

The promise and the potential consequences of the global transport of mycorrhizal fungal inoculum

Mark W. Schwartz,^{1*} Jason D. Hoeksema,² Catherine A. Gehring,³ Nancy C. Johnson,³ John N. Klironomos,⁴ Lynette K. Abbott⁵ and Anne Pringle⁶

¹Department of Environmental Science & Policy, University of California, Davis, CA, USA

²Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA, USA

³Department of Biological and Environmental Sciences, Northern Arizona University, Flagstaff, AZ, USA

⁴Department of Integrative Biology, University of Guelph, Guelph, Ontario, Canada

⁵School of Earth and Geographical Sciences, The University of Western Australia, Perth, WA, Australia

⁶Organismic and Evolutionary Biology, Harvard University, Cambridge, MA, USA

*Correspondence: E-mail: mwschwartz@ucdavis.edu

Abstract

Advances in ecology during the past decade have led to a much more detailed understanding of the potential negative consequences of species' introductions. Moreover, recent studies of mycorrhizal symbionts have led to an increased knowledge of the potential utility of fungal inoculations in agricultural, horticultural and ecological management. The intentional movement of mycorrhizal fungal species is growing, but the concomitant potential for negative ecological consequences of invasions by mycorrhizal fungi is poorly understood. We assess the degree to which introductions of mycorrhizal fungi may lead to unintended negative, and potentially costly, consequences. Our purpose is to make recommendations regarding appropriate management guidelines and highlight top priority research needs. Given the difficulty in discerning invasive species problems associated with mycorrhizal inoculations, we recommend the following. First, careful assessment documenting the need for inoculation, and the likelihood of success, should be conducted prior to inoculation because inoculations are not universally beneficial. Second, invasive species problems are costly and often impossible to control by the time they are recognized. We recommend using local inoculum sources whenever possible. Third, non-sterile cultures of inoculum can result in the movement of saprobes and pathogens as well as mutualists. We recommend using material that has been produced through sterile culture when local inoculum is not available. Finally, life-history characteristics of inoculated fungi may provide general guidelines relative to the likelihood of establishment and spread. We recommend that, when using non-local fungi, managers choose fungal taxa that carry life-history traits that may minimize the likelihood of deleterious invasive species problems. Additional research is needed on the potential of mycorrhizal fungi to spread to non-target areas and cause ecological damage.

Keywords

Agriculture, dispersal, horticulture, inoculum, invasive species, mutualism, mycorrhizae, restoration, symbiosis.

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INTRODUCTION

As humans continue to intentionally, and unintentionally, move species around the planet, it is increasingly important to understand both the benefits and costs of these actions. Understanding the potentially large consequences of globalization of species distributions has become a major focus of ecological studies during recent decades. This globalization of biota has resulted in: (a) ecological degradation and degraded ecosystem services (Mack *et al.* 2000); (b) biodiversity losses; and (c) increased biotic homogenization

(McKinney & Lockwood 1999), and costly management of noxious invaders (US Congress Office of Technology Assessment 1993; Pimentel *et al.* 2000, 2005). As a response to these negative ecological consequences, databases (e.g. Global Invasive Species Database), councils (e.g. US National Invasive Species Council; Clinton 1999) and numerous local laws and policies (Miller & Fabian 2004) have been created to slow the wave of invasion. Nevertheless, there have also been enormous economic benefits associated with intentional species movement. For example, virtually all of agricultural production is a product of species

in non-native habitats. Although it is not often discussed in the current ecological literature on invasive species, the societal benefits and economic gains as a consequence of moving biota in an effort to support human societies is considerable.

Within this context, the rate and volume of the intentional movement of non-indigenous mycorrhizal fungi is increasing as a consequence of the promise of harnessing beneficial soil organisms for improved agriculture (Gianinazzi *et al.* 2002), horticulture (Azcon-Aguilar & Barea 1997), habitat restoration (Miller & Jastrow 1992), bioremediation (Leyval *et al.* 2002), and forestry (Brundrett *et al.* 1996, Duponnois *et al.* 2005). The approach of this paper is to jointly examine our understanding of mycorrhizal ecology along with general patterns of invasive species in order to produce a preliminary assessment of the potential for costly unintentional outcomes of mycorrhizal inoculation. We then make recommendations to help minimize the risk of management mistakes using mycorrhizal fungi. Further, we suggest a research agenda to help fill existing knowledge gaps that make it difficult to predict outcomes of inoculation with mycorrhizal fungi. Our goal is to highlight ways by which we might maximize beneficial utility while minimizing risks associated with harmful species introductions.

To our knowledge, there are no documented cases where the intentional movement of mycorrhizal fungi has led directly to a widespread, persistent invasive species problem. It is difficult to ascertain, however, whether this lack of knowledge is because problems do not exist, or because they go undetected. The absence of documented problems from introduced mycorrhizal fungi is in stark contrast to problems caused by invasions of pathogenic fungi (e.g. Dutch elm disease or chestnut blight). With respect to plant disease issues, Anderson *et al.* (2004) reviewed the literature and surmised that the problem lies in a lack of detection. With the recent upsurge in the use of mycorrhizal inoculum, the potential for problem invasions may be increasing.

