REVIEW ARTICLE

A review of the influence of root-associating fungi and root exudates on the success of invasive plants

Cindy Bongard[1]

1 *Department of Physical and Environmental Sciences, University of Toronto at Scarborough, 1265 Military Trail, Toronto, Ontario, Canada, M1C 1A4,*

Corresponding author: *Cindy Bongard* (bongard@utsc.utoronto.ca)

Abstract

Plant-fungal interactions are essential for understanding the distribution and abundance of plants species. Recently, arbuscular mycorrhizal fungal (AMF) partners of non-indigenous invasive plants have been hypothesized to be a critical factor influencing the invasion processes. AMF are known to improve nutrient and moisture uptake, as well as disrupt parasitic and pathogenic microbes in the host plant. Such benefits may enable invaders to establish significant and persistent populations in environments previously dominated by natives. Coupling these findings with studies on invader pathogen-disrupting root exudates is not well documented in the literature describing plant invasion strategies. The interaction effects of altered AMF associations and the impact of invader root exudates would be more relevant than understanding the AMF dynamics or the phytochemistry of successful invaders in isolation, particularly given that AMF and root exudates can have a similar role in pathogen control but function quite differently. One means to achieve this goal is to assess these strategies concurrently by characterizing both the general (mostly pathogens or commensals) and AM-specific fungal colonization patterns found in field collected root samples of successful invaders, native plants growing within dense patches of invaders, and native plants growing separately from invaders. In this review I examine the emerging evidence of the ways in which AMF-plant interactions and the production of defensive root exudates provide pathways to invasive plant establishment and expansion, and conclude that interaction studies must be pursued to achieve a more comprehensive understanding of successful plant invasion.

Keywords

Introduction

Approximately 10% of non-indigenous plant species can significantly suppress or eliminate native populations (henceforth 'invaders'), and have successfully established in regions around the globe, while others merely become naturalized and integrate with the native community (Richardson et al. 2000a). Explaining why some species are widely successful, with large impacts on native biota, is an active area of research (Rejmánek and Richardson 1996, Mack et al. 2000, Inderjit et al. 2008). In particular, herbaceous species such as *Vincetoxicum rossicum*, *Euphorbia esula*, *Cirsium arvense*, *Alliaria petiolata*, *Polygonum cuspidatum*, and *Phragmites australis* (dog-strangling vine, leafy spurge, Canada thistle, garlic mustard, Japanese knotweed, and common reed, respectively) have established widespread monocultures in Canada and become ecologically and economically problematic, threatening both native biota and reducing agricultural production (Lorenz 1991, Meekins and McCarthy 1999, Ailstock et al. 2001, Klironomos 2002, Kruger-Mangold et al. 2002, Cappuccino 2004).

The hypotheses explaining invader success are multifaceted and continue to evolve (Mack et al. 2000, Inderjit 2005). Explanations of why certain invaders successfully establish in novel ranges generally include reduced negative interactions or key facilitative interactions that allow certain species to overcome biotic barriers to invasion. A number of these theories attempt to explain invader success as a function of fungal associations, both beneficial and detrimental, or as a function of invader root exudates, which have also been shown to cause significant shifts in the life-history strategy of native plants such as reproductive timing and characteristics (Parepa et al. 2012). The Enemy Release hypothesis proposes that invaders flourish because they are released from natural enemies that are either not found or have not successfully adapted to the invader in the novel environments, including fungal pathogens (Keane and Crawley 2002). The Novel Weapons hypothesis suggests that invaders possess chemical exudates that are harmful to previously unexposed native organisms in the novel environment, thus disrupting plant communities and abetting invader establishment (Callaway et al. 2008). The Diversity-stability hypothesis holds that more diverse ecosystems are likely to contain at least one or more species prone to thriving under conditions of environmental perturbation, and are therefore able to fill niches of competitors that falter under such conditions—thus increasing resistance to invasion (Tilman and Downing 1994). Consequently, dampening of diversity due to the success of invading species can also result in 'invasional meltdown', whereby the proliferation of one invader can increase the likelihood of successful establishment of subsequent invaders (Simberloff and Von Holle 1999). As well, the concept of a 'unifying theory' was put forward by Hallett (2006), suggesting that successful invasions result from a combination of dislocation from antagonistic relationships, the availability of generalist microbial mutualists in the novel environment, and allelopathy.

The benefits attributed to mutualisms such as mycorrhizal (root-fungal) associations have recently become well represented in the literature (Johnson et al.

1997, Bever 1999, Smith and Read 1997). Similarly the advantages derived from powerful allelopathic and anti-pathogenic root exudates (novel weapons) have been linked to successful plant invasions. These effects are generally categorized as either i) benefits derived from associations with arbuscular mycorrhizal fungi (AMF) which are symbionts in the order Glomales, known to enhance nutrient and moisture uptake as well as provide protection from pathogens, or ii) benefits derived from root exudates that contain antibiotic (allelopathic, antipathogenic or anti-feedant) or signaling compounds. These investigations have typically been carried out in isolation of one another, although it is evident that there are distinct interdependencies and interactions operating between mutualistic and chemical strategies (Newsham et al. 1994, Klironomos 2002, Hallett 2006). Invaders are also suspected of being fungal generalists, a trait that can result in successful establishment and significant seedling recruitment, leading to the formation of monocultures and loss of community diversity.

My objective in this review is to summarize the current understanding of plant-fungal associations in conjunction with root phytochemistry dynamics of successful invaders, and to suggest where research needs to be expanded in order to demonstrate the potential interdependencies between these two areas of research (see Figure 1). Knowledge of how they jointly influence invaders will further our understanding of processes supporting highly successful plant invasions.
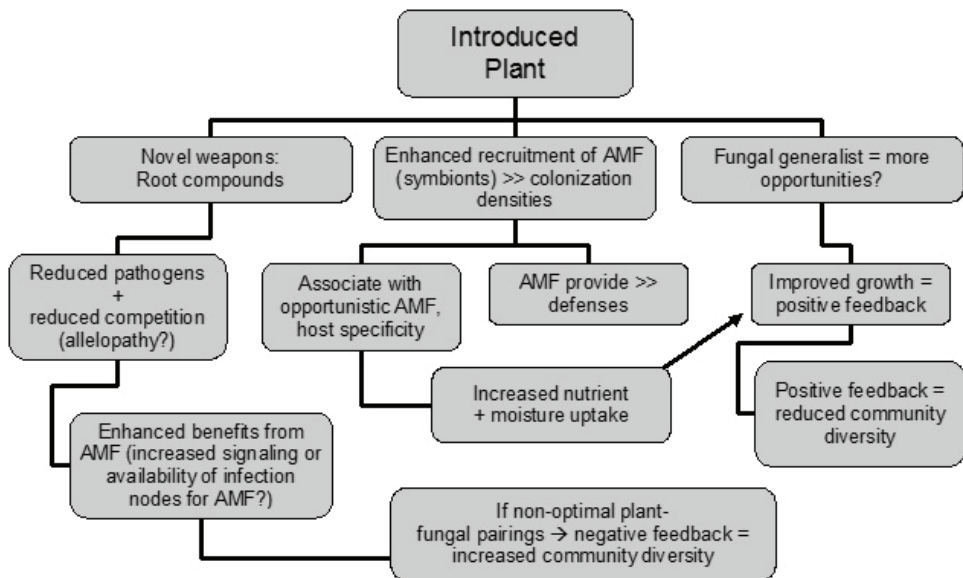

Figure 1. Possible dynamics within the rhizosphere and local soil environments subsequent to invasion by introduced plant species. The invader may possess novel or unique root compounds, an enhanced ability to establish associations with AMF, and/or the ability to associate with a wide range of beneficial fungi (some opportunistic P providers) relative to native plants.

AMF and invaders

Research related to plant-fungal association influences on invaders tends to bifurcate into two groups: investigations on fungi providing beneficial mutualisms, such as AMF and ectomycorrhizal fungi, and investigations on the impacts of parasitic/pathogenic fungi. In the case of the former, hyphal networks (vegetative filamentous structures) of mycorrhizae can extend as much as 200 times farther into the soil than the roots they colonize (Quinn 2011), providing increased resource availability that the plant would not otherwise have access to. Fungal partners may also mediate plant-to-plant transfer of carbohydrates and other nutrients among different individuals of the same plant species, as well as among different plant species within the community by linking together the roots of two or more plants. Such mycorrhizal communities are referred to as "common mycorrhizal networks" (Selosse et al. 2006, Egerton-Warburton et al. 2007). These generalist networks can result in the creation of inoculum reservoirs that promote selective seedling establishment within a plant community. However, plants differ in their responses to mycorrhizal fungi, and the fungi differ in their ability to distribute nutrients between coexisting plants. Arbuscular mycorrhizal plant-fungal symbioses form highly specialized nutrient-exchange structures (vesicles and arbuscules) at the plant-fungus interface and are recognized as being a particularly beneficial group of root endophytes. Plants associating with AMF are typically more competitive and better able to tolerate environmental stresses than are non-mycorrhizal or poorly colonized plants (Biermann and Linderman 1983, Daniell et al. 2001, Bianciotto and Bonfante 2002, Vandenkoornhuyse et al. 2002, Bonfante 2003, Brundrett 2004, De-Bellis and Widden 2006, Greipsson and DiTommaso 2006, Parniske 2008, Shah et al. 2010), and AMF associations may contribute to the diversity of plant communities.

