

Ecology, 87(7), 2006, pp. 1627–1636
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MUTUALISTIC STABILITY IN THE ARBUSCULAR MYCORRHIZAL SYMBIOSIS: EXPLORING HYPOTHESES OF EVOLUTIONARY COOPERATION

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Abstract. The 450-million-year-old symbiosis between the majority of land plants and arbuscular mycorrhizal fungi (AMF) is one of the most ancient, abundant, and ecologically important mutualisms on Earth. Yet, the evolutionary stability of mycorrhizal associations is still poorly understood, as it follows none of the constraints thought to stabilize cooperation in other well-known mutualisms. The capacity of both host and symbiont to simultaneously interact with several partners introduces a unique dilemma; detecting and punishing those exploiting the mutualism becomes increasingly difficult if these individuals can continue to access resources from alternative sources. Here, we explore four hypotheses to explain evolutionary cooperation in the arbuscular mycorrhizal symbiosis: (1) pseudo-vertical transmission and spatial structuring of plant and fungal populations leading to local adaptation of partners; (2) luxury resource exchange in which plants trade surplus carbon for excess fungal nutrients; (3) partner choice allowing partners to associate with better cooperators; and (4) host and symbiont sanctions which actively reward good partners and punish less cooperative ones. We propose that mycorrhizal cooperation is promoted by an exchange of surplus resources between partners and enforced through sanctions by one or both partners. These mechanisms may allow plant and fungal genotypes to discriminate against individuals employing exploitative strategies, promoting patterns of partner choice. Together these selection pressures provide a framework for understanding the stabilization of mycorrhizal cooperation over evolutionary time.

Key words: cheaters; coevolution; defection; evolutionary strategy; exploitation; host specificity.

INTRODUCTION

Explaining mutualistic cooperation between species remains a major challenge for biologists. Given the selfish interest of individuals, why expend resources to benefit another species, when resources could be redirected for one's own fitness? The 450-million-year-old symbiosis between the majority of plants and arbuscular mycorrhizal fungi (AMF) is an ancient mutualism, primarily involving the exchange of carbohydrates for mineral nutrients between plant host and fungus (Redecker et al. 2000). About 60% of all land plants enter into symbiosis with arbuscular mycorrhizal fungi (Trappe 1987). The evolutionary persistence and widespread nature of this mutualism is a testament to

cooperation between species (Selosse and Le Tacon 1998). Moreover, the fact that a mycorrhiza specific plant gene has been found that is activated by members of all major AMF families (even the ancient families that are estimated to have diverted over 350 million years ago; Karandashov et al. 2004) points to the persistence and evolutionary stability of this symbiosis.

Although mycorrhizal relationships are considered reciprocally beneficial, the evolutionary stability of cooperation between plants and AMF is poorly understood. For instance, it is typically assumed that AMF have a shared interest in increasing overall plant growth of their hosts because this presumably increases overall resources to themselves. Plants are thought to cooperate because, “[they] ... cannot afford to cheat as their success is interdependent with that of their fungi” (Brundrett 2002:297). Under this logic, cooperation is predicted to be the favored strategy by plant and fungal partners. In contrast, evolutionary theory predicts that

Manuscript received 6 October 2005; revised 23 December 2005; accepted 6 January 2006. Corresponding Editor (ad hoc): M. W. Schwartz.

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TABLE 1. Overview of factors that favor and limit evolutionary stability in the arbuscular mycorrhizal symbiosis. The *H* column indicates the hypothesis to which each factor applies.

Factors	<i>H</i>
Favorable	
AMF are completely dependent on plants for C supply.	2
Plants that are not carbon limited can invest in mycorrhizal associations with few additional costs.	2
Plants show AMF preferences and may select for a succession of beneficial or neutral partnerships.	3
Partners may be able to monitor resource exchange.	4
Plants have the ability to reduce mycorrhizal colonization under unfavorable conditions (e.g., high P availability or low light availability).	4
Limiting	
High energy costs for host plants to support AMF and benefit is temporally and environmentally variable.	2
Diverse communities of unrelated AMF types colonize a single root. This makes it difficult to reward and select beneficial fungi.	1
Reproductive success of partners is not strictly aligned.	1
No reliable correlation between AMF genetics and fungal effectiveness may hinder the development of host preference or specificity.	3
Punishment by a single host may be less effective because AMF can simultaneously interact with several plant hosts, allowing AMF access to alternative resources.	4
Host plants are unable to assess symbiont performance at time of infection.	4

