b).

Humans might inadvertently be altering the relationships between plants and mycorrhizal fungi and so might be affecting the cost:benefit balances. Use of fertilizers has increased exponentially in the past several decades (Vitousek, 1994). Also, wet and dry deposition of N emitted from livestock production, agricultural operations and internal combustion engines now exceeds natural N inputs in many ecosystems (Vitousek & Matson, 1993). Anthropogenic inputs of N might be linked to the alarming disappearance of mushroom-forming fungi, including a disproportionate number of ectomycorrhizal taxa (Arnolds, 1991). Whether the loss

of ectomycorrhizal fungi is a cause or a symptom of forest decline still needs to be resolved (Cherfas, 1991; Jaenike, 1991). Nitrogen fertilization can also change the species composition of AM fungal communities (Johnson, 1993). Experiments suggest that the fungal taxa that proliferate in fertilized soils might be less beneficial as mutualists to native prairie grasses than fungal taxa in unfertilized prairie soil (Johnson, 1993). Again, whether the shift in mycorrhizal fungal communities is a cause or a symptom of the loss of plant species diversity in eutrophied grasslands (*sensu* Wedin & Tilman, 1996) is yet unresolved.

Just as fertilization can cause mycorrhizal costs to exceed benefits, so can insufficient light; only here the benefits of a mycorrhizal association might remain constant while relative costs increase (Fig. 3c). Low light intensities can restrict photosynthetic capabilities of plants. Allocation of a *limited supply* of photosynthate to a fungal associate might potentially reduce plant allocation to functions related to its fitness. This constitutes a relatively greater cost because C has become relatively more limiting than soil resources. Mycorrhizal growth reductions associated with low light intensities have been commonly observed experimentally (e.g. Björkman, 1942; Hayman, 1974; Daft & El Giahmi, 1978; Son & Smith, 1988). Anthropogenic pollution can alter radiation levels and photosynthetic potential of host plants, thus changing the balance between mycorrhizal costs and benefits. For example, Duckmantion and Widden (1994) found that ozone changed the morphology of arbuscular mycorrhizas in sugar maple (*Acer saccharum*) seedlings. The relative abundance of arbuscules decreased while the abundance of vesicles and hyphal coils increased. These changes suggest that mycorrhizas are extremely sensitive to ozone generated plant stress. Again, the relationship between mycorrhizal morphology and functioning needs to be considered in light of the recent decline of maples in many forest ecosystems (Klironomos, 1995).

The biotic components of the environment in which a mycorrhizal plant grows are known to influence mycorrhizal functioning (e.g. Garbaye & Bowen, 1987; Linderman, 1988; Hetrick & Wilson, 1991; Fitter & Garbaye, 1994), but the mechanisms involved are often elusive. The complexity of biotic interactions is great enough to overwhelm probably even the most advanced super-computer. Yet, simple hypotheses concerning the effects of *functional groups* of organisms on mycorrhizal plants can be constructed using a cost-benefit framework. For example, herbivores consume photosynthetic organs and deplete plant reserves of photosynthate. For facultatively mycotrophic hosts, high levels of herbivory could deplete plant C reserves to the extent that the cost of maintaining a mycorrhizal association outweighs its benefits (e.g. Daft & El Giahmi, 1978;

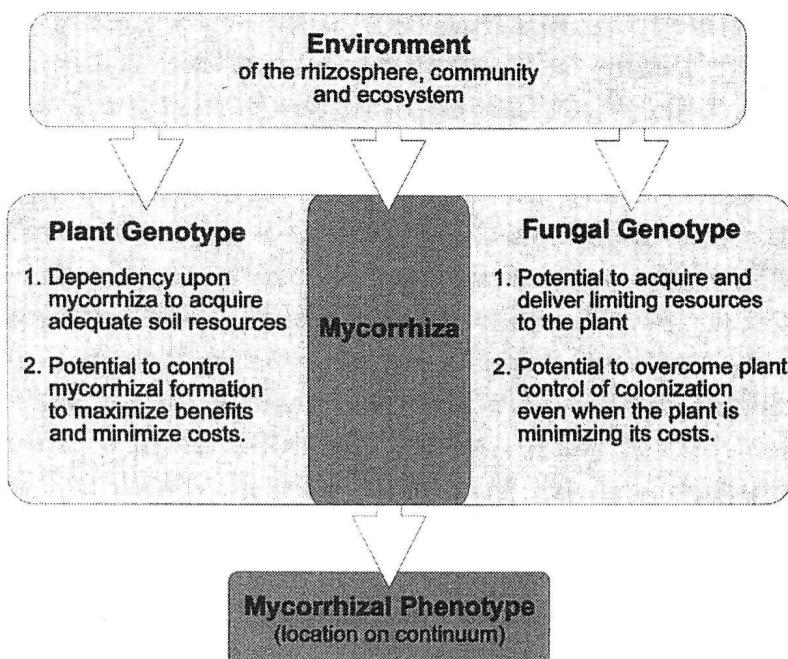


Figure 4. Mycorrhizal phenotypes are manifestations of the interaction between plant and fungal genotypes and environmental conditions. These factors determine the functioning of mycorrhizas along the mutualism-parasitism continuum.