Bever (2002) noted that there is evidence of negative feedback on abundance of a given plant species resulting from the asymmetries between plant and AM fungus: plant-fungal associations are not always established in such a way as to maximize the benefit realized by either partner. For example, in the case where Plant-1 grows best when partnered with AMF-1, AMF-1 may be more inclined to establish associations with Plant-2, and so on. This dynamic is thought to contribute to the successful coexistence of a variety of plant species functioning within species guilds, thus preventing dominance by one or a few species. In this scenario, negative feedback due to non-ideal plant-fungal pairings is a mechanism that promotes diversity in plant communities. An introduced plant may disrupt this type of system balance where it differentially promotes or disrupts fungi in the plant community, suggesting that AMF research must be coupled with investigations on established plant-fungal community pairings within a local environment. These as well as other findings would indicate that species identity is also relevant to invasion biology when considering plant-fungal mutualisms (Crawley et al. 1999).

Root structure is another factor for consideration with regard to plant-AMF associations. Seifert et al. (2009) noted that introduced plants generally had finer root architecture relative to their native European counterparts, a characteristic consistent

with a tendency to correspondingly increase reproductive biomass in newly introduced species. These findings suggest a reduced colonization by AMF in introduced plant variants, as finer roots are more typical of species with lower mycorrhizal responsiveness (Baylis 1975, Hetrick et al. 1992, Vogelsang and Bever 2009). Given that the structure and development of mycorrhizal hyphae is substantially altered in the presence of roots of host plants (Brundrett 2009), a shift in plant species representation post-invasion has the ability to significantly impact local AMF.

Plant community structure can be influenced by the presence/absence, density, and species richness of AMF in local soils, as plants can differ in their response to AMF colonization (Klironomos 2003). Less competitive plant species may establish a foothold within a community where they otherwise may have failed to persist in the absence AMF in the rhizosphere, suggesting that AMF promote plant coexistence and therefore contribute to community diversity (Moora and Zobel 1996, van der Heijden et al. 1998). For example, when small heal-all *Prunella vulgaris* plants were inoculated with AM fungi, they were able to successfully compete with larger neighbouring woodland strawberry *Fragaria vesca* plants that they had failed to successfully compete with pre-inoculation in greenhouse experiments (Moora and Zobel 1996). AMF associations would therefore increase biodiversity by decreasing the interspecific suppression of small plants by larger neighbours. It should be noted that fine-scale studies look at the impact of composition and diversity of AMF rather than just presence or absence of AM fungi (Hart et al. 2003), and therefore these studies consider factors such as host specificity and have more relevance for later-successional stages of invader range expansion. It has been proposed that AMF may be either disrupted or harnessed by aggressive invasive plant species, resulting in altered native fungal communities in the soil as the invader attains dominance in the system (van der Heijden et al. 1998, Daniell et al. 2001, Griepsson and DiTommaso 2006, Bastias et al. 2007, Curlevski et al. 2010).

The mechanisms by which AMF association provides advantages to successful invaders as they establish and attain dominance in a novel range typically include: i) increased general AMF colonization density of invaders relative to natives can lead to improved nutrient and moisture uptake and increased competitiveness, ii) host specific AMF that support plant community structure and diversity can be significantly altered by invaders, and iii) pathogen protection by AMF may be provided selectively to invaders.

Key findings for each category are summarized below.

AMF colonization, dependence, and density

Some aggressive plant invaders have been observed to sustain significantly increased AMF colonization densities relative to local native plants in the field. An example of this is *Vincetoxicum rossicum*, colloquially known as dog-strangling vine (DSV) because its twining tendencies lead to dense interconnected mats of impenetrable vegetation.

DSV has been shown to be more densely colonized by mycorrhizal fungi than co-occurring native plants in Henderson Harbour, New York (Greipsson and DiTommaso 2006, Smith et al. 2008). Smith et al. (2008) used bright field microscopy to detect evidence of significantly greater fungal colonization of DSV relative to leek *Allium ampeloprasum* bait plants (frequently used as a predictor of AMF density in soils), and local natives such as milkweed *Asclepias syriaca*, Canada goldenrod *Solidago canadensis*, or naturalized blueweed *Echium vulgare* L. Additionally, DSV colonized by fungal partners had a significantly greater total biomass relative to DSV grown in sterilized soil reamended with AMF-free microbial wash (Smith et al. 2008).

Soil microbial communities have been observed to change progressively as invasion advances from year to year (Wolfe and Klironomos 2005, Batten et al. 2006), and it has been suggested that invaders benefit disproportionately from symbiotic mutualists, particularly in disturbed sites (Reinhart and Callaway 2006, Sun and He 2010). Plants are capable of controlling the density of mycorrhiza representation by root growth, digestion of old interface hyphae in plant cells, or altered root system formation (Brundrett 2008). These types of mechanisms may be at play in the field when invasions occur, followed by shifts in fungal colonization patterns. A study by Liang et al. (2004) showed a significant positive correlation between invasion time and AMF colonization rate of goldenrod *Solidago canadensis*, a successful invader in China, though there was differential colonization evidenced by the different AMF species, depending on the environmental characteristics. They noted that one species of AMF, *Glomus mosseae*, demonstrated increased colonization density over time in *S. canadensis*, while another AMF species, *G. constrictum*, showed decreased colonization density over time. It was suggested that *G. constrictum* may be an early successional species, and *G. mosseae* a late-successional species. The authors concluded that AMF aided establishment and proliferation of *S. canadensis* in its introduced range in China.

In contrast to the above studies, soil/AMF conditioning studies and bioassays by Vogelsang and Bever (2009) demonstrated that the invasive herbaceous forb Italian thistle *Carduus pycnocephalus* exhibited strong growth in soil lacking arbuscular mycorrhizal fungi, as well as in soil conditioned by a diverse mix of non-native plant species. As well, *C. pycnocephalus* growth was inhibited by the soil that best promoted the native herbaceous forb California cudweed *Gnaphalium californicum*. Mycorrhizal density investigations showed a reduction of AMF in the invader-conditioned soil relative to the native-conditioned soil, suggesting that in some cases invader species do not promote the growth of mycorrhizal fungi in the same way that native species do. Given that most crop plants are hosts to AMF, this association is potentially an important resource for agriculture (Sieverding 1991, Oehl et al. 2003), and should be considered for further study.

AMF host specificity, richness, and opportunism

Given the observed low AM fungi:host plant ratio (i.e. approx. 150 described AMF species to 300,000 plant species), it is generally assumed that there is a high functional

redundancy among AM fungal species, and therefore low host specificity (Klironomos 2000). However, it has been shown that there are differential phosphorus uptake and pathogen protection responses that are highly plant- and fungus-species specific for different plant-fungus combinations (van der Heijden et al. 1998, Helgason et al. 2002, Duponnois et al. 2005, Gustafson and Casper 2006, Gogoi and Singh 2011). Optimal plant-AM fungi combinations are more likely to be established where higher AMF species diversity is present. As such, mycorrhizal fungal species richness has been shown to affect plant productivity, and observed shifts and loss of diversity in AMF groups post invasion could impact plant community structure (Maherali and Klironomos 2007). It has been observed that certain aggressive invading plant species can alter the existing native fungal communities in a densely invaded environment, thus disrupting native plant communities (Helgason et al. 2002, Kourtev et al. 2002, Mummey et al. 2005, Batten et al. 2006, Greipsson and DiTommaso 2006, Hawkes et al. 2006, Stinson et al. 2006, Meinhardt and Gehring 2012). Hawkes et al. (2006) described a dramatic shift in the composition of AMF communities in native North American grasses *Nassella pulchra* and *Lupinus bicolor* subsequent to invasion by introduced grasses *Avena barbata* and *Bromus hordeaceus*. There was a shift away from species originally colonizing natives toward those colonizing the invader, and fungal species richness in the natives was reduced as a result of the shift (Hawkes et al. 2006). Compositional changes in AM fungi pre- versus post-invasion supports host specificity as a factor, given that reduction in native plant species representation correspondingly reduced the associating fungi. The authors concluded that invading plants could influence the network of mycorrhizal fungi available to natives, thus providing a mechanism for successful establishment and subsequent invasion. Similarly, Mummey et al. (2005) used terminal restriction fragment length polymorphism (T-RFLP) and multivariate analyses to show that AMF communities associating with *Dactylis glomerata*, a common forage grass species naturalized in mid-western US, shifted to reflect the community composition associated with *Centaurea maculosa*, a noxious weed native to eastern Europe, post invasion. As well, Stinson et al. (2006) observed that the non-mycorrhizal exotic invasive forb garlic mustard *Alliaria petiolata* suppressed both AMF and ectomycorrhizal fungi, the latter being instrumental in tree seedling establishment and growth. Disruption of AMF by successful invaders could result in loss of natives dependent on such species, supporting competitive exclusion by the invader.

Vandenkoornhuyse et al. (2003) used PCA analyses to determine plant-fungal association patterns generated by T-RFLP using AMF-specific primers. They demonstrated that three different co-occurring grass species (*Agrostis capillaries*, *Festuca rubra*, and *Poa pratensis*) were differentially colonized by AMF phylotypes, suggesting that recognition mechanisms exist that confer fungal-host plant specificity. Another study by Helgason et al. (2002) similarly investigated host specificity in mycorrhizal fungal associations using small-subunit rRNA gene amplification and sequencing. They found that the only species of AMF colonizing field collected *Acer pseudoplatanus* in North Yorkshire (UK) was *Glomus hoi*, while several other species of AMF (*Scutellospora dipurpurescens*, *Archaeospora trappei*, and *Glomus sp.* isolate UY1225) were found

differentially colonizing four neighbouring plant species (*Rubus fruticosus agg. L., Epilobium angustifolium L.*, *Ajuga reptans L.* and *Glechoma hederacea L.*). The *Glomus hoi* consistently outperformed other AM fungi in improving P uptake in all the woodland plants in greenhouse experiments, thus enhancing the growth of these mycorrhizal plant species (Helgason et al. 2002), particularly in P-limited environments. Consequently, disruption or promotion of specific AMF by invaders would significantly impact existing plant community structure.