cooperation should be the exception, rather than the norm (Schwartz and Hoeksema 1998, Doebeli and Hauert 2005). Evolutionary theory views mutualisms as reciprocal exploitations (Herre et al. 1999) in which both partners are attempting to gain additional resources, maximizing their own benefits through counter-exploitation, while minimizing their own costs. Here we use this framework, and rather than assuming that AMF are generally mutualists, we approach the problem from an evolutionary vantage point and ask the question: why are there not more AMF types that exploit their hosts? If maximum exploitation is a favorable strategy, what prohibits an AMF mutant that only takes up enough phosphorus to meet its own needs from spreading and displacing wild-type fungi competing for the same host plants? Despite the potential of either partner to defect from mutualistic duties, how has this symbiosis persisted over millennia? Here we present a conceptual framework to explain mycorrhizal cooperation in this evolutionary context.

SELECTION FOR COOPERATION

A number of factors have been proposed to explain evolutionary stability in other mutualistic associations. For example, alignment of reproductive interests between partners through vertical transmission, as in the association between aphids and their endosymbiotic bacteria (*Buchnera*; Douglas 1997) will tend to promote cooperation over evolutionary time. Similarly, cooperative relationships can be favored through positive feedback mechanisms when host and symbiont repeatedly interact, such as in the ant-acacia mutualism (Palmer et al. 2000) or when there are restricted reproductive opportunities for partners outside the symbiosis (de Mazancourt et al. 2005). Additionally, if individuals interact with only a single partner genotype (West et al. 2002a, b), there is generally less opportunity for simple defection from mutualistic duties.

With the exception of restricted reproductive opportunities for AMF (an obligate biotroph) outside the host, the mutualism between plants and AMF follow none of the constraints thought to stabilize other symbioses (Table 1). Horizontal transmission of symbionts among unrelated hosts and multiple symbiont genotypes per host (as well as multiple hosts per symbiont genotype) are common. Host plants are typically colonized by three to 10 different AMF types on a single root or a few roots (Fig. 1; Vandenkoornhuyse et al. 2002, Scheublin et al. 2004). As this number of partners per individual increases, selection for cooperation decreases because partners supplying their host with resources are also indirectly benefiting competing strains colonizing the same individual. As a result, "free-riders" (Denison et al. 2003), "exploiters" (Egger and Hibbett 2004), or "cheaters" (Smith and Smith 1996), partners extracting resources with little or no benefit in return, are predicted to spread at the expense of cooperating partners. Furthermore, in the AMF symbiosis there is an inability to assess costs of particular associations at time of initial infection because there is no reliable correlation between AMF genetics and symbiotic effectiveness (see: host choice section). Eventually these factors could lead to the destabilization of the mutualism (Table 1). Before exploring the four hypotheses to explain evolutionary stability in the mycorrhizal symbiosis, we review the costs and benefits of mycorrhizal associations.

COSTS AND BENEFITS OF SYMBIOSIS

The mycorrhizal symbiosis is distinguished as a functionally diverse mutualism. Benefits to host plants include, but are not limited to increased phosphorus and nitrogen uptake, protection against plant pathogens, and improved drought tolerance (Newsham et al. 1995). In return, AMF receive photosynthate from the plant to support their growth and reproduction. Supporting