There is a need to consider the possibility of both overt as well as subtle undesirable effects of the movement of mycorrhizal fungi. Undesirable consequences of inoculation, where they occur, are likely to go unnoticed because large-scale monitoring of the consequences of inoculation is rarely conducted. A case study illustrates some of these possible complexities associated with fungal invasions. The ectomycorrhizal fungus *Amanita muscaria* was introduced to Australia and New Zealand in the 19th century (Bougher 1996; Orlovich & Cairney 2004) and frequently associates with trees endemic to its introduced habitats, e.g. *Nothofagus* spp. (Orlovich & Cairney 2004). The mushroom of *A. muscaria* is typically bright red with white spots and it is easily identified by even the casual naturalist. The morphological species is found in Europe, Asia and North America. However, molecular markers suggest the presence

of at least three cryptic species including a Eurasian lineage, a Eurasian sub-alpine lineage, and a North American lineage (Oda *et al.* 2004). Thus, *A. muscaria* appears to be a widespread distributed morphospecies with cryptic genetic species, at least one of which has been introduced to a novel continent. An isolate from New Zealand groups with Japanese *A. muscaria*, suggesting an Asian origin for *A. muscaria*'s invasion (Oda *et al.* 2004). The example illustrates two points. First, cryptic species have the potential to invade each other's ranges without detection and so, potentially, displace native species. In this case, *A. muscaria*'s invasion of Australia is obvious because it is the morphological species that has invaded. If a cryptic species were to invade the range of another cryptic species (e.g. if a Eurasian lineage were to invade North America) then that invasion might well go unnoticed. Second, the impact of the invasive *A. muscaria* in Australia and New Zealand is unknown, as we neither know if it is displacing native species nor if, through altered biogeochemistry, it has ecosystem consequences.

Mycorrhizal fungi are generally considered mutualistic, and accordingly, there has been little concern over potential negative consequences of their introduction. Nevertheless, evidence is growing that mycorrhizal function can range from mutualistic to parasitic (Johnson *et al.* 1997; Klironomos 2003; Jones & Smith 2004) with host plant and edaphic conditions mediating their functioning. Within an old-field plant community, *Glomus etunicatum* can stimulate the growth of certain plants but be detrimental to many others (Klironomos 2003). Enormous functional variability also exists among species of ectomycorrhizal fungi in attributes such as the utilization of organic nitrogen sources (e.g. Abuzinadah and Read 1986) and tolerance of water stress (e.g. Coleman *et al.* 1989). Thus, inoculation treatments must be supported by consideration of possible negative consequences along with the potential for benefit (Table 1). Jonsson *et al.* (2001) observed threefold differences among mycorrhizal species in their ability to influence shoot biomass in *Pinus sylvestris* growing under the same environmental conditions. In addition, mycorrhizal fungi can facilitate plant growth both through nutrient exchange as well as pathogen control (Whipps 2004). It is important to recognize this variability in function because mycorrhizal fungi can influence crop yields, tree survival, plant community structure and ecosystem properties (e.g. Johnson *et al.* 1992; van der Heijden *et al.* 1998; Jonsson *et al.* 2001).

We focus this essay on arbuscular mycorrhizal (AM) and ectomycorrhizal (EM) fungi, because they are the most widespread and economically important types of mycorrhizal fungi. These groups differ fundamentally in the morphology of their root associations, as their names suggest. The AM fungi produce arbuscules within roots that function as exchange surfaces with plants. In contrast, EM

Table 1 Potential beneficial and detrimental outcomes of inoculation with mycorrhizal fungi

Potential beneficial consequences	Potential detrimental consequences
Increased yields and survival of desirable plant species (Bethlenfalvay & Linderman 1992)	Decreased yields and survival of desirable plant species (e.g. Hendrix <i>et al.</i> 1992)
Reduced fitness of noxious invasive weeds (Johnson 1998)	Increased fitness of noxious invasive weeds (e.g. Marler <i>et al.</i> 1999)
Decreased uptake of toxic compounds (e.g. Rufyikiri <i>et al.</i> 2004)	Increased uptake of toxic compounds (e.g. Killham & Firestone 1983)
Improved soil aggregation and stability (Miller & Jastrow 2000)	Reduced diversity of indigenous mycorrhizal fungi
Enhanced carbon storage in soils (e.g. Hogberg & Hogberg 2002)	Reduced carbon storage in soils (Chapela <i>et al.</i> 2001)

fungi are named for their characteristic coat of hyphae that surrounds the external surface of roots. Although these groups differ in numerous other significant traits (Table 2), in both cases, the fungi receive carbon from the plants with which they associate in exchange for providing nutrients and/or pathogen protection to their host plants (Smith & Read 1997).

Production and application of mycorrhizal inoculum

In 2001, there were more than 30 companies worldwide marketing one or multiple products containing mycorrhizal fungal inoculum (Gianinazzi & Vosatka 2004). These products are marketed as plant growth promoters to be used in horticultural, agricultural, restoration and forestry

Table 2 Ecological attributes of AM and EM fungi.