Greipsson and DiTommaso (2006) predicted that highly invasive species such as *Vincetoxicum rossicum* will tend to associate with fast-growing opportunistic or highly beneficial AMF species, enabling rapid establishment of invaders in their novel range. *Glomus* species have been shown to comprise a subset of such AMF because they have the advantage of readily forming anastomoses (connections between hyphae) with other fungi and are able to colonize via hyphal fragments, whereas other AM fungi typically require intact mycelia to colonize host plants, or direct infection from spore dispersal (Figure 2) (Biermann and Linderman 1983, Giovannetti et al. 1999, Fumanal et al. 2006). *Glomus intraradices*, *G. caledonium*, and *G. mosseae* were observed to form anastomoses between hyphae originating from the same spore as well as different spores from the same isolate, while this was not the case for *Gigaspora* or *Scutellospora spp.* tested (also AMF) (Giovannetti et al. 1999). As such, these *Glomus* species have been shown to behave opportunistically relative to commonly co-occurring AMF (Giovanetti et al. 1999, Helgason et al. 2002). As well, preferential P uptake by *G. intraradices* has been observed in several studies (Graham and Eissenstat 1994, Appoloni et al. 2008, Van Aarle et al. 2009), suggesting that this species of AMF would be particularly beneficial in low P environments. DSV was observed to associate with *G. intraradices* and *G. caledonium* in field studies in Southern Ontario, where several co-occurring native plants were not observed to form such associations based on molecular investigation of root-colonizing AMF communities (Bongard et al., unpublished data).

Glomus species with demonstrated ability to colonize roots via hyphal fragments also appeared to be more beneficial in promoting plant growth over *Gigaspora* species (Bever et al. 2009), which have no demonstrated ability to colonize roots via hyphal fragments (Biermann and Linderman 1983, Bever et al. 2009). Maherali and Klironomos (2007) also noted that members of the Glomaceae (includes *Glomus* species) have demonstrated reduced pathogen abundance in roots; however, Gigasporaceae generally enhanced nutrient uptake in their plant hosts. Highly beneficial influences on plant growth was observed in the shrub *Acacia holosericea* inoculated with *Glomus intraradices* in a study by Duponnois et al. (2005), who observed that *G. intraradices* optimized P solubilization and uptake from mineral phosphate. Maldonado-Mendoza et al. (2001) observed that a phosphate transporter gene (GiPT) in the extra-radical mycelium of *G. intraradices* was expressed during associations with carrot *Medicago truncatula* roots. Their analyses revealed that GiPT expression is regulated in response to phosphate concentrations in the environment and modulated by the overall phosphate status of the mycorrhiza, suggesting that *G. intraradices* can detect phosphate
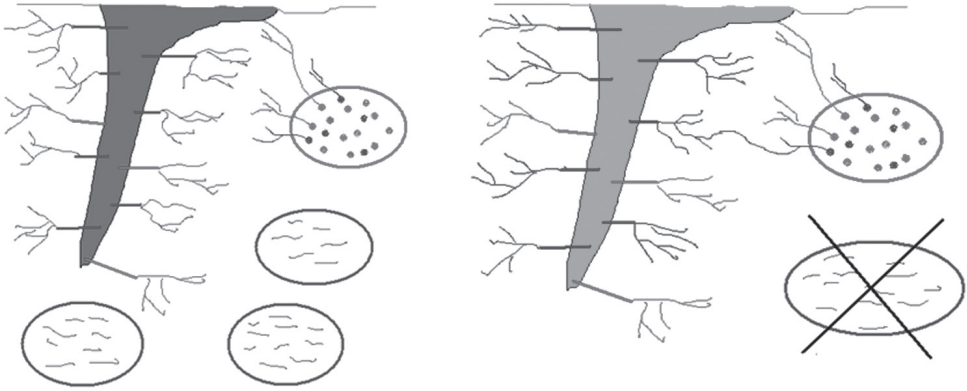
Figure 2. The root on the left represents an invasive plant that is able to form associations with opportunistic AM fungal fragments, while the root on the right cannot form such associations, but must form associations with hyphae of germinating spores or intact mycelia (i.e. established hyphal networks). The ability to form these opportunistic associations with hyphal fragments would be highly advantageous in mechanically disrupted sites.

levels in the external environment, as well as having an internal phosphate sensing mechanism. This ability in the propagative units among glomalean families would provide enhanced early successional establishment opportunities for plants capable of forming associations with these species (Giovannetti et al. 1999). In heavily mechanically disrupted sites, mycorrhizal networks may be in a slow state of recovery and therefore respond in a manner similar to early successional behavior (Hart et al. 2003), suggesting that colonization via mycelial fragments, or opportunistic *Glomus spp*., may be the predominant method of forming associations. Where invaders are preferentially colonized by this subset of AMF, establishment advantages would be gained.

While plant-fungal host specificity has been described in various studies, it has been observed that some invaders are most likely fungal generalists (Richardson et al. 2000b, Miller 2008, Moora et al. 2011), a characteristic that may provide advantages for establishment and spread in a novel environment. For example, DSV has been observed to form associations with a greater variety of fungal colonizers relative to proximal native plants, and has also demonstrated greater fungal colonization densities (Smith et al. 2008, Bongard et al., unpublished data).

AMF pathogen protection

AMF species with the ability to protect their host plants from a variety of microbial pathogens have been described in the literature (Newsham et al. 1994, Borowicz 2001, Klironomos 2002, Pozo and Azćon-Aguilar 2007, van der Putten et al. 2007, Appoloni et al. 2008, Mogg et al. 2008, Krüger et al. 2009, Wehner et al. 2009). It has been suggested that plants associating with these highly beneficial AMF could

have defensive enzyme and chemical production induced in their roots by their my-corrhizal partners, and subsequent damage to roots of non-host plants may occur while host roots remain protected (Brundrett 2004, Bais et al. 2006). Disruption of protective AMF by invaders would increase the susceptibility of natives that typically benefit from this type of protection, while the invader may simultaneously benefit from enemy release provided in the novel environment (Keane and Crawley 2002). Possible differential exploitation of these AM fungi by invaders would also provide advantages in the novel environment.

In a study using meta-analysis of AMF and plant pathogen data gathered from papers published between 1970 and 1998, it was determined that AMF tended to decrease the harmful effects of fungal pathogens (Borowicz 2001), and were shown to reduce parasitic nematode *Meloidogyne incognita* damage in white clover *Trifolium repens* L. (Habte et al. 1999). In experiments testing three AMF *Glomus* species (*G. aggregatum*, *G. mosseae*, and *G. intraradices*) for their relative effectiveness in provid-ing protection against nematode infestation, *G. intraradices* was found to provide the most effective protection (Habte et al. 1999). The authors noted that colonization by *G. intraradices* in particular was enhanced in the presence of nematodes, and that nematodes did not have a significant influence on plants colonized by *G. intraradices*. *G. intraradices* has been described as a promiscuously associating generalist (Graham and Eissenstat 1994, Appoloni et al. 2008, Van Aarle et al. 2009).

Maherali and Klironomos (2007) found that increased Glomaceae richness in roots generally increased competition against pathogenic soil fungi in lab experiments. Shah et al. (2010) observed reduced Glomaceae representation in soils post invasion by two highly invasive European herbaceous species *Anthemis cotula* and *Conyza canaden-sis* (Asteraceae) using rhizosphere spore analysis, thus potentially resulting in the loss of AMF-induced pathogen protection to natives. As well, Vigo et al. (2000) observed that tomato plants *Lycopersicon esculentum* colonized by *Glomus mosseae* had reduced infec-tion by the soil pathogen *Phytophthora parasitica* relative to plants not colonized by *G. mosseae*, with results showing 39% fewer infection loci from the pathogen seven days after zoospore inoculation with *G. mosseae*. These findings suggest that one mechanism by which AMF protect against fungal pathogen infection is via efficient colonization of the plant infection points or loci, which are limited in number. As such, this hy-pothesis supports the necessity of combining AMF colonization density studies with those investigating AMF host specificity and AMF as agents of protection. Wright and Upadhyaya (1998) hypothesized that glomalin, a glycoprotein unique to AMF, is used for pathogen protection of the AMF hyphae that extend into the soil and facilitate nu-trient transfer. Sub-groups of AMF may also be activating defense mechanisms within the host plant: 'defensin', a cysteine-rich plant protein demonstrating anti-fungal ac-tivity was only upregulated in roots colonized by *G. intraradices* relative to roots that were colonized by *G. mosseae* (Wehner et al. 2009).

Though AMF have been shown to confer protection against pathogenic fungi, it has been observed that there could be synergistic and/or additive effects produced by different AMF species combinations (Gustafson and Casper 2006, Wehner et al. 2009).

Wehner et al. (2009) hypothesized that protection against pathogens could be due to the combined effects of increased access to nutrients provided by AMF, enhancement of plant defense mechanisms stimulated by AMF associations, and altered root architecture (increased lignin concentrations) as a response to AMF colonization. However, depending on the soil environment and other factors, AMF can function on a continuum from parasitism to facultative exploitation by their plant hosts (Brundrett 2004); hence environment nutrient load must also be considered. Because of the variability in the benefits provided by AM fungi, it is important to understand more about the dynamics of the local fungal community as a whole, not just AM fungal density or dominant species type.