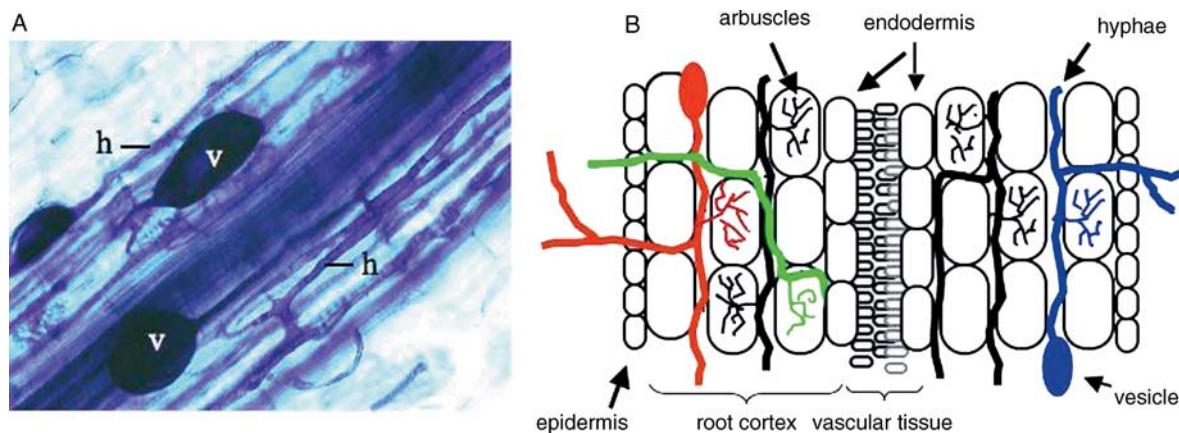


FIG. 1. (A) Plant root colonized by arbuscular mycorrhizal fungi with fungal hypha (h) and vesicles (v). (B) Schematic drawing of a plant root showing that hyphae of different AMF types simultaneously colonize the same root. Different colors represent hyphae from different AMF types.

AMF can be energetically expensive to host plants (Bago et al. 2000). The formation, maintenance and functioning of mycorrhizal structures can consume between 5% and 20% of the host's photosynthetically fixed carbon (Douds et al. 2000). Calculating the costs of symbiosis to the fungal partner is more difficult. Even if costs of providing other benefits (nitrogen uptake, protection against drought stress, etc.) are not considered, a number of energy-consuming steps are necessary to supply P to a plant host (e.g., P uptake by fungus, conversion to polyphosphate, transport and efflux to the plant [Ezawa et al. 2003, Viereck et al. 2004]). As the cost of supplying these benefits to the partner increases, cooperation becomes a less favorable strategy (Schwartz and Hoeksema 1998, Hoeksema and Schwartz 2003), and unless there are mechanisms to control against exploitative strategies, natural selection will favor those that maximize their own fitness.

EXPLOITATION BY PLANT AND FUNGAL PARTNERS

Virtually all mutualisms are characterized by some form of exploitative cheating (Yu 2001). In the mycorrhizal symbiosis, there are the roughly 400 species of achlorophyllous epiparasitic plants that obtain carbon and nutrients through tapping into mycorrhizal networks (Bidartondo et al. 2002, Taylor et al. 2002). These epiparasitic plants represent the most extreme end of the mutualism–parasitism continuum (Johnson et al. 1997), parasitizing AMF directly and the green plants connected in the mycorrhizal network indirectly. Exploitative strategies employed by AMF symbionts are difficult to demonstrate directly because benefits to host plants are less well defined and costs may be context dependent (Fitter 2001, Jones and Smith 2004) and temporally variable (Merryweather and Fitter 1998), depending on the time scale (ecological or evolutionary) in which costs are assessed (see de Mazancourt 2001, 2005). Although benefits may be context dependent, the consistently poor performance of certain strains (Burleigh et al. 2002,

Smith et al. 2003) suggests that symbiotic performance has some genetic basis. This poor performance may be an evolutionary strategy, not a mis-matched partnership. For instance, AMF differ in amount of carbon extracted from their hosts (Pearson and Jakobsen 1993), amount of lipids allocated to storage (van Aarle and Olsson 2003), in sporulation investment (Douds and Schenck 1990), in transport capacities of symbiotic interfaces (Dickson et al. 1999), in colonization and hyphal allocation strategies (Graham and Abbott 2000, Hart and Reader 2002), and in ability to exploit nutrient patches (Cavagnaro et al. 2005). Poor symbiotic performance of AMF strains collected from the field (Klironomos 2003, Reynolds et al. 2005) could be indicative of these successful exploitative evolutionary strategies. In general, negative AMF impacts are demonstrated most convincingly when nutrient availability is high (Johnson et al. 2003) or when light availability is low (Fig. 2), suggesting that cheating can be conditional (Egger and Hibbett 2004). However, antagonistic AMF relationships can be found under a wide range of conditions (Francis and Read 1995, Jones and Smith 2004).

A breakdown in cooperation in mycorrhizal symbiosis seems almost inevitable given (i) the high energy costs of mutualism for both partners; (ii) the genetically diverse partnerships of both the host and the symbiont; (iii) the inability to assess costs of particular associations at time of initial infection; and (iv) the ability of some fungi and plants to exploit the mutualism (Table 1). Here, we examine four hypotheses to explain this stability of cooperation between plants and fungi in the mycorrhizal symbiosis.