	AM fungi	EM fungi
Number of described species worldwide	< 200, but many undescribed species are known to exist (Bever <i>et al.</i> 2001; Clapp <i>et al.</i> 2002)	> 5000 (Molina <i>et al.</i> 1992)
Typical number of species found locally	< 50 (Bever <i>et al.</i> 2001; Clapp <i>et al.</i> 2002)	Varies from < 10 to > 200 (Horton & Bruns 2001)
Host plants and habitats	Herbaceous and woody plant hosts in many habitats from grasslands to forests, low to high latitude, on <i>c.</i> 90% of all plant species (Smith & Read 1997)	Woody plants in families Betulaceae, Dipterocarpaceae, Fagaceae, Myrtaceae, and Pinaceae, typically in forested habitats that have lower plant diversity than AM-dominated habitats (Smith & Read 1997)
Host specificity	Generalists with respect to ability to form association, but strong intra- and interspecific variation in relative preference for and performance with different host plant species is recently being discovered (Bever <i>et al.</i> 2001)	Varies widely: some are species-specific, some genus-specific, some family-specific, and some are broad generalists (Molina <i>et al.</i> 1992)
Trophic capability	Obligate biotrophs – cannot obtain carbon without host plant association (Smith & Read 1997)	Some species have some saprobic capability (Smith & Read 1997)
Spore size	Small to large (10–1000 microns) (Smith & Read 1997)	Small (usually < 15 microns) (Smith & Read 1997)
Spore dispersal mode	Animal vectors and/or physical soil movement (Allen 1991)	Aerial dispersal, animal vectors, and/or physical soil movement (Allen 1991)
Colonization speed	Significant variation within and among species with respect to ability to quickly colonize host plants from spores (EM: e.g. Kennedy & Bruns 2005; AM: e.g. Hart & Reader 2002). Similar variation may exist for the ability to colonize by growing from one plant root system to another.	
Growth effect on host plants	Both AM and EM fungi vary intra- and interspecifically with respect to impact on host plants, which can range from negative to neutral to positive (Smith & Smith 1996; Johnson <i>et al.</i> 1997; Klironomos 2003; Jones & Smith 2004)	
Competitive ability for host plant resources	The sparse experimental evidence suggests that species vary widely in their ability to compete for access to host roots, and that competition is often asymmetric (AM fungi: Lopez-Aguillon & Mosse 1987; Hepper <i>et al.</i> 1988; Pearson <i>et al.</i> 1993 and 1994; Wilson & Trinick 1983; Wilson 1984; Sen <i>et al.</i> 1989; EM fungi: Wu <i>et al.</i> 1999; Landeweert <i>et al.</i> 2003; Kennedy & Bruns 2005; AM vs. EM: Chen <i>et al.</i> 2000)	

applications. Typically, only a small number of different mycorrhizal taxa are included in these products, the most common being *Pisolithus tinctorius* (an EM fungus) and *Glomus intraradices* (an AM fungus). Numerous methods are used to prepare and apply mycorrhizal fungal inoculum; and the technical sophistication of these approaches varies greatly. The simplest method is to apply soils that are known to contain propagules of desirable mycorrhizal fungi to areas that either lack these fungi or contain very low population densities. This method is often used during reclamation operations when 'living topsoil' is added back to mining wastes to help restore biotic interactions (e.g. Paschke *et al.* 2003). This whole-community soil inoculum is undefined, and much more is added than the mycorrhizal fungi, possibly including saprobic or pathogenic fungi, soil invertebrates and prokaryotes. This approach may be desirable in mine lands and other areas that lack functioning soil biota; however, other applications may require more precise application of mycorrhizal fungi.

Production of mycorrhizal inoculum for commercial purposes has evolved considerably in recent years (Douds *et al.* 2000; Gianinazzi & Vosatka 2004) ranging from fungal propagation in on-site nursery plots (Sieverding 1991; Douds *et al.* in press) to axenic *in vitro* production in root organ culture (Adholeya *et al.* 2005) and liquid fermentation in bioreactors (Rossi *et al.* 2002). In all of these preparations, the source of the fungi is of critical concern, both in terms of the beneficial performance of the symbiosis, and in the potential risks associated with the product use. If proper hygiene is not practiced during inoculum production, there is a high risk of accidentally transferring pests or pathogens along with mycorrhizal inocula (Douds *et al.* 2000). Gianinazzi & Vosatka (2004) stress the importance of instituting industry-wide quality control measures to ensure the production of viable mycorrhizae that meet the expected requirements of end-users and are free from agents (e.g. pests) that might negatively affect normal plant growth and development.

POTENTIAL CONCERNS

We highlight three potential concerns associated with inoculation with mycorrhizal fungi: undesirable direct consequences for host plants in managed systems; direct and indirect negative consequences to biodiversity; and negative consequences to ecosystem function.

Undesirable direct consequences for crop production, horticulture and forestry

Inoculum that is intended to increase plant production and fitness may, in some cases, actually reduce it. Although there are many reports of mycorrhizal enhancement of crop yields and tree survival (e.g. Perry *et al.* 1987; Bethlenfalvay &

Linderman 1992), there are also many reports of neutral or even detrimental effects of mycorrhizal fungi on crops and trees in reforestation sites (e.g. Bledsoe *et al.* 1982; Teste *et al.* 2004). The examples cited in Table 1 illustrate a striking symmetry between positive and negative outcomes of many mycorrhizal functions, which underscores the importance of knowing the ecological context in which mycorrhizal fungi are introduced (Abbott & Robson 1991). One recent review concluded that often AM fungi do not improve the growth of plants in production agricultural systems as they are currently managed, particularly when soil phosphorus is not in limiting supply (Ryan & Graham 2002). Similarly, meta-analysis has demonstrated an average positive effect on crop yield of mycorrhizal colonization, but suggested that such positive effects are much less likely when either soil P or indigenous mycorrhizal inoculum potential are high (Lekberg & Koide 2005).

There is evidence that in some systems, certain species of mycorrhizal fungi may actually be detrimental to their hosts. For example, *Glomus macrocarpum* was shown to be the causal agent of stunting in tobacco (Modjo & Hendrix 1986; Hendrix *et al.* 1992); and yield decline associated with continuous cropping of corn and soybean has been linked to particular AM fungi (Johnson *et al.* 1992). Similarly, inoculation with the EM fungi *Laccaria proxima* and *Thelephora terrestris* isolate TT3 resulted in growth depressions of Sitka spruce 6 years after outplanting into natural soils with low additions of phosphate (Le Tacon *et al.* 1992). The likelihood that inoculation with EM fungi will improve tree performance following planting for reforestation appears to be highly dependent on ecological context (Bledsoe *et al.* 1982; Perry *et al.* 1987; Castellano 1996).

This variance in mycorrhizal function is cause for concern because the purpose of including the fungi in commercially produced mycorrhizal products is to capitalize on their abilities to promote plant growth and survival across a narrow range of environments. However, only fungal isolates that are most conducive to large-scale production will be included in these products. There is no reason to assume that production efficacy of a fungus corresponds with its ability to increase host plant vigour.