Bayne, Brown & Bethlenfalvay, 1984). By contrast, for obligately mycotrophic hosts (such as the Pinaceae) that cannot survive without mycorrhizae, no C cost is too great to maintain a mycorrhizal associate and costs never exceed benefits. Fungivores also potentially affect mycorrhizal functioning. By consuming the network of external mycelium, fungivores might potentially reduce the ability of mycorrhizal fungi to supply limiting soil resources to its host (e.g. McGonigle & Fitter, 1988; Gange & Brown, 1992; Fitter & Garbaye, 1994).

Positive mycorrhizal growth responses decrease as the density of plants increase (Sanders, Koide & Shumway, 1995). Where large numbers of roots and mycorrhizal fungal hyphae are close together the mycorrhizal roots appear to compete with each other (and with any non-mycorrhizal root), so that growth of all the individual plants is reduced compared with growth of plants spaced well apart. This might be one reason why in the field AM associations sometimes exhibit little benefit in improving growth.

(3) Genotypic factors

Parasitic mycorrhizal associations occur when the genotypes of plants and fungi involved in the mycorrhizas do not establish 'win-win' symbioses. Extreme examples of this are *Armillaria mellea* and *Rhizoctonia solani* which are beneficial mutualists in orchid mycorrhizas, but potentially destructive parasites (pathogens) to many woody and herbaceous plants (Smith & Douglas, 1987; Leake, 1994). Ultimately, it is the genotypes of the plants and fungi involved that determine the potential functioning of the symbiosis. However, mycorrhizal phenotypes are manifestations of interactions between plant and fungal genotypes and environmental conditions (Fig. 4).

Mycorrhizal dependency varies greatly among taxa and varieties of plants (e.g. Lambert & Cole, 1980; Burgess, Malajczuk & Grove, 1993; Graham & Eissenstat, 1994). At one extreme are non-host plants that do not form functioning mycorrhizas, and if inoculated with mycorrhizal fungi can exhibit growth depressions and root necrosis (Allen & Allen, 1984; Allen, Allen & Friese, 1989; Francis & Read, 1994). However, truly non-mycorrhizal plant species and genera are remarkably rare in nature and the great majority of plants are mycotrophic to some degree (Newman & Reddel, 1987). One might hypothesize that the greater the mycorrhizal dependency of a plant, the smaller the probability of a parasitic effect of mycorrhizas because obligate mycotrophs have a greater cost:benefit differential than facultative mycotrophs. Alternatively, because plant genotypes that are highly dependent on mycorrhizas for nutrient uptake appear to have a greater propensity to allocate C to support of higher rates of colonization than do less dependent plant genotypes (Graham, Duncan & Eissenstat, 1997), in highly fertilized systems, more dependent plants might have a greater risk of mycorrhizal parasitism where they do not closely control 'unnecessary' root growth or rate of colonization to reduce cost of colonization when benefit is not forthcoming.

Just as plant taxa vary in mycorrhizal dependency, fungal taxa and isolates vary in mycorrhizal effectiveness. When tested on a single host species, mycorrhizal fungal isolates can increase, decrease, or have little effect on plant growth (e.g. Molina, 1979; Miller, Domoto & Walker, 1985; Bethlenfalvay *et al.*, 1989; Dosskey, Linderman & Boersma, 1990; Burgess, Dell & Malajczuk, 1994; see also references in Smith & Smith, 1996). An extreme example of a mycorrhizal fungal association that decreases plant performance is observed in an intensively managed agricultural system in Kentucky, USA. A series of field and glasshouse studies has shown that colonization of tobacco by an endemic isolate of *Glomus macrocarpum* significantly reduces root length, aboveground biomass, and flowering (Modjo & Hendrix 1986; Jones & Hendrix, 1987; Modjo, Hendrix & Nesmith, 1987; Hendrix, Jones & Nesmith, 1992). Although this isolate of *G. macrocarpum* is strongly parasitic (pathogenic) on tobacco in field soils with extremely high P, it does not appear to have parasitic effects on other crops. Furthermore, it appears to have some specificity for tobacco because, in field studies, *G. macrocarpum* populations (and stunt-disease) can be controlled by rotation with *Festuca* (containing an endophyte that inhibits *G. macrocarpum*) as effectively as by fumigation (Hendrix *et al.*, 1992; An, Guo & Hendrix, 1993; Hendrix, Guo & An, 1995).