HYPOTHESIS 1: SPATIAL STRUCTURING

I. Pseudo-vertical transmission.—Cooperation can be stabilized when the fitness of individuals (or their decedents) is increasingly coupled with that of their

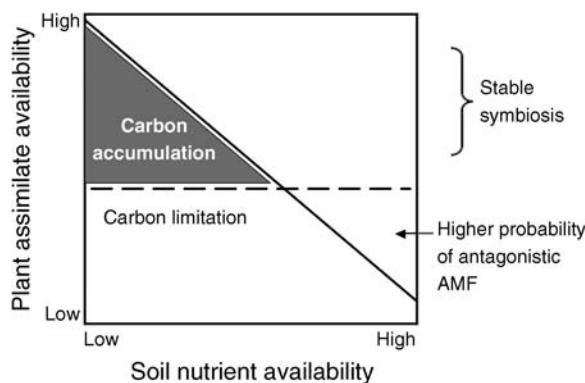


FIG. 2. Hypothetical model showing plant assimilate availability as a function of nutrient availability (solid line). The dashed line shows the amount of carbon required for growth, maintenance, and respiration. At low nutrient availability, carbon will tend to accumulate, while, at high nutrient availability, carbon is a limiting resource. The symbiosis between plants and AMF is predicted to be most stable under surplus C supplies. At high nutrient and low C availability, there is a higher probability of antagonistic AMF relationships.

partner (Herre et al. 1999). Such situations can arise when dispersal limitations force partners to associate for a series of exchanges, for example in vertically transmitted symbioses and in spatially structured populations (Bull and Rice 1991, Frank 1998). It has been suggested that host plants and their mycorrhizal symbionts are spatially co-constrained (through dispersal limitations), and cooperation is stabilized through “pseudo-vertical transmission” mechanisms (Wilkinson 1997). Under this hypothesis, the fitness of the plant host and fungal community become increasingly coupled because seedlings are thought to associate with fungal communities genetically identical to that of their parent plant as they become incorporated in the same fungal mycelium. Non-random patterns of association between host plants and specific AMF symbionts have indeed been documented (Eom et al. 2000, Helgason et al. 2002, Lovelock et al. 2003), suggesting some feedback mechanism is operating (Bever 2002a, b). However, there is little evidence to support the claim that seedlings and their parents harbor similar fungal communities. Recent work suggested that seedlings and adults of the same tropical tree species were colonized by significantly different fungal communities (Husband et al. 2002b). Moreover, competition among AMF strains on a single host will likely undercut any “group-selected benefits” generated from repeated associations between partners. Pseudo-vertical transmission of AMF strains may promote a loose genetic association between generations of plant hosts and their fungal communities, but as a selection pressure, it appears insufficient to stabilize cooperation over evolutionary time as this would require some relatively extreme structuring that does not seem to take place.

II. Kin selection in structured soil habitats.—In populations with spatial structure, there is also an

increased probability that the benefits of cooperation will be shared with related kin (kin selection) rather than non-kin (both are potential competitors) (Hamilton 1964). As a consequence, investment in cooperation (i.e., P uptake) is potentially favored because closely related strains benefit from the increased resources of healthy plant hosts. Constraints on fungal dispersal in soils (Chanway et al. 1991) could lead to an increase in relative relatedness of AMF strains; root portions would be colonized by AMF descended from a single individual. If plant hosts directed resources to root portions containing related AMF strains, this would select for more beneficial AMF strains because the rewards of cooperation are shared among AMF kin, rather than non-related competitors. However, two lines of evidence suggest that this spatial structuring does not increase cooperation (via kin selection) in mycorrhizal communities. First, if kin selection were operating, we would predict that root portions would contain highly related AMF strains. Instead, root portions tend to be colonized by genetically diverse AMF strains belonging to different AMF families (Husband et al. 2002a, Scheublin et al. 2004). In one study, root samples taken from two plant species at one single site, contained approximately 15% of all known AMF species (Vandenkoornhuyse et al. 2002). Second, even if spatial structuring tends to increase kin selection among mycorrhizal strains, recent experiments suggest that benefits to cooperation may be offset by the increased competition generated between kin in highly structured populations (Griffin et al. 2004). In the case of mycorrhizal fungi, this means that even though strong spatial structuring of soil could increase the benefits of kin-selected cooperation, competition for local resources between these same relatives could completely negate this potential advantage (West et al. 2002c). Hence, kin selection, as a mechanism to increase cooperation, falls short of explaining the evolutionary stability of the mycorrhizal symbiosis.