In planning studies on invasion success, it would be useful to consider multiple effects attributable to simultaneous colonization by AMF as well as other fungi, plant traits such as root architecture, and variation in benefits derived from different AMF species, which may or may not afford unique chemical protection to colonized roots (Seifert et al. 2009). Having a more complete picture of the plant-fungal dynamics would offer a better view to plant invasion processes, as well as elucidate how AM fungal specialists interact with the general (non-AMF exclusive) fungal community in supporting plant diversity and competition.

Fungal pathogens and invader root exudates

Fungal pathogens

Some invasive plant species have demonstrated significantly reduced infection by fungal pathogens in their introduced range relative to their native range, an effect that may not be directly attributed to associations with AMF (Keane and Crawley 2002, Callaway et al. 2003, Mitchell and Power 2003). This could be explained by the Enemy Release hypothesis described previously. However, Eppinga et al. (2006) used mathematical modeling to account for distribution patterns and success of the invasive species *Ammophila arenaria* (marram grass or European beach grass) in California that resulted from *A. arenaria*'s ability to tolerate accumulation of local soil pathogens rather than enemy release. The authors hypothesized that while the accumulation of pathogens may initially limit invader abundance in the novel environment, it might feed back more negatively to the native plant community. As such, they concluded that in California *A. arenaria* accumulated local generalist pathogens that had a more negative effect on the native plant species than on *A. arenaria*. Alternatively, Blumenthal et al. (2009) examined the effects of fungal pathogens hosted by invaders in the US relative to the effects of the same plants in their native European ranges. Their results suggested that plants from resource-rich native environments (strong competitors) are more likely to experience release from pathogens in their non-native range than plants originating in low resource habitats (stress-tolerant plants). The authors hypothesized that successful invaders will possess high growth characteristics and demonstrate a lower pathogen burdens in their introduced range.

Root exudates

Plant root exudates are substances that alter the conditions of the rhizosphere by changing pH levels and mineral availability via desorption, as well as influencing the growth and interactions of microorganisms (Rovira 1969). Plant-plant interactions are often mediated by root exudates (Bais et al. 2006, Parepa et al. 2012). Allelopathy, the suppression of germination or growth of neighboring plants by the release of toxic secondary chemical compounds, has been explored as a pathway for successful plant invasion (Callaway and Aschehoug 2000, Inderjit 2005, Callaway and Howard 2007, Antunes et al. 2008, Douglass 2008, de Souza et al. 2010, Cantor et al. 2011). De Souza et al. (2010) used multiscale mathematical models to determine that plant invasion patterns and success based on allelopathy depends on both the nature of the local native plants in the invaded site, as well as the nature of the invader phytotoxins (root exudates). Both the celerity and success of invasion increase in the presence of weakly resistant and relatively homogeneous native plants and effective invader phytotoxins. For example, in the case of spotted knapweed *Centaurea maculosa* in the western US, invasion is particularly successful due to the phytotoxin (-)-catechin exuded from roots, which inhibits germination and triggers the death of root systems of susceptible native grass species (Bais et al. 2003). Allelopathy has also been suggested as a means of successful expansion of invaders in North America (Callaway et al. 1999, de Souza et al. 2010), including DSV (Milbrath 2010, Milbrath et al. 2011), as well as invaders in other countries such as Japanese knotweed *Fallopia japonica* in Wales (Hollingsworth and Bailey 2008) and Canada goldenrod *Solidago canadensis* in China (Zhang et al. 2009). Extracts of *S. canadensis* roots were also shown to significantly suppress the growth of soil oomycete and fungal pathogens *Pythium ultimum* and *Rhizoctonia solani* relative to extracts of common local native plants in culture experiments (Zhang et al. 2010).

Studies have shown that root exudates of invaders can decrease colonization by pathogenic fungi in their novel range (Bais et al. 2006, Mogg et al. 2008). However, the impacts of root pathogens can range from reduced plant growth and fecundity to total plant failure; the interaction of plant and pathogen depends upon the class of pathogen as well as the defense-relative-to-growth strategies of the plant. Strong competitors in resource rich environments tend to allocate resources to growth (large leaf area) rather than defense, but often cope relatively well with a high pathogen load, whereas stress-tolerant competitors that excel in resource poor environments tend to make use of defensive root exudates that keep pathogens in check (Seastedt 2009). Consequently, in resource rich novel environments with reduced plant-specific pathogens (release from enemies), invaders are able to become strong competitors, while in disturbed, resource poor novel environments, invaders can gain an advantage when their root compounds (anti-pathogenic or anti-feedant chemicals) are particularly effective against pathogens and herbivores.

Invader root exudates may disrupt AM fungal associations of nearby natives, thereby decreasing competitiveness (Vierheilig et al. 2003, Stinson et al. 2006), or even comprise chemicals that are both allelopathic toward neighbouring plants and disruptive to

AMF (Zhang et al. 2010, Hale et al. 2011). Zhang et al. (2007) demonstrated that root extracts of *S. canadensis* added to several native plants in China (*Echinochloa crusgalli*, *Kummerowia striata*, and *Ageratum conyzoides*) significantly inhibited AMF colonization by several *Glomus* species common to natives one year post invasion. Broeckling et al. (2008) observed that two model plant species, *Arabidopsis thaliana* (non-mycorrhizal Brassicaceae) and *Medicago truncatula* (AMF-associating), demonstrated the ability to maintain associations with local soil fungus communities consistently over time, while not being similarly capable of maintaining non-resident soil fungus associations. The authors compared the resident soil fungus phylotype community profiles between native and non-native plant conditioned soils (or soils conditioned with their root exudates) using real-time PCR. The presence of non-native plants growing in soils, or their root exudates alone, influenced the fungal community by both positively and negatively impacting the relative abundance of individual phylotypes, while the native plants (or their root exudates) maintained consistent fungal community profiles over multiple plant generations. Accordingly, where an invader brings fungi new to the introduced range, natives dependent on resident fungal communities that are prone to disruption would be disadvantaged. As such, root exudates may serve as a selective agent enabling regulation of the fungal community in the rhizosphere (Broeckling et al. 2008). Roots of common milkweed *Asclepias syriaca* (in the same family as DSV, Asclepiadaceae) gained significant biomass when grown in DSV-conditioned soil relative to plants grown in uninvaded soils (DiTommaso 2006). This was attributed to a possible escape from fungal pathogens induced by the phenthorindolizadine alkaloid chemical (–)-antofine exuded by DSV roots (Mogg et al. 2008). DSV has demonstrated antifungal activity against plant pathogenic yeast-like and filamentous fungi, as well as broad-host-range plant pathogens such as *Fusarium spp*. (Mogg et al. 2008). These findings suggest that there is a strong likelihood that fungal communities associating certain aggressive invaders will differ from those associating with native plants that do not demonstrate similar phyto-chemistry, resulting in native community disturbance.

Stinson et al. (2006) reported that the mutualistic associations between native tree seedlings and mycorrhizal fungi were disrupted by the non-mycorrhizal European native garlic mustard *Alliaria petiolata*, resulting in decreased seedling survival. They found that hardwood seedlings grown in garlic mustard-conditioned soil showed significantly reduced AMF colonization of roots and slower growth than those grown in non-garlic mustard conditioned soil, based on lab experiments conducted in Waterloo, Ontario. The authors attributed the ability of *A. petiolata* to dampen seedling growth of AMF-dependent competitors to the glucosinolate root exudates manufactured by these members of the Brassicaceae family. These findings were supported by Callaway et al. (2008), who found that the anti-fungal influence of *A. petiolata* had far greater inhibitory effects in North America than in their native European ranges. Root exudates that are relatively harmless to resistant mycorrhizal symbionts in the home range as a result of adaptation, may therefore be disruptive to native mutualists in the introduced range, and indirectly suppress the plants that rely on them (Callaway et al. 2004).

Some plant root exudates have also been shown to increase the signaling pathways attracting AM fungi, and consequently increase hyphal growth and colonization by these beneficial symbionts (Vierheilig 2004, Akiyama et al. 2005, Greipsson and DiTommaso 2006). A net increase in fungal biomass was observed in the experiments by Broeckling et al. (2008) when non-resident root exudates were added to resident plant treatments (*Arabidopsis thaliana* and *Medicago truncatula*), which the authors suggested could be attributed to increased production of signaling compounds in the roots triggered by the root exudates. Where invaders are selectively able to benefit from increased AMF colonization due to unique signaling compounds, they will experience advantages relative to proximal native plants, particularly in moisture- or P-limited environments.

Prevailing plant-fungal post invasion responses are listed in Table 1.

Table 1. Alternative plant-fungal strategies of invasive plants in a novel range. Shifts in soil fungi will vary in the plant rhizosphere as invasion progresses, depending on the nature of the fungi introduced by or associating with the invader, and the root exudates of the invader. Native versus invader responses are suggested.