Biodiversity concerns

Introduced mycorrhizal fungi may directly impact local diversity of fungal communities and indirectly impact plant community composition. There are no documented cases of introduced AM fungi facilitating the spread of invasive herbaceous plants, but given the widespread and general associations of these fungi with vascular plants, there are few locations where potential plant invaders are limited by access to AM fungi. However, introduced AM fungi may contribute to plant invasions if invasive plants benefit more

from introduced AM fungi than the native plant species, an important point to consider when applying AM fungal inoculum in restoration efforts. It appears that *Bromus tectorum* may more readily invade sagebrush steppe of the United States when forming arbuscular mycorrhizae, whereas individual plant growth is greater in isolation when lacking a mycorrhizae (Richardson *et al.* 2000). In addition, competitive exclusion of native grasses by spotted knapweed may involve facilitation by AM fungi (Marler *et al.* 1999).

Facilitation of invasive plants by mycorrhizal fungi may be more likely with EM fungi (Richardson *et al.* 2000). This potential is perhaps best illustrated among the EM fungi that were introduced along with their host plants for the establishment of pine and eucalypt plantations. Nineteen species of *Pinus* are considered problem invasives in the southern hemisphere (Higgins & Richardson 1998), and members of the genus *Eucalyptus* are included on invasive weed lists in the US and Europe (Warner 1999; Diez 2005). For example, Monterey pine (*Pinus radiata*) has a restricted native distribution in California and Mexico, but has been widely planted for agroforestry, especially in Spain, New Zealand, South America, and Australia where it now covers more than 4 million hectares (Rogers 2002). Similarly, several species of *Eucalyptus* native to Australia have been introduced to North America, South America, Asia and Europe (Richardson 1998). Successful introduction of these trees required that EM fungi be imported, providing early evidence of the importance of the symbiosis to host trees (Smith & Read 1997). The application of EM inoculum can be viewed as positive for agroforestry operations; however, there may also be unintended negative consequences if these fungal introductions contribute to the spread of their introduced host plants beyond plantation sites into neighbouring habitats (Richardson *et al.* 2000). For example, eucalypts in Spain have become invasive in areas near large forestry plantations (Diez 2005). These eucalypts are colonized almost exclusively by fungal species or strains of Australian origin (Diez 2005).

The direct impacts of fungal introductions on native fungal communities are also important to consider. Several studies have shown that exotic EM fungi are highly persistent in their novel environments (e.g. De La Bastide *et al.* 1995; Selosse 1997; Selosse *et al.* 1998a,b, 1999). For example, *Laccaria bicolor* isolates from North America were detected in Douglas fir (*Pseudotsuga menziesii*) plantations in Europe 10 years after inoculation of out-planted seedlings (Selosse *et al.* 1998a,b), and were also found to colonize nearby uninoculated trees (Selosse *et al.* 1999). Isolates of *Amanita muscaria* have survived for > 36 years in *Pinus radiata* plantations in Australia (Sawyer *et al.* 2001). In addition, exotic EM fungi may establish on native hosts where they could alter the distribution of native EM fungi.

Fruiting body observations and molecular analyses revealed that EM fungi introduced with *Eucalyptus* in Spain were present on native shrubs (Diez 2005). Similarly, *Amanita muscaria* is now associated with *Nothofagus* forests in Tasmania and New Zealand, presumably as a consequence of its introduction with pines (Fuhrer & Robinson 1992, <http://www.landcareresearch.co.nz/research/biosecurity/fungal/>).

Even if care is taken to introduce fungal species that may already be present in native habitats, problems may still arise. Novel genotypes may outcompete native genotypes and spread beyond the site of introduction, and may interact differently than native genotypes with native hosts, soil communities, and abiotic conditions. Different strains of mycorrhizal fungi vary widely in their responses to the environment and in the benefits they provide to host plants (e.g. Cairney 2002), and there is evidence that some local genotypes of mycorrhizal fungi may be better adapted to their native environment and/or may provide greater benefits to their native host plants than non-local genotypes (e.g. Gildon & Tinker 1983; Stahl & Smith 1984). If novel genotypes outcompete local strains, locally adapted combinations of fungi and their host plants may be disrupted. This disruption could also occur through introgression between native and non-native fungal strains, if native and non-native strains are vegetatively or sexually compatible with each other. For example, North American *L. bicolor* strains used to inoculate Douglas fir plantation trees in Europe have been shown to be genetically distinct from, but sexually compatible with, European strains at these sites (Mueller & Gardes 1991; De La Bastide *et al.* 1995). Hybridization or introgression between introduced and native populations of plants and animals has been shown to have significant negative consequences for the native populations, including extinction (Rhymer & Simberloff 1996), especially when the native populations are small or rare.

Ecosystem function

At the international scale, there is increasing interest in the establishment of tree plantations to sequester carbon dioxide from the atmosphere. These forestation plans frequently include exotic trees (e.g. the BioCarbonFund, <http://carbonfinance.org/biocarbon/router.cfm>). The introduction of a more diverse community of EM fungi has been proposed to improve yield of trees in these plantations (Dell *et al.* 2002). However, Chapela *et al.* (2001) have shown that the EM fungus, *Suillus luteus*, introduced with Monterey pine into Ecuador grasslands, contributed to the removal of up to 30% of stored soil carbon in less than 20 years. Stable and radioactive carbon isotope analyses revealed that *Suillus luteus* utilized stored carbon to support abundant sporocarp

production, while plantation trees performed poorly (Chapela *et al.* 2001). This dramatic impact on the soil carbon cycle was not consistent with the biology of the fungus in its native habitat. Notably, *S. luteus* does not associate with Monterey Pine in California (E.C. Vellinga, personal communication). Further, sporocarp abundance in Ecuador was threefold greater than that of all sporocarp species combined in native California habitats (Chapela *et al.* 2001). This simple example suggests the possibility of negative consequences of introduced mycorrhizal fungi on ecosystem functioning under some circumstances.

