Arbuscular-mycorrhizal fungi: potential roles in weed management

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Summary

The importance of interactions between arbuscular-mycorrhizal fungi (AMF) and weeds of agro-ecosystems is reviewed. Considerable evidence suggests that AMF can affect the nature of weed communities in agro-ecosystems in a variety of ways, including changing the relative abundance of mycotrophic weed species (hosts of AMF), and non-mycotrophic species (non-hosts). These effects may merely change the composition of weed communities without affecting the damage that these communities cause. However, it is quite plausible that interactions with AMF can increase the beneficial effects of weeds on the functioning of agro-ecosystems. Through a variety of mechanisms, weed:AMF interactions may reduce crop yield losses to weeds, limit weed species shifts, and increase positive effects of weeds on soil quality and beneficial organisms. If beneficial effects of AMF on the composition and functioning of weed communities can be confirmed by more direct evidence, then AMF could provide a new means of ecologically-based weed management. Intentional management will be required to increase diversity and abundance of AMF in many cropping systems, but these actions (e.g. conservation tillage and use of cover and green-manure crops) typically will confer a range of agronomic benefits in addition to potential improvements in weed management.

Keywords: weed ecology, biodiversity, biocontrol, integrated weed management.

Introduction

Farmers face very strong pressures to be cost-effective in production of food and fibre, while reducing the environmental impact of farming. In response, conservation tillage systems have gained popularity in recent years (Swanton & Weis, 1991). These systems reduce fuel and labour costs, as well as losses of nutrients and soil (Brown *et al.*, 1989; Hildebrand, 1990). Also, cover and green-manure crops are being used by a growing number of farmers to improve soil quality and tilth, reduce fertility and pest-control inputs, and limit soil erosion (Lal *et al.*, 1991; Liebman & Dyck, 1993). One significant effect of increased use of conservation tillage and cover crops is a substantial increase in diversity and abundance of soil organisms (Doran & Linn, 1994; Neher & Barbercheck, 1998). Soil organisms are fundamentally important to plant function, and can

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strongly affect plant population and community dynamics (Watkinson, 1998). In particular, it is clear that soil biota can affect weed biology and management (Boyetchko, 1996). We argue that a more thorough assessment should be made of the potential value of increased soil biodiversity for weed management, in order to expand the range of biotic interactions that can be employed in the service of sustainable approaches to weed management (National Research Council, 1996).

This assessment should certainly encompass interactions between weeds and arbuscular-mycorrhizal fungi (AMF). Many aspects of plant biology are known to be strongly affected by AMF, which form symbiotic relationships with most vascular plants (Perez-Moreno & Ferrera-Cerrato, 1997; Smith & Read, 1997). Furthermore, AMF can affect the dynamics, diversity and productivity of plant communities (Zobel *et al.*, 1997; Van Der Heijden *et al.*, 1998a). It is evident that increased use of conservation tillage and cover crops will increase the diversity and abundance of AMF in soils (Johnson & Pfleger, 1992). We propose that agronomic management to favour AMF may provide a means of directing weed community dynamics (Aldrich, 1984; Swanton *et al.*, 1993) so as to reduce negative effects of weeds, and increase their beneficial effects.

In this review, we briefly survey knowledge of AMF in agro-ecosystems, and describe mechanisms by which AMF might affect the functional ecology of weeds (i.e. their functional biology considered in an ecological context). We then consider the possible influence of AMF on dynamics and agro-ecological functioning of weed communities, and suggest important research directions.