Increase in AM fungal diversity and abundance	Decrease in AM fungal diversity and abundance	No change in fungal community	Main references
Invader has caused fungal shift or brought novel AMF, increasing AMF diversity/abundance, potentially resulting in increased nutrient uptake or pathogen protection Natives may benefit if host specificity is either suitable or not a factor	Invader introduced a novel AMF species into the soil environment that is unable to colonize natives, but becomes pervasive Invader sustains decreased AMF colonization density or richness, while simultaneously increasing potential fungal pathogen load in rhizosphere	Invader is able to form associations with existing AMF but experiences escape from resident pathogens in novel environment Invader is a fungal generalist that associates with a variety of local AMF without causing significant disruption or change to fungal community	Appoloni et al. 2008, Bastias et al. 2007, Batten et al. 2006, Beckstead and Parker 2003, Callaway et al. 2003, Graham and Eissenstat 1994, Hawkes et al. 2006, Keene and Crawley 2002, Meinhardt and Gehring 2012, Mogg et al. 2008, Moora et al. 2011, Mummey and Rillig 2006, Richardson et al. 2000b, Van Aarle et al. 2009
Increased signaling compounds (root exudates) added to rhizosphere by Invader enables increased AM and general fungal colonization Benefits to natives vary	Invader releases toxins that decrease general and AM fungal persistence in the rhizosphere; allelopathy; possibility of decreased pathogen protection and/or nutrient/moisture uptake in proximal natives	Invaders capitalizes on alternate strategies to dominate the system such as allelopathy, ability to compete in resource-depleted or disturbed environments more successfully than natives	Antunes et al. 2008, Bais et al. 2003, Broeckling et al. 2008, Callaway et al. 2004, Callaway et al. 2008, Douglass 2008, Parniske 2008, Pozo and Azcón-Aguilar 2007, Stinson et al. 2006
Reduced fungal pathogens occupying root infection loci due to infusion of novel chemicals by Invader; AMF are able to take up residence in newly available loci of Invader (possibly natives)	Invader is able to form associations with existing AMF via hyphal fragments or anastamoses, where natives are not and such AMF species become pervasive in the rhizosphere	Increased fungal pathogens occupying infection loci cause reduced AMF colonization – net effect is decrease in symbionts but increase in commensalists and pathogens	Biermann and Linderman 1983, Callaway et al. 2003, Daniell et al. 2001, Giovannetti et al. 1999, Helgason et al. 2002, Mogg et al. 2008, Vigo et al. 2000

AMF and invader root exudate interaction studies

Although most authors have focused their research on either the benefits/anti-pathogenic properties of AMF or the benefits associated with invader plant root exudates independently, there are some examples of much needed interaction studies. Newsham et al. (1994) explored the relative effects ascribed to both AMF and fungal pathogens (potentially controlled by either AMF or root exudates) in the field, and determined how the two groups of fungi interacted to determine plant response and fitness. They found that while AMF colonization of winter annual grass *Vulpia ciliata* ssp. *ambigua* was reduced by the application of anti-fungicides, the root, shoot, total plant biomass, and phosphorus inflows were unaffected. The authors hypothesized that this somewhat unexpected finding arose due to the fungicidal depression of pathogenic root-inhibiting fungi such as *Fusarium oxysporum* or *Embellisia chlamydospora* isolated in the roots of *V. ciliata* that might otherwise be compromising plant growth and fecundity. Newsham et al. (1994) concluded by suggesting that the main benefit supplied by arbuscular mycorrhizal fungi to the plant was apparently protection from pathogenic attack, not phosphorus uptake. Significant reductions in fecundity resulted from the root pathogen associations in *V. ciliata*, though the infections were otherwise asymptomatic, presenting a specialized case of plant-pathogen interaction. The authors postulated that there was an interaction effect between the AMF and pathogenic fungi on some level, resulting in the ostensibly asymptomatic nature of the infection by pathogens. Observations of both sets of fungi in an invaded environment provide insights as to simultaneous shifts that could be instigated by exposure to invader root exudates or alterations to AMF initiated by the invader via diverse strategies.

In a study by Klironomos (2002), local fungal pathogens demonstrated a negative impact on growth and spread of rare plants when grown in local or home soil over time, while invasive plants demonstrated net positive growth when grown in their own local soil (and associated fungi), suggesting reduced susceptibility to local pathogens over time. The effects of AMF, however, did not differ between the rare and invasive plant groups. For both groups (native and invaders), AMF isolated from soil with a history of the same plant species had a more positive effect on plant growth than fungi isolated from a different plant host. With both groups of plants, inoculations using AM fungi from foreign plants rarely resulted in significant growth depressions. These findings suggest that most plants can potentially experience positive feedback with AMF communities, but this effect is not realized unless negative feedback resulting from pathogens is limited. This arises as a consequence of the differential effect of pathogenic fungi on invasive plants relative to rare plants, rather than a differential response to the AMF. When introduced to previously uncultured soil at low densities, plants that ultimately achieve high abundance do not seem to accumulate species-specific pathogens at the same rate as plants that remain in low abundance (Klironomos 2002). Pathogen accumulation in highly successful invasive plant species tends to happen more slowly than that of natives demonstrating low abundances due to negative feedback mecha-

nisms, including dense colonization by microbial pathogens (Bever 2002, Klironomos 2002, Mitchell and Power 2003, Inderjit and van der Putten 2010).

Studies investigating simultaneous shifts in both the general fungal community and AMF would provide clarification as to the role of each subsequent to plant invasion. In doing so, they would elucidate the combined mechanisms of invader root exudates invoking pathogen reduction via allelopathy, as well as the response of altered or introduced AMF subsequent to invasion. While other interaction study methods have been suggested, including use of microbial microarrays and detailed assays of root exudates to differentiate phytochemicals that signal AMF hyphenation and infection from those targeting disruption of rhizosphere pathogens (Bais et al. 2006), the use of molecular alternatives such as T-RFLP and other fingerprinting methods could provide the same result at a reduced effort. Primers targeting the general fungal community differentially from primers targeting AMF produce both a proxy for the rhizosphere response to allelopathic chemicals in invaders roots (shifts in general fungal community), as well as directly observable shifts in the AMF community.

Conclusions and future directions

It is necessary to design experiments that can account for the multiplicity of events taking place in local soil environments post invasion to gain a greater understanding of the fungal-chemical interactions in the rhizosphere (local scale), and within the ecosystem (regional scale) as the plant invasion progresses. Investigating fungal communities (both general and AMF) in pre- and post-invaded sites over time would be useful in determining how each factor, such as the state of AMF or non-AM fungi (comprised of fungal pathogens, commensalists, and mutualists), as well as the influence of invader root exudates or the interaction of all of these factors, might contribute to invasion success. For example, if amplified AMF colonization of invaders via increased signaling compounds were to confer a highly successful invasion pathway relative to the anti-pathogenic effects of invader root exudates, it would suggest that AMF inoculation may not be an effective restoration strategy. If the opposite were true, inoculation of a restored site with local AM fungi might be useful for the establishment of select re-introduced native plants, even where residual invader root exudates persist in the soil.

Investigations pairing a highly successful invader and a native plant species that are both known for producing allelopathic root exudates, along with non-allelopathic natives would be useful for AMF and general fungal phylotype comparisons using molecular analyses such as T-RFLP. The terminal restriction fragment analyses would enable comparison of the variation in both general and AM fungal communities, with the variable TRFs serving as a proxy for different fungal phylotypes associating with the plant groups. Where TRF data show a tendency for the general fungi associating with allelopathic plants to differ from the non-allelopathic plants in both natives and invaders, but not similarly for the AMF community, allelopathy is then recognized as a factor rather than the various scenarios linked to benefits associated

with increased or altered AMF post invasion. Where pathogenic fungi are being depressed or are well tolerated in invader plant roots but AM fungi are not similarly altered, it suggests that natives growing in an invaded patch may be susceptible to higher pathogen loads relative to natives that are unexposed, supporting the hypotheses of both Eppinga et al. (2006) and Klironomos (2002). Alternatively, natives may be more negatively affected by specific pathogen introductions associated with an invader than the invader itself. This effect will likely vary considerably for different native plant species, and individual investigations that are relevant to the invasion site would be informative. These types of molecular investigations also allow for comparisons of AMF diversity and density changes relative to those occurring in the general fungal community (including pathogens) as invasions progress. It would be expected that the general fungal community would be less diverse/abundant in invader roots relative to natives if pathogenic fungi are being depressed or virtually eliminated by phytochemicals (root exudates) in invaders that are not present in natives. As well, looking at the response of AM fungi relative to responses in the general fungal community would also potentially reveal the relative role of AMF as invasion progresses (Hawkes et al. 2006, Mummey and Rillig 2006).

In considering alteration of soil fungal communities by invasive plants, differential fungal association dynamics need to be quantified and compared, a process that is well supported by molecular investigation methods. Comparing both AMF and general fungal community fingerprints within a variety of native plant roots in pre- and post-invaded sites will provide insight as to whether shifts in AMF or the general fungal community (or both) are facilitating the invasion process. Molecular fingerprinting techniques could also be used to investigate variation in the diversity and density of fungal colonization during different stages of invader succession to determine which species are supporting the establishment and progression of invaders, particularly in light of the fact that delayed proliferation in time and space (due to Allee effect) has been observed in many invasive plant species.