Assessment of risks associated with species introductions

Ecologists have long tried to ascertain predictable ecological patterns in the propensity of introduced species to become costly noxious invaders. Attempts to identify universal traits of successful invaders (e.g. Baker 1965) have generally failed but attempts to understand traits that predict the invasive potential of smaller, more constrained suites of species have met with more success (e.g. Rejmanek & Richardson 1996; Reichard & Hamilton 1997; Kolar & Lodge 2001).

Thinking very generally about the potential of non-native biota to cause ecological harm, we know that: (1) numerically, most introductions fail (Simberloff & Stiling 1996; Mack *et al.* 2000); (2) among the species that successfully establish, most are relatively innocuous and do not require costly management responses (Hiebert 1997); (3) for species that establish and create costly problems there is often a lag time between introduction and ecological damage (Mack *et al.* 2000; Sakai *et al.* 2001); (4) invasive species and their novel interactions with the existing biota can result in strong selection, rapid evolution and novel and unpredictable interspecific interactions (Parker & Gilbert 2004); and (5) noxious problem species cost societies billions of dollars per year (U.S. Congress Office of Technology Assessment 1993; Naylor 2000; Pimentel *et al.* 2000). As a result, there is great value in identifying where the low probability but exceedingly costly problem introductions may occur and working to adopt management practices that minimize the likelihood of these situations (Mack *et al.* 2000; Mack 2000).

Generally speaking, the larger the species, the more likely we know the timing, source and consequences of species introductions. We may know, for example, when, where and why various vertebrates were introduced, areas where they are now invasive, as well as their rate of spread (Shigesada & Kawasaki 1997; Abbott 2002). The corollary to this observation is that the smaller the organism, the less, in general, we know about invasions. Relatively little is known, for example, regarding the invasion of earthworms to North America, despite our current understanding of the dramatic ecosystem effects that they have once they are established

(James 1991; Bohlen *et al.* 2004). We know even less about microbes in natural environments (e.g. Galan & Moreno 1998). We often do not know, for example, exactly when or how particular fungi have been introduced, or sometimes even if they are native or introduced in particular places (Orlovich & Cairney 2004; Pringle & Vellinga, 2006).

There are at least four problems associated with diagnosing introductions of mycorrhizal fungi. Foremost is that identifying species of fungi can be difficult. Traditionally mycologists have relied on morphological species concepts but abundant evidence demonstrates that morphological species possess cryptic reproductively isolated (Perkins & Raju 1986; Dettman *et al.* 2003) or genetic species (Koufopanou *et al.* 1997; Dettman *et al.* 2003; Pringle *et al.* 2005; Taylor *et al.*, in press). When species are defined according to morphology, often for practical purposes, what are identified as different 'ecotypes' of the same morphospecies can function very differently (e.g. Stahl & Smith 1984; Bethlenfalvay *et al.* 1989). Invasive species may be difficult to identify because the concept of a fungal species can vary among biologists. AM fungi pose a unique challenge because they are often defined according to morphology, but the genetic system is a focus of ongoing research (Pawlowska & Taylor 2004; Hijri & Sanders 2005). The individual nuclei within a single morphologically defined species of AM fungus may differ, for example, making it possible for an introduced nuclear type to introgress into a native population of nuclei, even if the morphotype does not establish or invade. This kind of invasion is rarely considered by ecologists but is exactly analogous to the introgression of genes after hybridization events, or the horizontal transmission of genes between bacterial lineages. In other kingdoms hybridization may serve as a stimulus to invasion (Ellstrand & Schierenbeck 2000; Ayres *et al.* 2004; Petit 2004).

Second, because soil is a cryptic environment, it has proven difficult to assess the abundance and distribution of mycorrhizal fungi (Johnson *et al.* 1999). We lack adequate knowledge of the biogeography of mycorrhizal fungi (Pringle and Vellinga, 2006). Available studies suggest that many AM fungi, and some EM fungi, are remarkably cosmopolitan in their distributions (Molina *et al.* 1992; Morton & Bentivenga 1994; Stutz *et al.* 2000). Once again, however, there is a conflict between morphological and genetic species concepts. When species are defined according to reproductive or genetic isolation the different cryptic lineages generally have constrained distributions (Petersen & Hughes 1999; Taylor *et al.*, 2000). Only one fungus has been demonstrated to possess cryptic genetic species with global distributions (Pringle *et al.* 2005). Global distributions of reproductively isolated or genetically defined species are an exception. Additional biogeographical data are crucial to our understanding of invasive fungi. If morphological species

are globally distributed, the intentional movement of mycorrhizal fungi may be of little concern. Alternatively, if cryptic species are endemic, then they are susceptible to displacement and extinction by introduced types.

Third, information on the endemic diversity of especially AM fungal communities is sparse. For example, one intensively sampled North Carolina field possessed at least 37 AM fungal species; one-third of these species were discovered at that site and have not been found elsewhere (Bever *et al.* 2001). It will be impossible to understand how fungal communities change without an understanding of baseline community composition.

Fourth, perhaps because of the difficulties associated with defining species, assessing fungal biogeography, and describing fungal communities, there has been little effort to track inadvertent international transport of mycorrhizal fungi found in horticultural products or through other means of transport (Perrings *et al.* 2002). These challenges result in a great deal of difficulty discerning whether or not mycorrhizal fungi are native to a particular location. Mycologists need to further develop and apply molecular techniques that will allow us to track the establishment, invasion and persistence of fungal isolates in novel environments (for an example with EM fungi, see Selosse *et al.* 1998a,b, 1999). Gianinazzi & Vosatka (2004) conclude that current DNA technologies for tracking inoculated AM fungi only allow detection at the species level (where species is defined according to morphology), and stress the need for further development of 'strain'-specific probes and the construction of kits to better track the persistence of commercially produced mycorrhizal inoculum. Towards this goal, 'bar-coding' technology may be important for future research (<http://www.barcoding.si.edu>).