AMF in agro-ecosystems

Agronomic management can strongly affect AMF abundance in agro-ecosystems, although linkages between particular management factors and specific patterns of AMF abundance often appear to be inconsistent. An increasing number of case studies demonstrate that high AMF populations will develop in soils where certain conditions are met. These conditions include (i) avoidance of bare-soil fallow, (ii) low inputs of tillage, synthetic fertilizers, and certain high-phosphorus animal manures, and (iii) minimal rotation to crops that are poor or non-hosts to AMF (Baltruschat & Dehne, 1988; Rosemeyer & Gliessman, 1992; Douds *et al.*, 1993; Kurle & Pfleger, 1994; Glavez, 1995; McGonigle & Miller, 1996; Boswell *et al.*, 1998; Douds & Millner, 1999). Conventional high-input cropping systems often do not meet these conditions, and can substantially reduce AMF diversity and abundance (Hamel, 1996; Smith & Read, 1997; Douds & Millner, 1999). Prolonged failure to meet these conditions can result in very low population densities of AMF in some high-input cropping systems (I Charvat, pers. comm.; Johnson *et al.*, 1992), although some AMF can persist in such situations (Ellis *et al.*, 1992; Khalil *et al.*, 1992; Hooker & Black, 1995). Moreover, evidence is accumulating that crop monocultures or high-nutrient inputs may cause a rapid shift in behaviour of AMF species or communities, resulting in reduction in benefits provided to plants by AMF (Johnson, 1993; Johnson *et al.*, 1997; Scullion *et al.*, 1998; Feldmann & Boyle, 1999). However, as we argue below, when AMF are present in agro-ecosystems, they may be capable of strongly affecting the ecology of weeds.

AMF effects on weed functional ecology: nutrition, seed germination, pathogen resistance and stress tolerance

AMF colonize roots of 'mycotrophic' plant species ('host' species hereafter) and form mycorrhizae, which are intimate connections between fungus and plant root. Mycorrhizae are

not formed with non-mycotrophic species ('non-host' species hereafter). The net effect of colonization on plant function and fitness can vary widely, from strongly beneficial to strongly deleterious (Johnson *et al.*, 1997) and evidence is accumulating that these effects are typically specific to a particular combination of AMF and plant genotypes (Bever *et al.*, 1996). This more nuanced view of AMF:plant relations is replacing the notion that the response of a given plant species to AMF can be described categorically (Van der Heijden *et al.*, 1998a).

For the plant, potential benefits of colonization include greatly increased uptake of soil nutrients, especially phosphorus. Mycorrhizae serve to increase the volume of soil available for acquisition of mineral nutrients by host plants (Smith & Read, 1997), via the nutrient uptake capacity of the fungal mycelium in the soil (a network of fungal tissue within the soil). AMF-facilitated nutrient uptake allows mycorrhizal plants to tolerate wide variation in soil fertility (Varma, 1995). In addition to P, AMF have been reported to facilitate absorption and accumulation of ammonium N, K, Ca, Mn, Fe, Cu, Zn, and Ni in various plants (Marschner & Dell, 1994; Medeiros *et al.*, 1994; Smith & Read, 1997). In a number of cases (e.g. Martensson *et al.*, 1998; Nasholm *et al.*, 1999) AMF have been shown to play a significant role in N nutrition.

Among agricultural weeds that are AMF hosts, AMF infection has been shown to improve growth, seed production and seed quality (Koide *et al.*, 1988; Koide & Lu, 1992; Stanley *et al.*, 1993; Shumway & Koide, 1994a; Koide & Lu, 1995; Heppell *et al.*, 1998). This effect has been shown to be variable within the growing season, and to decline at higher plant densities (Koide & Li, 1991; Shumway & Koide, 1994b). Such work has begun to characterize the effects of AMF on the ecological functioning of weeds and weed populations. However, the focus has been on species that are AMF hosts, and on effects on individual plant function or intraspecific interactions. Processes critical to population and community dynamics, e.g. germination and establishment, interspecific interactions, and stress tolerance in both host and non-host species, have only begun to be examined in agricultural weeds.

There is some indication that germination and early growth of weedy species can be strongly affected by AMF, and that some of these effects indicate parasitic or antagonistic behaviour of AMF towards plants (Johnson *et al.*, 1997). Francis & Read (1995) developed an experimental system that modelled establishment of ruderal weeds in gaps in grassland ecosystems. A fine-mesh filter was used to exclude plant roots from growing into the experimental soil volume, while allowing development of an AMF mycelium. Very strong AMF effects on seed germination, early growth and survival of target weeds were observed. Non-host species, including several important agricultural weeds (*Chenopodium album* L. and *Spergula arvensis* L.) had germination, early growth and survival rates sharply reduced by the presence of AMF mycelia. In these interactions, fungal hyphae penetrated the roots of non-host species. Penetration was associated with disrupted and distorted morphological development of roots, absence of arbuscules (presumed sites of plant:fungus nutrient exchange), and a strong stunting effect on seedling and plant growth (Francis & Read, 1995). Host species (e.g. *Plantago lanceolata* L.) showed the opposite pattern, benefiting strongly from mycelium presence.