Acknowledgments

References

Ailstock MS, Norman CM, Bushmann PJ (2001) Common reed *Phragmites australis*: control and effects upon biodiversity in freshwater nontidal wetlands. Restoration Ecology 9 (1): 49–59. doi: 10.1046/j.1526-100x.2001.009001049.x

Akiyama K, Matsuzaki K, Hayashi H (2005) Plant sesquiterpenes induce hyphal branching in arbuscular mycorrhizal fungi. Nature 435 (9): 824–827. doi: 10.1038/nature03608

Antunes PM, Miller J, Carvalho LM, Klironomos JM, Newman JA (2008) Even after death the endophytic fungus of *Schedonorus phoenix* reduces the arbuscular mycorrhizas of other plants. Functional Ecology 22: 912–918. doi: 10.1111/j.1365-2435.2008.01432.x

Appoloni S, Lekberg Y, Tercek MT, Zabinski CA, Redecker D (2008) Molecular community analysis of arbuscular mycorrhizal fungi in roots of geothermal soils in Yellowstone National Park (USA). Microbial Ecology 56: 649–659. doi: 10.1007/s00248-008-9384-9

Bais HP, Vepachedu R, Gilroy S, Callaway RM, Vivanco JM (2003) Allelopathy and exotic plant invasion: From molecules and genes to species interactions. Science 301:1377–1380. http://www.jstor.org/stable/3835029

Bais HP, Weir TL, Perry LG, Gilroy S, Vivanco JM (2006) The role of root exudates in rhizosphere interactions with plants and other organisms. Annual Review of Plant Biology 57: 233–266. doi: 10.1146/annurev.arplant.57.032905.105159

Bastias BA, Anderson IC, Xu ZH, Cairney JWG (2007) RNA and DNA- based profiling of soil fungal communities in a native Australian eucalypt forest and adjacent *Pinus eliotti* plantation. Soil Biology and Biochemistry 39: 3108–3114. doi: 10.1016/j.soilbio.2007.06.022

Batten KM, Scow KM, Davies KF, Harrison SP (2006) Two invasive plants alter soil microbial community composition in serpentine grasslands. Biological Invasions 8: 217–230. doi: 10.1007/s10530-004-3856-8

Baylis GTS (1975) The magnolioid mycorrhiza and mycotrophy in root systems derived from it. In: F. Sanders E, Mosse B, Tinker PB (Eds) Endomycorrhizas. Academic Press (New York), 373–389.

Beckstead J, Parker IM (2003) Invasiveness of *Ammophlla arenaria*: release from soil-borne pathogens? Ecology 84 (11): 2824–2831. http://www.jstor.org/stable/3449954

Bever JD (1999) Dynamics within mutualism and the maintenance of diversity: inference from a model of interguild frequency dependence. Ecology Letters 2: 52–61. doi: 10.1046/j.1461-0248.1999.21050.x

Bever JD (2002) Negative feedback within a mutualism: host-specific growth of mycorrhizal fungi reduces plant benefit. The Proceedings of the Royal Society of London B. 269:2595-2601. doi: 10.1098/rspb.2002.2162

Bever JD, Richardson SC, Lawrence BM, Holmes J, Watson M (2009) Preferential allocation to beneficial symbiont with spatial structure maintains mycorrhizal mutualism. Ecology Letters 12: 13–21. doi: 10.1098/rspb.2002.2162

Bianciotto V, Bonfante P (2002) Arbuscular mycorrhizal fungi: a specialised niche for rhizospheric and endocellular bacteria. Antonie van Leeuwenhoek 81: 365–371. doi: 10.1023/A:1020544919072

Biermann B, Linderman RG (1983) Use of vesicular-arbuscular mycorrhizal roots, intraradical vesicles and extraradical vesicles as inoculum. New Phytologist 95: 97–105. http://www.jstor.org/stable/2434175

Blumenthal D, Mitchell CE, Pyšek P, Jarošík V (2009) Synergy between pathogen release and resource availability in plant invasion. Proceedings of the National Academy of Science U.S.A. 106: 7899–7904. doi: 10.1073/pnas.0812607106

Bonfante P (2003) Plants, mycorrhizal fungi and endobacteria: a dialogue among cells and genomes. Biological Bulletin 204 (2): 215–220. http://www.biolbull.org/content/204/2/215.full, doi: 10.2307/1543562

Borowicz VA (2001) Do arbuscular mycorrhizal fungi alter plant-pathogen relations? Ecology 82 (11): 3057–3068. http://www.jstor.org/stable/2679834

Broeckling CD, Broz AK, Bergelson J, Manter DK, Vivanco JM (2008) Root exudates regulate soil fungal community composition and diversity. Applied and Environmental Microbiology 74 (3): 738–744. doi: 10.1128/AEM.02188-07

Brundrett M (2004) Diversity and classification of mycorrhizal associations. Biological Review 79: 473–495. doi: 10.1017/S1464793103006316

Brundrett MC (2008) Mycorrhizal associations: the web resource. http://mycorrhizas.info/info.html [accessed January 2012]

Brundrett MC (2009) Mycorrhizal associations and other means of nutrition of vascular plants: understanding the global diversity of host plants by resolving conflicting information and developing reliable means of diagnosis. Plant Soil 320:37–77. doi: 10.1007/s11104-008-9877-9

Callaway RM, Aschehoug ET (2000) Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. Science 290 (5491): 521–523. doi: 10.1126/science.290.5491.521

Callaway RM, Cipollini D, Barto K, Thelen GC, Hallett SG, Prati D, Stinson K, Klironomos J (2008) Novel weapons: invasive plant suppresses fungal mutualists in America but not in its native Europe. Ecology 89 (4): 1043–1055. http://www.jstor.org/stable/27651643, doi: 10.1890/07-0370.1

Callaway RM, DeLuca TH, Belliveau WM (1999) Biological-control herbivores may increase competitive ability of the noxious weed *Centaurea maculosa*. Ecology 80 (4): 1196–1201.

Callaway RM, Howard TG (2007) Competitive networks, indirect interactions, and allelopathy: a microbial viewpoint on plant communities. Progress in Botany 68: 317–335. doi: 10.1007/978-3-540-36832-8_14

Callaway RM, Mahall BE, Wicks C, Pankey J, Zabinski C (2003) Soil fungi and the effects of an invasive forb on grasses: neighbor identity matters. Ecology 84(1): 129–135. http://www.jstor.org/stable/3108003, doi: 10.1890/0012-9658(2003)084[0129:SFATEO]2.0.CO;2

Callaway RM, Thelen GC, Rodriguez A, Holben WE (2004) Soil biota and exotic plant invasion. Nature 427: 731–733. doi: 10.1038/nature02322

Cantor A, Hale A, Aaron J, Traw MB, Kalisz S (2011) Low allelochemical concentrations detected in garlic mustard-invaded forest soils inhibit fungal growth and AMF spore germination. Biological Invasions 13: 3015–3025. doi: 10.1007/s10530-011-9986-x

Cappuccino N (2004) Allee effect in an invasive alien plant, pale swallow-wort *Vincetoxicum rossicum* (Asclepiadaceae) OIKOS 106: 3–8. doi: 10.1111/j.0030-1299.2004.12863.x

Crawley MJ, Brown SL, Heard MS, Edwards GR (1999) Invasion-resistance in experimental grassland communities: species richness or species identity? Ecology Letters 2 (3): 140–148. doi: 10.1046/j.1461-0248.1999.00056.x

Curlevski NJA, Xu Z, Anderson IC, Cairney JWG (2010) Converting Australian tropical rainforest to native Araucariaceae plantations alters soil fungal communities. Soil Biology & Biochemistry 42: 14–20. doi: 10.1016/j.soilbio.2009.08.001

Daniell TJ, Husband R, Fitter AH, Young JPW (2001) Molecular diversity of arbuscular mycorrhizal fungi colonising arable crops. FEMS Microbiology Ecology 36: 203–209. doi: 10.1111/j.1574-6941.2001.tb00841.x

de Souza DR, Martins ML, CarmoFMS (2010) A multiscale model for plant invasion through al-lelopathic suppression. Biological Invasions 12: 1543–1555. doi: 10.1007/s10530-009-9567-4

Debellis T, Widden P (2006) Diversity of the small subunit ribosomal RNA gene of the ar-buscular mycorrhizal fungi colonizing *Clintonia borealis* from a mixed-wood boreal forest. Microbial Ecology 58: 225–235. doi: 10.1111/j.1574-6941.2006.00150.x

DiTommaso A (2006) How to deal with two increasingly problematic exotic vines in NY State? The Swallow-worts: a multi-disciplinary approach http://www.css.cornell.edu/WeedEco [accessed May 22, 2006]

Douglass C (2008) The roles of allelopathy, morphology and genetic diversity in the invasion of swallow-wort species in New York State http://hdl.handle.net/1813/10367

Duponnois R, Colombeta A, Hienb V, Thioulouse J (2005) The mycorrhizal fungus *Glomus intraradices* and rock phosphate amendment influence plant growth and microbial activity in the rhizosphere of *Acacia holosericea*. Soil Biology & Biochemistry 37: 1460–1468. doi: 10.1016/j.soilbio.2004.09.016

Egerton-Warburton LM, Querejeta JI, Allen MF (2007) Common mycorrhizal networks pro-vide a potential pathway for the transfer of hydraulically lifted water between plants. Jour-nal of Experimental Botany 1–11. doi: 10.1093/jxb/erm009

Eppinga MB, Rietkerk M, Dekker SC, De Ruiter PC (2006) Accumulation of local patho-gens: a new hypothesis to explain exotic plant invasions. OIKOS 114 (1): 168–176. doi: 10.2307/40234860

Fumanal B, Plenchette C, Chauvel B, Bretagnolle F (2006) Which role can arbuscular mycor-rhizal fungi play in the facilitation of *Ambrosia artemisiifolia* L. invasion in France? Mycor-rhiza 17:25–35. doi: 10.1007/s00572-006-0078-1

Giovannetti M, Azzolini D, Citernesi AS (1999) Anastomosis formation and nuclear and pro-toplasmic exchange in arbuscular mycorrhizal fungi. Applied and Environmental Microbi-ology 65 (12): 5571–5575. http://aem.asm.org/content/65/12/5571#ref-list-1