PREDICTING TRAITS OF INVASIVE AND NON-INVASIVE MYCORRHIZAL FUNGI

Mycorrhizal fungi vary widely with respect to life-history attributes and ecological aspects of their interactions with plant hosts (Table 2). Ultimately, we may be able to use our knowledge of life-history attributes such as host specificity, competitive ability and dispersal mode to infer the likely ability of mycorrhizal fungi to become an invasive problem. This knowledge may allow us to develop general predictors of how and when undesirable AM and EM fungi may establish and spread to non-target species and habitats.

Life-history traits

Ecologists have identified a continuum of life-history traits in reproduction (allocation to numerous, small propagules vs. few, larger and well-provisioned propagules), dispersal

ability, and competitiveness (Grime 2001). Some of these life-history traits can be loosely associated with the potential for noxious behaviour. For example, a large number of problem invasive plant species are disturbance dependent, ruderal or weedy species with high dispersal but low competitive capacity (Kolar & Lodge 2001; Sakai *et al.* 2001). Among the worst of these invaders, however, are species (e.g. spotted knapweed, star thistle, purple loosestrife) that carry attributes that allow them to rapidly invade disturbed habitats and maintain competitive dominance through time. Some of the most costly and difficult to contain invasive species are the relatively few that successfully invade mature vegetation in relatively undisturbed habitats (e.g. garlic mustard and leafy spurge; Meekins & McCarthy 2001).

Aspects of life history may be used to predict relative risks associated with introductions to novel ecosystems. For example, many EM species produce small airborne spores that are likely to be circulated widely, while some EM and nearly all AM fungi produce belowground spores which are distributed only locally by animals and physical soil movement (Allen 1991). The risk of spread via spore dispersal into nearby non-target habitats is expected to be significantly different among these groups of fungi. In addition, recent theoretical studies of plant-parasite interactions suggest that parasites with higher rates of gene flow may be better able to adapt to local host populations, as long as gene flow does not completely homogenize parasite populations (Gandon & Michalakis 2002; Morgan *et al.* 2005). If these results are applicable to the mycorrhizal symbiosis, then differing dispersal abilities among types of mycorrhizal fungi may help predict the potential for non-native populations to adapt to novel environments.

Evidence in support of the importance of life-history attributes to predict invasion success comes from studies of EM fungi, where invasion may be less common for species with hypogeous or closed sporocarps and more likely for species with open sporocarps and wind or insect dispersed spores. Truffles and truffle-like fungi typically possess closed sporocarps, and such fungi have been introduced across continents at multiple times (Dennis 1975; Sogg 2000; Trappe & Cázares 2000; Fogel & States 2001; Yun & Hall 2004). Nevertheless, the available (albeit limited) data suggest that these taxa are not invasive.

In contrast, gilled and poroid mushrooms possess forcibly discharged spores that may be carried long distances by wind or in some cases, flying insects. Two obvious examples of invasive mycorrhizal fungi are *Amanita muscaria* (Bougher 1996; Orlovich & Cairney 2004) and *Amanita phalloides* (A. Pringle, unpublished data); both species make gilled mushrooms with airborne spores. An estimate of how quickly species with open sporocarps will travel can be made using data of the saprobe *Clathrus archeri* (Parent *et al.* 2000).

This fungus, whose spores are carried by insects, appeared in the Alsace region of France in 1920 and by 1999 (and perhaps earlier) *C. archeri* had travelled to and established in the Galicia region of Spain, a distance of at least 1400 km in *c.* 70 years.

Colonization and competition

Some ectomycorrhizal fungi have been shown to have different abilities to compete for space on the roots of their host plants. Kennedy & Bruns (2005) showed that *Rhizopogon occidentalis*, a ruderal EM fungus typically found only on the roots of pine seedlings in relatively early stages of plant succession (Horton *et al.* 1998; Baar *et al.* 1999), more quickly colonized host roots than *Rhizopogon salebrosus*, which exhibits some ruderal behaviour but is also found on the roots of trees in mature forest. Interestingly, rapid colonization by *R. occidentalis* seemed to give it a priority effect in competitive interactions with *R. salebrosus*, with *R. occidentalis* inhibiting colonization by *R. salebrosus* in mixed species treatments. This example illustrates an important distinction between different scales of colonization ability for mycorrhizal fungi – *Rhizopogon* species produce below-ground sporocarps that are dispersed locally, and thus would be considered to have more limited colonization ability than aerially dispersed species. However, within local populations, species such as *R. occidentalis* exhibit ruderal characteristics, quickly colonizing host plants through rapid spore germination after disturbances. *Rhizopogon* species have been used to inoculate ectomycorrhizal plants for commercial purposes, and a species such as *R. occidentalis* seems to possess a number of desirable characteristics for such uses: rapid colonization, initial competitive ability due to priority effects, and inability to persist in later stages of succession; however, for any particular management scenario, it would also be crucial to know whether inoculation with *R. occidentalis* is beneficial to the target host plant.