As we have seen, environmental factors mediate mycorrhizal effects. Fungal isolates have been shown

to increase plant growth in one experimental system and not in another experimental system (e.g. Anderson, Hetrick & Wilson, 1994). Alternatively, some isolates of AM fungi have been found that are equally effective in promoting plant growth over a wide range of edaphic and host conditions (Sylvia *et al.*, 1993). The question remains, are there genotypes of mycorrhizal fungi that are universally bad for plants i.e. are there constitutive fungal parasites? If so, there remains the unresolved evolutionary issue of why plants have not evolved mechanisms to prevent their colonization. In this context, it is dangerous to assume that the selective advantages of mycorrhizal associations lie only in the mutual exchange of nutrients or other simple physiological benefits, as emphasized by Fitter (1985, 1991).

The potential for parasitism by mycorrhizal fungi has been discussed in the context of 'cheating' by Janos (1985, 1987, 1996; see also Smith & Smith, 1996). A 'cheater' is an individual of a partner species that receives the benefits of mutualism but does not reciprocate (Soberon & Martinez del Rio, 1985). From an evolutionary context, the appearance of cheaters within mutualistic associations is highly probable (Boucher, James & Keeler, 1982). Based on an analysis of cheating in plant-pollinator mutualisms, Soberon & Martinez del Rio (1985) proposed that factors that impede the discrimination of cheaters and non-cheaters by the cheated partner, or decrease the interdependency of the partners, favour the evolution of cheating. Native plant populations have diverse gene pools that are continually modified through selection pressures exerted by their environment, including the endemic mycorrhizal fungal community. One would expect that over time, plant genotypes that maximize mycorrhizal benefits would be at a selective advantage, and come to predominate in the population. By contrast, crop plants and plantation stock have no mechanism to link their gene pool with mycorrhizal functioning. Farmers, fruit producers, and foresters generally do not choose plant genotypes on the basis of their functioning with local mycorrhizal fungi, and fertilization and tillage might further uncouple the interdependency of plants and mycorrhizal fungi. Consequently, management practices might actually select for mycorrhizal fungi that are cheaters (Johnson & Pfleger, 1992).

INDICATORS OF MUTUALISTIC/PARASITIC QUALITIES

The hypothesized formulas for parasitism describe types of situations in which parasitic effects might be expected to occur, but mechanistic details of the causes of these effects remain largely unexplored. Morphological, phenological, and physiological characteristics of the symbionts (both plants and fungi) influence the functioning of mycorrhizas (see

Smith & Smith, 1996). Can certain combinations of characteristics signal the mutualistic or parasitic qualities of mycorrhizal associations? Imbalances between transfer of inorganic nutrients and organic C might be the physiological events that determine whether the symbiosis is mutualistic or parasitic, but there are several possible causes of this imbalance, ranging from synthesis, operation and regulation of transport proteins to structural features of the plant-fungus interface. An example of the latter in arbuscular mycorrhizas is the number of arbuscules and their rate of formation and turnover (Dickson & Smith, 1991; Duckmanton & Widden, 1994). Recognition of appropriate indicators, and development of a predictive model of *mycorrhizal functioning* would be extremely useful for selecting appropriate fungi for management or inoculation efforts to maximize benefits of the symbiosis. A helpful start would be to construct a model that uses as its basis the approach of Barber and associates (Silberbush & Barber, 1983).

A predictive model of mycorrhizal functioning needs to incorporate variables and parameters that account for plant responses to, and control of, mycorrhizas. Plant genotypes differ measurably in their dependency on mycorrhizas. In general, plants with coarse root systems benefit more from mycorrhizal associations than the genotypes with fibrous root systems (e.g. Baylis, 1975; Pope *et al.*, 1983; Graham & Syvertsen, 1985; Hetrick, Kitt & Wilson, 1988). Similarly, plant species and cultivars with high shoot:root ratios can have a higher mycorrhizal dependency than those with low shoot:root ratios (Jakobsen, 1991). As noted above, the potential for plants to vary C allocation to roots and maintain control of mycorrhizal colonization appears to be important. Among citrus genotypes colonization rate varies in relation to non-structural carbohydrate allocation to roots. The more dependent the citrus genotype on arbuscular mycorrhizas for P acquisition, the greater the tendency to allocate carbohydrate to roots to support colonization (Graham *et al.*, 1997). Plasticity in shoot:root ratios can be another mechanism by which plants control C allocation to mycorrhizal fungi (Koide, 1991).