This experiment is unique in examining seedling:mycelium interaction free of confounding effects of seedling:root interactions. However, several other studies (Grubb, 1986; Allen *et al.*, 1989; Francis & Read, 1994; Muthukumar *et al.*, 1997; Johnson, 1998) have produced evidence consistent with this mechanism, in which early growth rates of non-host weedy species were reduced in the presence of AMF. These studies highlight the capability of some AMF to exert strongly antagonistic effects on some non-host species. There are also indications that non-host

species may be actively antagonistic to AMF, e.g. via inhibitory compounds released into soil (Fontenla *et al.*, 1999). Notably, many troublesome agricultural weeds belong to families that appear to be predominantly non-hosting (Hirrell *et al.*, 1978; Tester *et al.*, 1987; Brundrett, 1991; Francis & Read, 1994), including Amaranthaceae, Brassicaceae, Caryophyllaceae, Chenopodiaceae, Cyperaceae, and Polygonaceae. Moreover, agricultural weeds that are members of families that commonly host AMF (e.g. Poaceae, Compositae) have been shown in some cases to be non-mycorrhizal (Harley & Harley, 1987; Feldmann & Boyle, 1999). It is clearly premature to delimit the prevalence of hosting behaviour among agricultural weeds. However, there are good grounds to hypothesize that, when present, AMF may reduce the prevalence of non-host species in weed communities.

Other effects of AMF that are of potential importance to the distribution and abundance of weeds include effects on interactions between weeds and their pathogens and herbivores, and response of weeds to environmental stresses. Protective effects of AMF infection against a range of pathogens have been documented (Fitter & Garbaye, 1994; Newsham *et al.*, 1995a), in controlled environments (Linderman, 1992; Fitter & Garbaye, 1994) and field settings (West *et al.*, 1993; Newsham *et al.*, 1995b; Smith & Read, 1997; Little & Maun, 1996). Similar protective effects against above-ground herbivory by insects have been observed in some but not all cases (Gange & Bower, 1997).

AMF may affect weed responses to a number of forms of environmental stress. For example, AMF have been found to improve drought tolerance (Bethlenfalvay, 1992). AMF inoculation of corn increased growth and yield over a range of drought stress treatments (Sylvia & Williams, 1992). Mechanistically, it is clear that many physiological processes that influence plant water relations and drought tolerance are affected by AMF (Bethlenfalvay, 1992). AMF can also improve plant tolerance of other stresses, including high soil temperature, saline soil, adverse soil pH, and toxic metals (Mosse *et al.*, 1981; Bagyaraj, 1990; Munyanziza *et al.*, 1997). Also, weed species that are germinating in the understory of a mycorrhizal crop species may benefit from mycorrhizae that are subsidized by energy from other plants connected to the mycelium (Smith & Read, 1997). This subsidy may permit these species to survive and produce seeds despite low light levels and perhaps other stress factors.

Effects of AMF:weed interactions on dynamics and agro-ecological functioning of weed communities

As would be expected from the manifold effects of AMF on plant function at the individual level, AMF:plant interactions can also affect plant communities, particularly by affecting regeneration processes and outcomes of interspecific competition (Allen & Allen, 1990). From a weed-management perspective, we wish to draw attention to two possible effects of AMF on weed communities. First, as noted above, AMF are likely to influence the composition of weed communities and the relative abundance of species within them. Second, AMF may change the agro-ecological functioning of weed communities, so that the net effect of weeds becomes more beneficial.

The composition of plant communities can be strongly affected by AMF. Evidence from a variety of plant communities indicates that host species generally fare more poorly in competitive interactions with non-hosts when AMF are absent (Watkinson, 1998). Relevant studies have been conducted on experimental systems ranging from two-species competition experiments in pots, to studies of the dynamics of experimental plant communities in 'microcosms' established