HYPOTHESIS 2: LUXURY RESOURCE EXCHANGE

It has been suggested that initial mycorrhizal associations were based on an exchange of excess resources (Brundrett 2002). If neither carbon (for the plant) nor phosphorus (for the fungus) is limiting, exchange of surplus resources (Schwartz and Hoeksema 1998) could be beneficial to plant and fungal partners. Such “by-product mutualisms” should be more evolutionary stable because there are fewer net investment costs incurred by partners (Agrawal 2000, Hoeksema and Bruna 2000).

Of course, resources are never strictly in “excess” if they can be stored for future use. However as the availability of certain resources increase, they can be more freely allocated to the acquisition of the other nutrients most directly limiting to growth (Fig. 2). This can be best understood in a biological market-modeling framework (Noë and Hammerstein 1995) in which differences in (i)

capacity to acquire resources and (ii) requirements of resources determine potential benefits of exchange (Hoeksema and Schwartz 2003). For instance when plants develop under conditions of low nutrient supply, growth is more limited by nutrients than by carbon supply and carbohydrates actually accumulate in plant organs (e.g., Qiu and Israel 1992, Poorter and de Jong 1999). Therefore under nutrient poor conditions, cost : benefit ratios of the mutualism are altered and it becomes advantageous for plants to allocate more photosynthetic C to roots (or associated symbionts) if by doing so they can acquire more of the nutrients they need (Tinker et al. 1994, Tuomi et al. 2001). Increases in carbohydrate availability (i.e., when plants are grown under elevated CO₂ or in full light) will favor enhanced mycorrhizal abundance (Treseder 2004, Alberton et al. 2005), suggesting that AMF abundance is at least partially regulated by carbohydrate availability (Graham et al. 1997). Ultimately, the host plant may still pay an opportunity cost aboveground for allocating carbohydrates to the root system, however shifts in resource allocation enable the plant to capture more resources that most directly limit their growth, if carbohydrates can be directed to mutualistic partners. Antagonism may still permeate the system, and the mutualism may not reach an evolutionary optima, but the net effect of the interaction can still be positive (de Mazancourt et al. 2001).

Second, it has been suggested that carbon production (photosynthesis) depends, in part, on the relative strength of carbon sinks within a plant (Fitter 1991). Accumulation of carbohydrates can lead to a down regulation of genes and enzymes responsible for photosynthesis (Pego et al. 2000). Therefore, investment in the mycorrhizal symbiosis under nutrient limited conditions could actually enhance the host's photosynthetic capacity. Several studies report that AMF have a positive impact on host photosynthesis (Wright et al. 1998, Valentine et al. 2001, Miller et al. 2002), although this could be an indirect effect (Black et al. 2000). However, at equivalent P:N ratios, with plants of similar biomass, mycorrhizal plants were shown to have a higher overall C assimilation than their non-mycorrhizal counterparts (Miller et al. 2002). The increased sink potential in cells of mycorrhizal plants has been linked to increased transcription and activity (Blee and Anderson 2002, Ravnskov et al. 2003) of enzymes that stimulate sink function.

If increased sink potential of mycorrhizal cells optimizes the host's photosynthetic machinery, while AMF consumes the accumulated carbon, investment in the symbiosis could be less costly (Fig. 2). However, a delicate balance exists between the photosynthetic benefits of increased sink capacity and the costs of antagonistic carbon extraction by the symbiont. Is an AMF strain that extracts a hypothetical 10 units of carbon for every five units of phosphorous more mutualistic (i.e., due to higher sink strength) than an AMF strains that extracts five units of carbon for every

five units of phosphorous? Parasitizing plants have also been shown to stimulate photosynthesis of their host under certain conditions (Jeschke and Hilpert 1997), but the relationship is still clearly antagonistic. Similarly, aggressive mycorrhizal strains adapted to colonize and extract carbohydrates from plant roots may increase sink strength of their host plant, regardless of their benefits to host growth (Lerat et al. 2003). The potential importance of luxury resource exchange will likely depend on the availability of nutrients, among others (Fig. 2). The crucial part is that natural selection will continue to maximize an organism's ability to extract resources regardless of whether this is best for both partners. In the absence of mechanisms to regulate trading of resources, vulnerability to exploitation remains high.