Similarly, AM fungi differ in the rates at which they colonize plant roots as well as their abilities to compete with other AM fungi once they are inside roots. For example, Hart & Reader (2002) showed that isolates from the Glomaceae tend to colonize roots significantly more quickly, usually within 3 weeks, compared with isolates from the Acaulosporaceae and Gigasporaceae, some of which took up to 8 weeks. Studies of interactions among indigenous and introduced species of AM fungi show that competitive outcomes also vary with fungal taxa (Hepper *et al.* 1988), as well as proximity of the fungal propagules relative to plant roots (Lopez-Aguillon & Mosse 1987), population densities (Abbott & Robson 1981), and the presence or absence of hyperparasites in the system (Ross & Ruttencutter 1977). Although competitive outcomes may sometimes depend on initial relative inoculum densities, some taxa of AM fungi are

clearly more competitive than other species. For example, Hepper *et al.* (1988) showed that *Glomus caledonium* was more competitive than *Glomus mosseae*, and both species were much more competitive than the *Glomus* isolate known as 'E3'. Presence of one fungus in a root system can alter the ability of another to colonize roots (Pearson *et al.* 1993) but this can depend on the stage in the life cycle of the fungi (Pearson & Schweiger 1993). Colonization of roots by AM fungi is a complex phenomenon and seasonal dynamics (Merryweather & Fitter 1998) demonstrate that simple assessments at one point in time would offer incomplete descriptions of colonization success or failure.

Outcomes of competition among mycorrhizal fungi at decadal and longer time scales will ultimately be most relevant for determining whether introduced mycorrhizal fungi can establish and persist in non-target ecosystems. We need to understand whether there are consistent tradeoffs among species for initial colonization ability, long-term competitive ability, dispersal ability, and benefits to host plants. For example, more local dispersal, as in fungi with closed sporocarps, may be associated with higher levels of ecotypic variation and host specialization. Unfortunately, very few data exist to assess such tradeoffs. It is conceivable that the ability to compete for root space may favour long-term persistence by a fungus, but it may not be a good predictor of the ability to spread in an ecosystem, or of its influence on host plant fitness. For example, it may be that the mycorrhizal fungal species that have the best initial colonization ability, and thus are desirable for ease of inoculation, also tend to have poor long-term competitive ability, a relatively low growth benefit to host plants, and/or a high ability to spread into non-target plant communities, in which case these fungi would be undesirable from a management perspective.

CONCLUSIONS AND RECOMMENDATIONS

We believe that evidence suggests that there is clear potential for non-indigenous mycorrhizal fungi to persist and invade non-target habitats. These invasions may have positive, neutral, or negative effects on plant growth, local fungal and plant communities and ecosystem processes. Figure 1 summarizes these potential effects, and provides a general framework of testable hypotheses. We can no longer assume that all interactions with mycorrhizal fungi will result in positive or negligible effects. With ecological studies documenting the potential for serious negative by-product consequences of inoculation, more attention needs to be placed on research that can help elucidate best management practices for mycorrhizal treatments. Those applying fungal treatments should expect a range of outcomes from positive to negative within natural systems as well as in managed systems. Thus, careful consideration of need and techniques

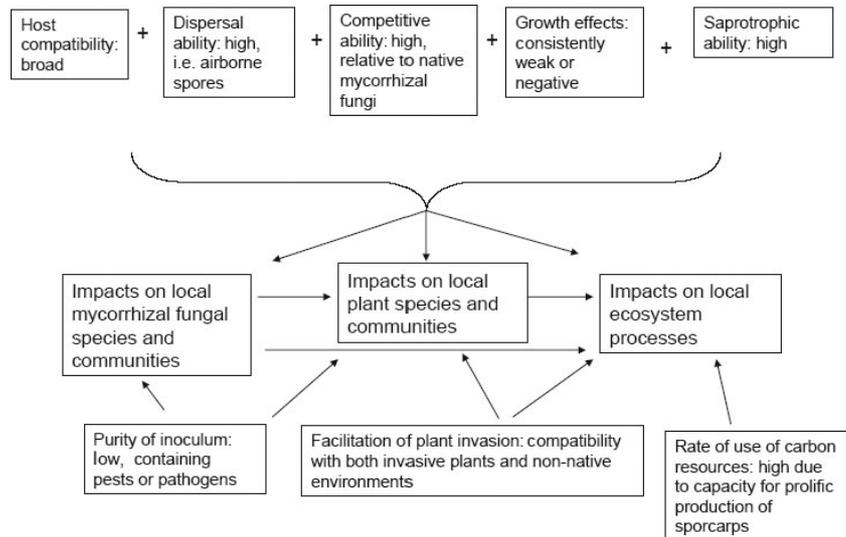


Figure 1 A conceptual model illustrating issues of primary concern when using fungal inoculum in plant management. The top row represents traits of non-native mycorrhizal inoculum that are hypothesized to be associated with impacts on native communities and ecosystem processes. These are often the very same traits sought after as favourable attributes for management use. The middle row represents three primary areas of potential impacts and their interactions. The bottom row represents mechanisms by which fungal inocula may either directly or indirectly affect natural systems.

are warranted. We make three specific recommendations with this in mind.

First, the primary consideration for each proposed application of mycorrhizal inoculation should be whether or not inoculation is necessary (Abbott & Robson 1991). Mycorrhizal fungi are ubiquitous and abundant in most agricultural systems (Olsson *et al.* 1999); consequently, inoculation is generally not necessary to produce mycorrhizae on crop roots. In addition, ecotypes of AM fungi in systems with a history of high fertilizer inputs may not be beneficial to plant growth (Johnson 1993, Bell *et al.* 2003). Alternatively, population densities of indigenous AM fungi in soils managed for agriculture and horticulture may be severely depressed due to soil sterilization, tillage and fallow (Douds & Johnson 2003). Both AM and EM fungi may be eliminated from severely disturbed ecosystems such as mine lands or eroded slopes so that inoculation with mycorrhizal fungi is necessary for successful reclamation or restoration (Jasper *et al.* 1987; Lumini *et al.* 1994). Finally, reforestation projects often benefit from the addition of EM inoculum when the abundance and diversity of natural inoculum is low due to previous land uses (Le Tacon *et al.* 1992).