in large pots, to field studies in which various treatments were applied to reduce or eliminate AMF (Fitter, 1977; Hall, 1978; Allen & Allen, 1984; Carey *et al.*, 1992; Hartnett *et al.*, 1994; West, 1996; Streitwolf-Engel *et al.*, 1997; Marler *et al.*, 1999). For example, the productivity of host species relative to non-hosts was increased by AMF in controlled-environment studies of experimental communities of grasses and forbs (Grime *et al.*, 1987; Wilson & Hartnett, 1997). Grime *et al.* (1987) found that biomass production of host species was suppressed by certain dominant non-hosts in the absence of AMF, and this suppression was greatly relieved (over 300% increase in biomass) when AMF were present. AMF can also cause reductions in performance of non-host weeds. For example, in a field experiment in a non-agricultural setting, density of the non-host weed *Salsola kali* L. was reduced 30–50% by AMF inoculation (Allen & Allen, 1988).

For weeds of agro-ecosystems, AMF effects on interactions between host and non-host species have been assessed in several controlled-environment studies involving pair-wise interactions (Crowell & Boerner, 1988; Boerner & Harris, 1991; Koide & Li, 1991; Borowicz, 1993). In each case, experimental suppression of AMF resulted in substantial reduction in the relative performance of the host weed species. In preliminary work extending these comparisons to a weed community context (N R Jordan, S Huerd & J Zhang, unpubl. obs.), we found that a multispecies field-collected AMF inoculum significantly increased the overall density and biomass of host weeds in experimental communities grown in large pots in a greenhouse. In one experiment, presence of AMF also reduced the total density of non-host weeds. Responses of host-weeds to AMF were consistent across two soil media, providing a first indication of the potential effect of AMF in shaping weed communities. A single published study has examined field-crop weeds in a field setting (Sanders & Koide, 1994). Survival, growth, seed production and quality, and P concentration were compared in two host species [*Abutilon theophrasti* Medic. and *Setaria lutescens* (Weigel) F T Hubb] and a non-host species (*Amaranthus retroflexus* L.). Soil fumigation was used to remove AMF, and this treatment was compared with fumigated soil inoculated with AMF and an unfumigated soil. For most measures of performance, *A. theophrasti* benefited and *A. retroflexus* suffered when AMF were present, while *S. lutescens* responded little. Host species that are strongly responsive to mycorrhizae (i.e. are strongly benefited by AMF colonization, Smith & Read, 1997) would be expected to suffer more in the absence of AMF than less responsive hosts. In this experiment, *S. lutescens*, which has been observed to have little response to AMF infection (Koide & Li, 1991), provides an example of a less-responsive species.

Many mechanisms may be responsible for the observed beneficial effects of AMF on host species in mixtures of hosts and non-host species. First, these effects may result from antagonistic effects of AMF on non-host species, as described above. In preliminary work, we have found a consistent pattern of inhibition of non-host species when seedlings of single weed species were exposed to a multispecies AMF inoculum. Most notably, we found that exposure to the inoculum caused a 90% reduction in biomass production by *A. retroflexus*. Overall, we observed a mean biomass reduction of 60% for that species and five other non-host species [*Chenopodium album*, *Polygonum lapathifolium* L., *Rumex obtusifolium* L., *Portulaca oleracea* L., *Brassica kaber* (DC) L C Wheeler; N R Jordan, S Huerd & J Zhang, unpubl. obs.]. If subsequent experiments confirm this result, it will suggest that AMF have considerable potential as a broad-spectrum biocontrol agent of non-host weed species.

Alternatively, any of the various mechanisms by which AMF can benefit host species may be at work, e.g. nutrient uptake, or amelioration of effects of natural enemies or environmental

stresses. Conversely, given that AMF effects on individual plant function and fitness vary widely between positive and negative impacts (Johnson *et al.*, 1997; Van der Heijden *et al.*, 1998a), it is quite possible that AMF could negatively affect the relative performance of certain host species in plant mixtures.

The implication of these studies is that increased diversity and abundance of AMF is likely to increase the relative abundance of host species in weed communities, although many exceptions may occur. The question becomes how this effect of AMF, and others that may occur, bears upon the issue of practical concern: the agro-ecological functioning of weed communities. The functioning of weed communities should be viewed broadly, to include such emergent properties as dynamic responses to management (e.g. rapidity of weed species shifts) and beneficial effects, such as those on soil quality, nutrient cycling, and populations of beneficial organisms, as well as the harmful effects that are the usual focus of investigation. Little direct evidence exists to indicate how AMF might affect the functioning of weed communities, but a variety of indirect evidence exists. We review what is known regarding AMF effects on two potentially significant attributes of weed communities: species diversity, and interspecific facilitative (i.e. beneficial) effects of weeds (Callaway, 1995) that are mediated by the AMF mycelium.