Gogoi P, Singh RK (2011) Differential effect of some arbuscular mycorrhizal fungi on growth of *Piper longum* L. (Piperaceae). Indian Journal of Science and Technology 4(2): 119–125. http://www.indjst.org/archive/vol.4.issue.2/feb11purnima-11.pdf

Graham JH, Eissenstat DM (1994) Host genotype and the formation and function of VA my-corrhizae. Plant and Soil 159: 179–185. doi: 10.1007/BF00000107

Greipsson S, Ditommaso A (2006) Invasive non-native plants alter the occurrence of arbuscular mycorrhizal fungi and benefit from this association. Ecological Restoration 24 (4): 236–241. http://weedecology.css.cornell.edu/pubs/Published%20Ecol.%20Restoration%20 24%20236-241%202006.pdf

Gustafson DJ, Casper BB (2006) Differential host plant performance as a function of soil arbuscular mycorrhizal fungal communities: experimentally manipulating co-occurring *Glomus* species. Plant Ecology 183: 257–263. doi: 10.1007/s11258-005-9037-8

Habte M, Zhang VC, Schmitt DP (1999) Effectiveness of *Glomus* species in protecting white clover against nematode damage. Canadian Journal of Botany 77 (1): 135–139. doi: 10.1007/BF00016287

Hale AN, Tonsor SJ, Kalisz S (2011) Testing the mutualism disruption hypothesis: physio-logical mechanisms for invasion of intact perennial plant communities. Ecosphere 2 (10): 1–15. doi: 10.1890/ES11-00136.1

Hallett SG (2006) Dislocation from coevolved relationships: a unifying theory for plant invasion and naturalization? Weed Science 54: 282–290. http://www.jstor.org/stable/4539389

Hart MM, Reader RJ, Klironomos JN (2003) Plant coexistence mediated by arbuscular mycorrhizal fungi. TRENDS in Ecology and Evolution 18 (8): 418–423. doi: 10.1016/S0169-5347(03)00127-7

Hawkes CV, Belnap J, D'Antonio C, Firestone MK (2006) Arbuscular mycorrhizal assemblages in native plant roots change in the presence of invasive exotic grasses. Plant and Soil 281: 369–380. doi: 10.1007/s11104-005-4826-3

Helgason T, Merryweather JW, Denison J, Wilson P, Young JPW, Fitter AH (2002) Selectivity and functional diversity in arbuscular mycorrhizas of co-occurring fungi and plants from a temperate deciduous woodland. Journal of Ecology 90: 371–384. http://www.jstor.org/stable/3072140 doi: 10.1046/j.1365-2745.2001.00674.x

Hetrick BAD, Wilson GWT, Todd TC (1992) Relationships of mycorrhizal symbiosis, rooting strategy, and phenology among tallgrass prairie forbs. Canadian Journal of Botany 70: 1521–1528. doi: 10.1139/b92-191

Hollingsworth ML, Bailey JP (2008) Evidence for massive clonal growth in the invasive weed Fallopia japonica (Japanese Knotweed). Botanical Journal of the Linnean Society 133 (4): 4463–4472. doi: 10.1111/j.1095-8339.2000.tb01589.x

Inderjit (2005) Soil microorganisms: An important determinant of allelopathic activity. Plant and Soil 274: 227–236. doi: 10.1007/s11104-004-0159-x

Inderjit, van der Putten WH (2010) Impacts of soil microbial communities on exotic plant invasions. Trends in Ecology and Evolution 25 (9): 512–519. doi: 10.1016/j.tree.2010.06.006

Inderjit, Seastedt TR, Callaway RM, Pollock JL, Kaur J (2008) Allelopathy and plant invasions: traditional, congeneric, and bio-geographical approaches. Biological Invasions 10: 875–890. doi 10.1007/s10530-008-9239-9

Johnson NC, Graham JH, Smith FA (1997) Functioning of mycorrhizal associations along the mutualism-parasitism continuum. New Phytologist 135 (4): 575–586. http://www.jstor.org/stable/2558989, doi: 10.1046/j.1469-8137.1997.00729.x

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends in Ecology & Evolution 17 (4): 164–170. doi: 10.1016/S0169-5347(02)02499-0

Klironomos JN (2000) Host-specificity and functional diversity among arbuscular mycorrhizal fungi. In: Microbial Biosystems: New Frontiers In: Proceedings of the 8th International Symposium on Microbial Ecology In: Bell CR, Brylinsky M, Johnson-Green P (Eds) Atlantic Canada Society for Microbial Ecology (Halifax), 845–851.

Klironomos JN (2002) Feedback with soil biota contributes to plant rarity and invasiveness in communities. Nature 417: 67–70. doi: 10.1038/417067a

Klironomos JN (2003) Variation in plant response to native and exotic arbuscular mycorrhizal fungi. Ecology 84(9): 2292–2301. http://www.jstor.org/stable/3450135, doi: 10.1890/02-0413

Kourtev PS, Ehrenfeld JG, Haggblom M (2002) Exotic plant species alter the microbial community structure and function in the soil. Ecology 83 (11): 3152–3166. http://www.jstor.org/stable/3071850, doi: 10.1890/0012-9658(2002)083[3152:EPSATM]2.0.CO;2

Krüger M, Stockinger H, Krüger C, Schüßler A (2009) DNA-based species level detection of Glomeromycota: one PCR primer set for all arbuscular mycorrhizal fungi. New Phytologist 183: 212–223. doi: 10.1111/j.1469-8137.2009.02835.x

Krueger-Mangold J, Sheley RL, Roos BD (2002) Maintaining plant community diversity in a waterfowl production area by controlling Canada thistle (*Cirsium arvense*) using glyphosate. Weed Technology 16 (2): 457–463. http://www.jstor.org/stable/3989575, doi: 10.1614/0890-037X(2002)016[0457:MPCDIA]2.0.CO;2

Liang J, Gu Y, Xiao M, Chen J, Li B (2004) The history of *Solidago canadensis* invasion and the development of its mycorrhizal associations in newly-reclaimed land. Functional Plant Biology 31: 979–986. doi: 10.1071/FP04061

Lorenz RJ (1991) Leafy spurge research and education programs in the Great Plains: The leafy spurge task force. Proceedings of the Great Plains Agricultural Council June 4-6/1991: 151–154.

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications 10: 689–710. http://www.jstor.org/stable/2641039, doi: 10.1890/1051-0761(2000)010[0689:BICEGC]2.0.CO;2

Maherali H, Klironomos JN (2007) Influence of phylogeny on fungal community assembly and ecosystem functioning. Science 316: 1746–1748. doi: 10.1126/science.1143082

Maldonado-Mendoza IE, Dewbre GR, Harrison MJ (2001) A phosphate transporter gene from the extra-radical mycelium of an arbuscular mycorrhizal fungus *Glomus intraradices* is regulated in response to phosphate in the environment. MPMI 14 (10): 1140–1148. http://apsjournals.apsnet.org/doi/pdf/10.1094/MPMI.2001.14.10.1149, doi: 10.1094/MPMI.2001.14.10.1140

Meekins JF, McCarthy BC (1999) Competitive ability of *Alliaria petiolata* (garlic mustard Brassicaceae), an invasive, non-indigenous forest herb. International Journal of Plant Science 160: 743–752. doi: 10.1086/314156

Meinhardt KA, Gehring CA (2012) Disrupting mycorrhizal mutualisms: a potential mechanism by which exotic tamarisk outcompetes native cottonwoods. Ecological Applications 22 (2): 532–549. doi: 10.1890/11-1247.1

Milbrath LR (2010) Phytophagous arthropods of invasive swallow-wort vines (*Vincetoxicum* spp.) in New York. Environmental Entomology 39 (1): 68–78. doi: 10.1603/EN09116

Milbrath L, Biazzo J, Gibson D (2011) Research update swallow-wort biological control program, USDA-ARS Ithaca, NY. USDA Agricultural Research Service. http://www.ars.usda.gov/naa/ithaca/BioIPM

Miller G (2008) Dog-strangling vine (*Cynanchum rossicum*): review of distribution, ecology, and control. Rouge Park Report.