Second, we recommend adopting policies that favour the use of local mycorrhizal types, where feasible. A conservative approach to managing biotic integrity is to recommend managing indigenous mycorrhizal fungi that are already present in the soil (Trappe 1977; Abbott & Robson 1982; Sylvia & Burks 1988; Bethlenfalvay & Linderman 1992; Jasper 1994; Parlade *et al.* 1996; Berman & Bledsoe 1998; Douds *et al.* 2000). When mycorrhizal fungal propagules are absent, or in extremely low densities, then inoculum containing local strains of mycorrhizal fungi should be developed and utilized to the extent possible. Protocols are already in place for the selection and production of

mycorrhizal inoculum containing indigenous fungi (Abbott *et al.* 1992; Douds *et al.* 2000). On-farm production of AM fungal inoculum is feasible in most situations and it is highly desirable because it minimizes production costs (Douds *et al.* 2000). Also, producing inoculum locally will help minimize the potential risk of spreading non-indigenous pathogens and pests that may accidentally contaminate commercial mycorrhizal inoculum products. During every step of the process, care should be taken to ensure the production of pest-free mycorrhizal inoculum (Menge 1984).

Our third recommendation pertains to the use of non-indigenous fungi. Local strains or species may be unavailable or may be known to be incompatible with the target plant species in many managed systems. Mixed strain AM inocula might be viewed as increasing the probability of a positive target effect, but this strategy also carries risk. Strains beneficial to target plant growth do not always dominate and mixed inocula increase the likelihood of an unintended negative consequences, such as non-target invasion. As discussed above, when EM plants are planted as exotics for timber production, compatible exotic EM fungi are often introduced with them to ensure successful establishment. If non-indigenous fungi must be used, then steps should be taken to minimize the risk of introducing mycorrhizal fungi that could become problem invasive species. For such situations, we propose that the isolates used for inoculation should be selected to have the following traits when possible:

- (1) High benefit to the target host plant.
- (2) High specificity to the target host plant species.
- (3) Among EM fungi, low ability to utilize non-host carbon sources, in order to minimize the opportunity

Table 3 Research needs in mycorrhizal fungi needed to better predict invasion potential. There is currently insufficient knowledge to accurately predict ecological outcomes of inoculation with non-native isolates of mycorrhizal fungi. Future research is needed to develop assessment methods and provide ecological information to ensure inoculation safety

Assessment methods

- Develop protocols for rapid determination of the taxonomy of mycorrhizal fungi, with complementary use of morphological and molecular methods
- Develop protocols for determining the biogeographical distribution of mycorrhizal fungi, especially cryptic species
- Develop protocols for tracking specific genotypes of mycorrhizal fungi in novel environments
- Develop protocols for assessing the infectivity of inoculum of mycorrhizal fungi
- Develop protocols for screening of inoculum for the presence of pests and pathogens

Ecological information

- Assess life history traits of fungal taxa that are used as inoculum, particularly: host range, competitive ability against other mycorrhizal fungi and other fungal taxa, dispersal ability, and average impact on the growth of multiple host plant species, and comparative infectivity of fungi from different quantities of inocula
 - Characterize local communities of mycorrhizal fungi, especially in habitats near areas of frequent mycorrhizal inoculation
 - Determine the degree of compatibility of mycorrhizal fungi with invasive plant species in non-native environments
 - Assess potential impacts of colonization by mycorrhizal fungi on soil carbon storage
-

for EM fungi to exist as partial saprobes in introduced habitats.

- (4) Rapid colonization ability, for ease of inoculation.
- (5) Low dispersal ability, to reduce the potential for encroachment into non-target habitats.
- (6) Poor long-term competitive ability which would allow inoculation and establishment of host plants, followed by extirpation of the introduced fungus by native fungi.

Note that recommendations (2), (3), (5) and (6) would not apply if the management treatment utilizes indigenous fungi as inoculum because traits such as high dispersal ability and long-term competitive ability would then be desirable for building a sustainable ecosystem.

Unfortunately, we do not have sufficient data on all six of these traits for specific fungal strains to allow selection of fungi based on these traits. More research is necessary to increase our knowledge of the ecological attributes of mycorrhizal fungi, and our ability to assess persistence and spread by non-indigenous mycorrhizal fungi (Table 3). Research in these areas will allow us to better predict inoculation and growth responses as well as unwanted invasions into native ecosystems (Hart *et al.* 2001). We need to know whether the fungi that are being used most frequently in inoculation efforts tend to have positive benefits for the target host plant and high host specificity, the ability to compete with native fungi in the short and long term, and the ability to spread into and affect non-target plant species or habitats. Ultimately, scientists working on invasion biology and ecosystem health will need to work towards thoroughly documenting cases of non-native fungal impacts on native

plant species and ecosystem processes. It is of primary importance that the potential benefits of mycorrhizal inoculation be balanced with the potential costs of unwanted invasions. Policies that reduce the likelihood of ecologically costly introductions are unlikely unless mycorrhizal ecologists can develop a much better understanding of the ecological costs incurred by continuing current practices, and develop feasible alternative strategies to inoculation with non-local strains. However, until we develop better empirically based support for these concerns, as well as models for management, there is likely to be little impetus to alter management strategies. With inoculation treatments increasing, and new companies emerging to meet the demand for these products, mycorrhizal ecologists must respond quickly to fill the research void that currently exists in order to assess the need for the cautious approach that we advocate here. These research gaps can be closed with comparative studies linking phylogenetic relatedness, life-history traits, and ecological effects in commonly used fungal types, careful field studies of potential spread of fungi to non-target hosts, and a synthesis of the range of target effects expected from inoculation. This is an achievable research agenda. Several research groups are currently working on aspects of these problems. Care is needed to make sure that this emerging science is integrated into mycorrhizal management.

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