HYPOTHESIS 3: PARTNER CHOICE

The evolutionary stability of mutualisms will increase if partners associate with better cooperators (Ferrière et al. 2001). Partner choice, the ability to discriminate partners based on their symbiotic functioning, can result in both an immediate fitness benefit to individuals and to increased stabilization in many mutualisms (Bull and Rice 1991, Sachs et al. 2004). The AMF symbiosis lacks absolute specificity; plant species capable of entering into the symbiosis can be colonized by almost any AMF strain under greenhouse conditions (see Sanders 2002). However, coexisting plant species have been shown to harbor distinctive AM fungal communities (Vandenkoornhuysen et al. 2003) and plants may benefit from hosting particular AMF strains (van der Heijden et al. 1998). Do these patterns indicate that partners are able to selectively associate with better cooperators? There is little evidence to suggest that particular host-fungal combinations are optimal, or even that the relative fitness to either partner is greater in these than in other combinations (Fig. 3). One exception is the functional selectivity demonstrated by Helgason et al. (2002) between the host *Acer pseudoplatanus* and its fungal symbiont *Glomus hoi*. In the field, this fungus abundantly colonizes *Acer*. In the greenhouse, it is the only fungal species to increase *Acer* growth and promote P uptake; other species were incapable of colonizing *Acer* roots (Helgason et al. 2002). The discovery of similar cases will strengthen the argument for partner choice, but experiments are needed to explicitly test whether common partnerships are indeed the most beneficial. For instance, there are at least two examples showing that hosts can preferentially enrich the soil with *less* mutualistic mycorrhizal fungi (Johnson et al. 1992, Bever 2002a), which is consistent with (but does not prove), maladaptive partner choice (negative line, Fig. 3).

Partner choice can be seen as a two step process requiring (i) an evaluation of the effectiveness of the partner and (ii) a "decision" as to whether or not to enter (or remain) in the interaction (Sachs et al. 2004). Intricate molecular defense responses allow host plants

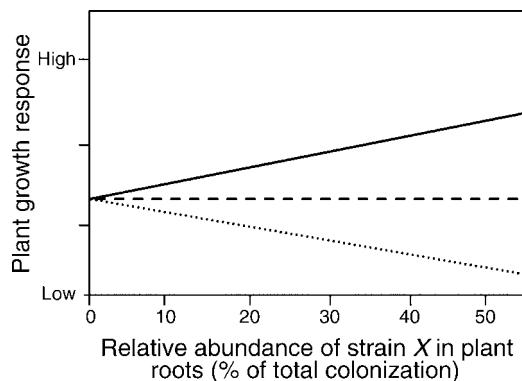


FIG. 3. Three possible relationships between relative abundance of AMF types in roots and plant growth response: (1) the solid line indicates a positive relationship between abundance of a particular AMF type and benefits to plant growth, suggesting that partner choice is operating; (2) the dotted line indicates a negative relationship, suggesting maladaptive partner choice; (3) the dashed line indicates that no relationship exists between the abundance of an AMF type and its impact upon plant growth, suggesting that plants lack ability to control and maintain specific partners.

to differentiate between AM fungal penetration and pathogen attack (García-Garrido and Ocampo 2002). However, the ability of host plants to assess symbiotic potential of AM fungal genotypes at time of infection is unlikely because exchange of products does not start immediately. Moreover, there may be no reliable correlation between AMF genetics and symbiotic effectiveness (Munkvold et al. 2004, van der Heijden et al. 2004). In addition to this, single spores of AMF may be genetically diverse, containing many different sequences of the same gene (Kuhn et al. 2001, Pawlowska and Taylor 2004). Such factors may limit the ability of a host plant to evaluate symbiotic potential of AMF partners at time of infection. Accumulating evidence argues for preference of association, but it is unlikely that this preference is based on a genetic evaluation. More likely, this preference of association is the result of dynamic interactions between partners altering or modifying either (i) the duration of the interaction or (ii) the amount of resources exchanged. This may be viewed in the evolutionary context of “on-going partner choice” and could result in a succession of partners, rather than static partnerings (West et al. 2002a). Recent studies reveal that AMF types that monopolize root system of tropical seedlings are almost entirely replaced in older seedlings by previously rare AMF types (Husband et al. 2002a, b). Though this pattern could have multiple explanations, it is possible that there is on-going partner choice and partner switching in the mycorrhizal symbiosis, resulting in a succession of AMF types within a single host. Partner switching is common in other mutualisms, such as between corals and their endosymbionts (Baker 2001). This type of on-going partner choice could be an important selection pressure in mycorrhizal cooperation, but how do

partners physiologically control associations with different partners? One mechanism could be to mediate resources to partners based on their symbiotic performance. We explore this possibility next.