A predictive model of mycorrhizal functioning also needs to account for fungal effects on, and responses to, the plant. As already noted, genotypes of mycorrhizal fungi differ in their ability to acquire and deliver limiting resources to their hosts (e.g. Sanders *et al.*, 1977; Graham, Linderman & Menge 1982; Jakobsen, Abbott & Robson, 1992). The rate and extent of colonization is likely to be important. Fungi that are rapid colonists appear to generate the greatest growth benefits in low-P-fertility soils, and also the greatest growth depressions in high fertility soils (Abbott & Robson, 1985; Graham *et al.*, 1996). This relationship between colonization rate and mutualistic or parasitic response is presently recog-

nized for a narrow range of *Glomus* spp., and needs to be investigated over a wider range of Glomalean and ectomycorrhizal fungi. Functional differences at the host-fungus interface is also likely to be important. For example, isolates of AM fungi that are rapid colonizers have higher rates of fungal fatty acid accumulation in roots than slower colonizers; and, a greater effect on allocation of nonstructural carbohydrates to roots in support of fungal and host construction and maintenance of the mycorrhizas (Peng *et al.*, 1993; Graham *et al.*, 1996). In heavily fertilized soils, fungal genotypes with the potential to overcome plant control of the rate and extent of colonization and C allocation would be at a selective advantage over genotypes that are more sensitive to plant regulation (Fig. 4).

METHODS TO STUDY PLANT RESPONSES TO MYCORRHIZAL COLONIZATION

What are the best approaches to study the dynamics of mycorrhizal functioning? Because of the ubiquity of mycorrhizas in most ecosystems, their manipulation in field trials is challenging. Fungicides and fumigation have been utilized experimentally with varying success to reduce the incidence of mycorrhizas and manipulate field function and cost benefit outcomes (Fitter & Nichols 1988; Gange & Brown, 1992; Graham & Eissenstat, 1996; Wilson & Hartnett, 1996). The nonselectivity of some biocides raises concerns that growth responses might be attributable to control of pathogens or altered nutrient dynamics rather than reducing colonization of mycorrhizas. Jakobsen (1994) suggests making comparisons between uninoculated and inoculated plants grown in fumigated field plots to reduce the confounding effects of enhanced nutrient availability following fumigation. Several agronomic and forestry practices can be used instead of biocides to reduce mycorrhizal colonization rate. Tillage as a form of soil disturbance is well known to disrupt hyphal networks and reduce colonization by arbuscular mycorrhizas (Jasper, Abbott & Robson, 1991; McGonigle & Miller, 1996). Forest clear-cutting and intensive site preparation is also known to reduce ectomycorrhizal colonization rates (Perry, Molina & Amaranthus, 1987). Pre-planting with non-host plants or maintaining fallow might also reduce mycorrhizal fungal populations moderately to drastically, depending on their duration, and reduce colonization rate in subsequent experimental plants (Black & Tinker, 1979; Thompson, 1987; Perry *et al.*, 1989).

For mycorrhizal systems in which enhanced P uptake is the dominant benefit and C drain is the dominant cost, the ideal experimental condition to study field functioning is in low-P soil that is experimentally treated to: (1) reduce mycorrhizal colonization using one of the methods described

above; and, (2) enrich P supply to provide for plant sufficiency without mycorrhiza-mediated uptake. Furthermore, to the extent possible, no resource other than C assimilation (e.g. nutrient or water) should be limiting plant growth. These experimental preconditions are not atypical of intensively fertilized and irrigated systems and are most easily interpreted with AM plants. The predicted outcomes of mycorrhizal reduction at low and high P supply are designed to demonstrate the extremes of mutualistic to parasitic effects of indigenous mycorrhizal fungi or those introduced through preinoculation of the plants or planting site. At low P supply, reduced colonization will reveal mycorrhizal benefits and result in early P limitation and reduced growth rate depending on the mycorrhizal dependency of the host, and the effectiveness of the fungi. Phosphorus fertilization eliminates mycorrhizal benefits due to enhanced P uptake, yet maintains the costs *if the fungi are actively colonizing roots in spite of high P availability*, as discussed above. In these circumstances, reduced colonization often reduces mycorrhizal cost and might increase plant growth rate and yield response. A similar approach can be used to test costs and benefits when increased uptake of another nutrient (e.g. Zn or NH₄⁺) is suspected or known to be the dominant benefit. However, this simplistic 'functional' approach has its dangers if the assumption that increased uptake of a single limiting nutrient is the only mycorrhizal benefit turns out to be incorrect. Thus, a positive mycorrhizal response in soil with non-limiting P would indicate another mycorrhizal benefit.