Mitchell CE, Power AG (2003) Release of invasive plants from fungal and viral pathogens. Nature 421: 625–627. doi: 10.1038/nature01317

Mogg C, Petit P, Cappuccino N, Durst T, McKague C, Foster M, Yack JE, Arnason JT, Smith ML (2008) Tests of the antibiotic properties of the invasive vine *Vincetoxicum rossicum* against bacteria, fungi and insects. Biochemical Systematics and Ecology 36: 383–391. doi: 10.1016/j.bse.2008.01.001

Moora M, Zobel M (1996) Effect of arbuscular mycorrhiza on inter- and intraspecific competition of two grassland species. Oecologia 108: 79–84. http://www.jstor.org/stable/4221389, doi: 10.1007/BF00333217

Moora M, Berger S, Davison J, Öpik M, Bommarco R, Bruelheide H, Kühn I, Kunin WE, Metsis M, Rortais A, Vanatoa A, Vanatoa E, Stout JC, Truusa M, Westphal C, Zobel M, Walther G-R (2011) Alien plants associate with widespread generalist arbuscular mycorrhizal fungal taxa: evidence from a continental-scale study using massively parallel 454 sequencing. Journal of Biogeography 38: 1305–1317. doi: 10.1111/j.1365-2699.2011.02478.x

Mummey DL, Rillig MC, Holben WE (2005) Neighboring plant influences on arbuscular mycorrhizal fungal community composition as assessed by T-RFLP analysis. Plant and Soil 271: 83–90. doi: 10.1007/s11104-004-2066-6

Mummey DL, Rillig MC (2006) The invasive plant species *Centaurea maculosa* alters arbuscular mycorrhizal fungal communities in the field. Plant Soil 288: 81–90. doi: 10.1007/s11104-006-9091-6

Newsham KK, Fitter AH Watkinson AR (1994) Root pathogenic and arbuscular mycorrhizal fungi determine fecundity of asymptomatic plants in the field. Journal of Ecology 82: 805–814. http://www.jstor.org/stable/2261445

Oehl F, Sieverding E, Ineichen K, Mäder P, Boller T, Wiemken A (2003) Impact of land use intensity on the species diversity of arbuscular mycorrhizal fungi in agroecosystems of Central Europe. Applied and Environmental Microbiology 69 (5): 2816–2824. doi: 10.1128/AEM.69.5.2816-2824.2003

Parepa M, Schaffner U, Bossdorf O (2012) Sources and modes of action of invasive knotweed allelopathy: the effects of leaf litter and trained soil on the germination and growth of native plants NeoBiota 13: 15–30. doi: 10.3897/neobiota.13.3039

Parniske M (2008) Arbuscular mycorrhiza: the mother of plant root endosymbioses. Nature Reviews Microbiology 6: 763–775. doi: 10.1038/nrmicro1987

Pozo MJ, Azcón-Aguilar C (2007) Unraveling mycorrhiza-induced resistance. Current Opinion in Plant Biology 10: 393–398. doi: 10.1016/j.pbi.2007.05.004

Quinn G (2011) Mycorrhizae help feed your plants. Fine Gardening 96: 82. http://www.finegardening.com/how-to/articles/mycorrhizae-help-feed-your-plants.aspx?nterms=74874

Reinhart KO, Callaway RM (2006) Soil biota and invasive plants. New Phytologist 170: 445–457. doi: 10.1111/j.1469-8137.2006.01715.x

Rejmánek M, Richardson DM (1996) What attributes make some plant species more invasive? Ecology 77: 1655–1660. doi: 10.2307/2265768

Richardson DM, Pysek P, Rejmanek M, Barbour MG, Panetta FD, West CJ (2000a) Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions 6 (2): 93–107. http://jstor.org/stable/2673320, doi: 10.1046/j.1472-4642.2000.00083.x

Richardson DM, Allsopp N, D'Antonio CM, Milton SJ, Rejmanek M (2000b) Plant invasions-the role of mutualisms. Biological Reviews 75: 65–93. doi: 10.1111/j.1469-185X.1999.tb00041.x

Rovira A (1969) Plant root exudates. The Botanical Review 35 (1): 35–57. doi: 10.1007/BF02859887

Seastedt T (2009) Traits of plant invaders. Nature 459: 783–785. doi: 10.1038/459783a

Seifert EK, Bever JD, Maron JL (2009) Evidence for the evolution of reduced mycorrhizal dependence during plant invasion. Ecology 90 (4): 1055–1062. http://www.jstor.org/stable/25592592, doi: 10.1890/08-0419.1

Selosse MA, Richard F, He X, Simard SW (2006) Mycorrhizal networks: des liaisons dangereuses? Trends in Ecology and Evolution 21 (11): 621–28. doi: 10.1016/j.tree.2006.07.003

Shah MA, Reshi ZA, Rasool N (2010) Plant invasions induce a shift in Glomalean spore diversity. Tropical Ecology 51 (2S): 317–323. http://www.tropecol.com/pdf/open/PDF_51_2S/J-03.pdf

Sieverding E (1991) Vesicular–arbuscular mycorrhiza management in tropical agrosystems. Deutsche Gesellschaft Technische Zusammenarbeit (GTZ). GmbH Eschborn: 371.

Simberloff D, Von Holle B (1999) Positive interactions of nonindigenous species: invasional meltdown? Biological Invasions 1: 21–32. http://vonholle.cos.ucf.edu/pubs/Simberloff_VonHolle1999.pdf, doi: 10.1023/A:1010086329619

Smith L, DiTommaso A, Lehmann J, Greipsson S (2008) Effects of arbuscular mycorrhizal fungi on the exotic invasive vine pale swallow-wort (*Vincetoxicum rossicum*). Invasive Plant Science and Management 1: 142–152. doi: 10.1614/IPSM-07-010.1

Smith SE, Read DJ (1997) Mycorrhizal symbiosis. Academic Press (San Diego and London): 605.

Stinson KA, Campbell SA, Powell JR, Wolfe BE, Callaway RM, Thelen GC, Hallett SG, Prati D, Klironomos JN (2006) Invasive plant suppresses the growth of native tree seedlings by disrupting belowground mutualisms. PLoS Biology 4 (5): 727–731. doi: 10.1371/journal.pbio.0040140

Sun Z-K, He W-M (2010) Evidence for enhanced mutualism hypothesis: *Solidago canadensis* plants from regular soils perform better. Plos One 5 (11) e15418:1–5. doi: 10.1371/journal.pone.0015418

Tilman D, Downing JA (1994) Biodiversity and stability in grasslands. Nature 367: 363–365. doi: 10.1038/367363a0

Van Aarle IM, de la Providencia IE, Rouhier H, Declerck S (2009) *Glomus intraradices* shows an opportunistic behaviour towards nutrient acquisition and actively re-allocates phosphorus. Manuscript. Université catholique de Louvain (UCL) (Belgium).

van der Heijden MGA, Boiler T, Wiemken A, Sanders IR (1998) Different arbuscular mycorrhizal fungal species are potential determinants of plant community structure. Ecology 79: 2082-2091. http://links.jstor.org/sici?sici=0012-9658%28199809%2979%3A6%3C2082%3ADAMFSA%3E2.0.CO%3B2-S, doi: 10.1890/0012-9658(1998)079[2082:DAMFSA]2.0.CO;2

van der Putten WH, Kowalchuk GA, Brinkman EP, Doodeman GTA, van der Kaaij RM, Kamp AFD, Menting FBJ, Veenendaal EM (2007) Soil feedback of exotic savanna grass relates to pathogen absence and mycorrhizal selectivity. Ecology 88 (4): 978–988. http://www.jstor.org/stable/27651187, doi: 10.1890/06-1051

Vandenkoornhuyse P, Husband R, Daniell TJ, Watson IJ, Duck JM, Fitter AH, Young JPW (2002) Arbuscular mycorrhizal community composition associated with two plant species in a grassland ecosystem. Molecular Ecology 11: 1555–1564. doi: 10.1046/j.1365-294X.2002.01538.x

Vandenkoornhuyse P, Ridgway KP, Watson U, Fitter AH (2003) Co-existing grass species have distinctive arbuscular mycorrhizal communities. Molecular Ecology 12: 3085–3095. doi: 10.1046/j.1365-294X.2003.01967.x

Vierheilig H (2004) Regulatory mechanisms during the plant—arbuscular mycorrhizal fungus interaction. Canadian Journal of Botany 82: 1166–1176. doi: 10.1139/B04-015

Vierheilig H, Lerat S, Piché Y (2003) Systemic inhibition of arbuscular mycorrhiza development by root exudates of cucumber plants colonized by *Glomus mosseae*. Mycorrhiza.13: 167–170. doi: 10.1007/s00572-002-0219-0

Vigo C, Norman JR, Hooker JE (2000) Biocontrol of the pathogen *Phytophthora parasitica* by arbuscular mycorrhizal fungi is a consequence of effects on infection loci. Plant Pathology 49: 509–514. doi: 10.1046/j.1365-3059.2000.00473.x

Vogelsang KM, Bever JD (2009) Mycorrhizal densities decline in association with nonnative plants and contribute to plant invasion. Ecology 90 (2): 399–407. http://www.jstor.org/stable/27650995, doi: 10.1890/07-2144.1

Wehner J, Antunes PM, Powell JR, Mazukatow J, Rillig MC (2009) Plant pathogen protection by arbuscular mycorrhizas: A role for fungal diversity? Pedobiologia doi: 10.1016/j.pedobi.2009.10.002

Wolfe BE, Klironomos JN (2005) Breaking new ground: soil communities and exotic plant invasion. BioScience 55 (6): 477–487. doi: 10.1641/0006-3568(2005)055[0477:BNGSCA]2.0.CO,2

Wright SF, Upadhyaya A (1998) A survey of soils for aggregate stability glomalin, a glycoprotein produced by hyphae of arbuscular mycorrhizal fungi. Plant and Soil 198: 97–107. http://resolver.scholarsportal.info.myaccess.library.utoronto.ca/resolve/0032079x/v198i0001/97_asosfabhoamf, doi: 10.1023/A:1004347701584

Zhang Q, Yao L, Yang R, Yang Y, Tang J, Chen X (2007) Potential allelopathic effects of an invasive species *Solidago canadensis* on the mycorrhizae of native plant species. Allelopathy Journal 20 (1): 71–77.

Zhang Q, Yang R, Tang J, Yang H, Hu S, Chen X (2010) Positive feedback between mycorrhizal fungi and plants influences plant invasion success and resistance to invasion. Invasive Plant and Mycorrhizae 5 (8): 1–10. doi: 10.1371/journal.pone.0012380

Zhang S, Jin Y, Tang J, Chen X (2009) The invasive plant *Solidago canadensis* L. suppresses local soil pathogens through allelopathy. Applied Soil Ecology 41: 215–222. doi: 10.1016/j.apsoil.2008.11.002