HYPOTHESIS 4: HOST AND SYMBIONT SANCTIONS

Cooperation between species can be enforced if individuals are able to actively reward good partners or punish less cooperative ones. Punishment mechanisms are thought to be critical in stabilizing an array of cooperative relationships such as cleaner fish mutualisms (Bshary and Grutter 2002), obligate pollination mutualisms (Pellmyr and Huth 1994), and even in the maintenance of cooperation in humans (Gardner and West 2004). In the legume–rhizobia mutualism, plant hosts have been shown to detect and punish rhizobial symbionts that defect from their N_2 fixing duties by cutting off important resources (Kiers et al. 2003). This idea has been termed “sanctions” (Denison 2000) and can be defined as the preferential supply of resources (or the curtailing of resources) to partners based on their symbiotic performance. If hosts can evaluate and actively punish cheating symbionts, this creates a strong selection pressure to favor cooperation, even under conditions where cooperation is predicted to be low (West et al. 2002a, b).

There are several mechanisms plants could employ to control AMF and particular AMF types. First, host control could be executed at a cellular level; for example, through inhibition of colonization (Douds 1994), hyphal digestion (Imhof 1999), or differential carbon supply (Lerat et al. 2003). Exploitative AMF strains could presumably be detected if host plants could monitor exchange of sugars and nutrients at plant–fungal interfaces. It is still unclear if C and P transfer is bidirectional at a specific interface (e.g., arbuscules) or if there is spatial separation of resource transfer. The lack of direct symplastic continuity between the organisms means that nutrients must be directed through an interfacial apoplast before adsorption, making reciprocal 1:1 exchange of C and P unlikely. Mechanics of transfer are important from an evolutionary standpoint because spatial separation of resource exchange could allow for increased incidences of cheating (Smith and Smith 1996).

Host control could also be executed at an organismic level, such as in the selective abortion of root tips containing less mutualistic fungi by ectomycorrhizal hosts (Hoeksema and Kummel 2003), mediation of competition between symbiont strains (Pearson et al. 1993), or host-specific sporulation rates (Bever 2002b). Plant roots are also able to respond to small nutrient patches in the soil by enhancing root density and by selective root placement (de Kroon and Hutchings 1995) and hosts may allocate more carbon to root parts colonized by beneficial AMF (but see Lerat et al. 2003).

Finally, plants could control AMF colonization at the whole root level. Mycorrhizal colonization tends to be

reduced when nutrient availability is high. For instance, in a meta-analysis of recent field studies, Treseder (2004) reported a 32% reduction in percent root colonized by mycorrhizal fungi after phosphorus fertilization. Under these conditions, plants may regulate AM colonization using various strategies (e.g., flavonoids, phytoalexins, H₂O₂) (Vierheilig 2004). Under P fertilization, host plants can accumulate compounds that are inhibitory for AMF hyphal growth (Guenoune et al. 2001) and AMF colonization (Tawarayama et al. 1998). These observations all suggest that plants have some degree of control of mycorrhizal colonization, but do not necessarily imply that plants can selectively punish individual AMF strains within a root system. If AMF species occupy characteristically distinct locations within the root system (i.e., inner vs. outer cortex) as has been reported for one plant species (Merryweather and Fitter 1998), host plants could utilize these spatial patterns to differentially supply resources to the AMF of their root systems.