Once differences in mycorrhizal functioning are identified it is then desirable to identify the fungi and study their interactions (Friese & Allen, 1991). Morphological characters of colonization cannot always be used to identify mycorrhizal fungi to the species level in the field where usually several morphological species coexist in the same root system. Strict identification and quantitative measurements of individual species require molecular probes and biochemical analyses. Molecular approaches involving amplification of nuclear DNA encoding the small rRNA and attendant ITS regions yield diagnostic PCR profiles for ectomycorrhizal basidiomycetes (Gardes & Bruns, 1993) but profiles for AM fungi from field soils are highly variable (Sanders *et al.*, 1995a; Sanders, Clapp & Wiemken, 1996). Until the basis for the genetic heterogeneity is understood, PCR techniques will be of limited use for study of AM fungi. Biochemical techniques, including isozyme polymorphisms and activities (Rosendahl, 1992), fatty acid profile analysis of fungal lipids (Graham, Hodge & Morton, 1995), and immunofluorescence (Friese & Allen, 1991; Hahn, Gianinazzi-Pearson & Hock, 1994) seem to hold some immediate promise for both identification and quantification of AM fungi in the roots.

Inability to monitor individual isolates of mycorrhizal fungi in roots imposes severe limitations on study of their competitive behavior. Necessarily, the ability of individual isolates to colonize roots and their effectiveness in providing net benefits must first be characterized under controlled environments with a minimum of competition from other fungi. However, competitive ability of the isolate becomes an important consideration in the field where many fungi co-occur in the same root system. Whether isolates that are highly successful colonists individually are more competitive in mixed populations, especially in the long term, is unknown.

CONCLUDING SUGGESTIONS

Mutualism and parasitism are extremes of a dynamic continuum of species interactions. Mycorrhizal associations are generally at the mutualistic end of the continuum, but they can be parasitic when the stage of plant development or environmental conditions make costs greater than benefits, or possibly when the genotypes of the symbionts do not form 'win-win' associations. In natural systems, plant genotypes exist because they successfully propagate more plants, and fungal genotypes exist because they successfully propagate more fungi. Usually, by living together, plants and mycorrhizal fungi improve each other's probability for survival and reproductive success. But sometimes, and being anthropomorphic, plant 'interests' are in conflict with those of fungi. In the words of Dawkins (1978) '... we must expect lies and deceit, and selfish exploitation of communication to arise whenever the interests of the genes of different individuals diverge.' The 'interests' of plants and mycorrhizal fungi are likely to diverge in highly managed agricultural systems, where fertilization eliminates shortages of soil nutrients, and plant genotypes are selected by humans and not by millennia of natural selection.

Based on earlier definitions proposed by Germann (1970) and Harley (1992), Trappe (1994) defined mycorrhizas in functional and structural terms as 'dual organs of absorption formed when symbiotic fungi inhabit healthy absorbing organs (roots, rhizomes, or thalli) of most terrestrial plants and many aquatics and epiphytes' and suggested that *mutualistic functioning* of these associations should be a defining criteria of the term mycorrhiza. However, defining mycorrhizas as healthy absorbing organs does not address their effects on whole-plant fitness, and the mutualistic criterion becomes problematic whenever the effects of these associations are neutral or negative to either the plant or the fungal partner. For example, a mycorrhizal root might be healthy, yet its presence might reduce the plant's fitness in its environment when compared with a non-mycorrhizal root. We suggest that the structural and functional accuracy of Trappe's excellent definition are not compromised if the dynamic nature of

plant responses to mycorrhizal associations is accepted and they are considered to be generally mutualistic, with occasional commensal and parasitic excursions from this norm.

Twenty years ago many mycorrhizal researchers optimistically predicted that mycorrhizal associations could be successfully managed to reduce reliance on chemical fertilizers, but, 'promises concerning the applied value of mycorrhizal fungi in agriculture, forestry and horticulture have been more rhetorical than deliverable' (Miller & Jastrow, 1992). Perhaps one reason for this is that we often underestimate the ecological complexity of mycorrhizal systems. If our long term goal is to understand and manage mycorrhizal functioning in the real world, then we must study the full spectrum of plant responses to formation of mycorrhizas, and better understand the factors generating these responses in complex systems.

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