These mechanisms of sanctioning of AMF by plants are potentially important in the mycorrhizal symbiosis, but the plant host may not be completely “enslaving” the symbiont (Freat and Abraham 2004). This is because, like the host plant, the AMF symbiont can simultaneously interact with several partners and may supply resources to plant hosts depending on the plant’s symbiotic performance. Unfortunately, little is known about possible mechanisms employed by AMF to punish or reward specific host plants. It has been suggested that AMF-mediated phosphate efflux and translocation to the plant increases in response to increasing carbohydrate availability (Solaiman and Saito 2001, Bücking and Shachar-Hill 2005). By linking efflux of P to carbohydrate availability, AMF could differentially supply P to plants hosts that supply them with the most C. There is also evidence to suggest that AMF may differentially control the expression of their host’s genes (Burleigh et al. 2002). Overall, it is clear that resource control by one or both partners is present in the mycorrhizal symbiosis but additional empirical data, coupled with a physiological understanding of the mechanisms of control are still needed.

CONCLUSION

Traditional constraints, thought to stabilize other mutualisms, fail to explain cooperation in the mycorrhizal symbiosis. The capacity of both host and symbiont to simultaneously interact with several partners introduces a unique dilemma; detecting and punishing cheaters becomes increasingly difficult if partners can access resources from alternative sources. Despite the potential for exploitation, cooperation has persisted. The failure of cheaters to completely displace their mutualistic counterparts speaks to the individual fitness benefits of cooperating.

Evolutionary strategies to constrain exploitation by plant and fungal partners will be shaped by many

factors, at various levels of selection. At the population level, spatial structuring (hypothesis 1) may facilitate a loose genetic association between generations of plant hosts and their fungal communities, but as a selection pressure, it is insufficiently strong to stabilize cooperation. At the level of the individual, exchange of surplus resources (hypothesis 2) will provide a mutual benefit to partners if exploitation can be controlled. Sanctions (hypothesis 4) provide a direct mechanism, at the organismic interface, to control exploitation by partners by preferentially supplying resources to the best symbionts, but experimental evidence is still weak. Taken together, these mechanisms may allow partners to associate with better cooperators, favoring specific plant–fungal combinations (hypothesis 3). More data are needed to determine if local patterns of plant–fungal preference seen in the field actually represent fitness-optimizing host–fungal combinations.

PERSPECTIVES

In order to better understand what regulates the evolutionary stability of the mycorrhizal symbiosis, several questions still need to be answered. First, many studies have shown that plant roots are colonized by diverse AMF communities. However, it is unclear whether the plants have actively selected those AMF and if these particular AMF are most beneficial in terms of enhancing plant growth or fitness. Experiments with split roots systems where different fungi occupy different parts of the roots system are needed to determine whether plants allocate resources to the most efficient symbionts. Surprisingly, such experiments have not been performed in an evolutionary and ecological context (but see Pearson et al. 1993). Second, we identify luxury resource exchange and sanctions as important mechanisms that can contribute to stability of the mycorrhizal symbiosis. However, these mechanisms only work if plants and AMF have the ability to evaluate the symbiotic effectiveness of their partner. Hence, future research should identify mechanisms for evaluating symbiotic effectiveness. Third, what factors are most important in determining fungal fitness? Studies tend to focus on spore production or percentage of mycorrhizal fungal root colonization. However both the size of the mycorrhizal mycelium and the persistence of hyphae in soil are likely to be important in determining fungal fitness, especially in undisturbed plant communities. Experiments are needed that (i) monitor relative fitness of AMF strains under host plants over multiple generations and (ii) relate the resulting strain fitness to the amount of benefit provided by those strains to the host. Fourth, the biogeography of different AMF types and their hosts needs to be better documented in order to understand the potential for coevolution and the development of specificity between plant–fungal combinations. Finally, there is large functional diversity between AMF strains with similar identity (Munkvold et al. 2004), making it difficult to relate fungal strategies

to fungal genotypes. Hence, the genetics of AMF need to be better understood. The genome of one of the most abundant AMF types, *Glomus intraradices*, will soon be known (Martin et al. 2004), giving us new tools to better understand the evolutionary success of this mutualism.

ACKNOWLEDGMENTS

We thank Andrew Smith, Ford Denison, Jason Hoeksema, Hendrik Poorter, Stuart West, Alastair Fitter, Jacinta Ellers, Tanja Scheublin, Susanne de Bruin, and Sebastiaan Verkade for fruitful discussion and comments, and the editor and anonymous reviewers for many useful suggestions. Funding was provided by a NWO-bezoekersbeurs B84-613, a NSF graduate fellowship (E. T. Kiers), and a NWO-Vernieuwingsimpuls 016.001.023 (M. van der Heijden).

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