AMF effects on weed species diversity are of interest because agro-ecological effects of weeds may be related to the species diversity of weed communities (Patriquin, 1986; Tilman, 1996; Tilman *et al.*, 1997), for example, the ability of weeds to maintain populations of desirable organisms (e.g. beneficial insects or mycorrhizal fungi) is likely to be related to weed community diversity (Altieri, 1994; Feldman & Boyle, 1999). For plant communities generally, mechanisms by which plant:AMF interactions affect plant community diversity have been explicitly examined only in the computer-simulation studies of Bever *et al.* (1997). Diversity can be promoted when AMF have a spatially heterogeneous distribution in the soil, or when AMF species and host species do not provide fully reciprocal benefits (Bever *et al.*, 1997). Other mechanisms by which AMF may affect diversity are more speculative. Newsham *et al.* (1995b) argued that a spectrum of beneficial effects of AMF association is distributed differentially among host species. For example, AMF may benefit plant species with poorly branched root systems by enhancing P uptake, while benefiting plants with highly branched roots by some other means, e.g. via protection against fungal pathogens. Their suggestion was that this distribution of benefits promoted plant community diversity. Also, AMF may maintain diversity within weed communities subjected to frequent environmental stresses, by preventing elimination of less stress-tolerant species. On the other hand, AMF may decrease community diversity by favouring a host species that is capable of competitive suppression of other species. As for effects of AMF on performance of individual species, the net effects of AMF on diversity may be contingent on the degree of AMF responsiveness of species that are capable of achieving community dominance (Hartnett & Wilson, 1999). If these species are highly responsive to the AMF community present at a particular location, then increased AMF may decrease diversity; conversely, if these species are less responsive or non-hosts, increased AMF may increase diversity.

Controlled-environment and field studies (Grime *et al.*, 1987; Streitwolf-Engel *et al.*, 1997; Van Der Heijden *et al.*, 1998b) have provided cases where AMF acted to increase community diversity. For example, Gange *et al.* (1993) monitored species richness in ruderal weed communities for 4 years after establishment and observed a significant positive association between AMF infection and plant species richness. In contrast, plant diversity in a grassland was decreased by increasing AMF (Hartnett & Wilson, 1999). In this case, experimental suppression

of indigenous AMF by soil fungicide applications reduced the dominance of a strongly AMF-dependent grass species, while a variety of less-responsive or non-mycorrhizal species became more abundant.

A second avenue by which AMF may affect agro-ecological functioning of weed communities involves interspecific facilitative effects mediated by the mycelial network. Mycelial interconnections among host species in a weed:crop mixture may cause patterns of resource uptake and distribution among host species that differ qualitatively from those occurring in plant communities where AMF are absent (Fitter *et al.*, 1998; Perry, 1998). Specifically, dying host species may release nutrients into the AMF mycelium (Newman & Eason, 1993; Smith & Read, 1997; Bethlenfalvay *et al.*, 1996; Rejon *et al.*, 1997), which then may be redistributed among other host species. This phenomenon may enable facilitative effects in crop:weed mixtures. For example, after selective weed control, nutrients acquired by host weeds may be transferred to host crop or cover crop via the mycelium (Bethlenfalvay *et al.*, 1996). Such processes may result in tighter nutrient cycling (Swift & Anderson, 1993) and reduced competitive effects of non-host weeds (Rejon *et al.*, 1997). If such phenomena occur and are qualitatively important, then AMF may be capable of significantly altering the agro-ecological functioning of weeds. For example, properly timed control operations – such as sublethal post-emergence herbicide applications – might be used to transfer nutrients from weeds to crops. In this scenario, the weeds would function in effect as a temporary nutrient sink, reducing pre-emption of nutrients by non-host weeds and leaching and other nutrient losses.

Also, facilitative effects may occur when one host species supports populations of mycorrhizal fungi that are beneficial to another species (Bethlenfalvay, 1992; Perry, 1995; Bever *et al.*, 1996; Feldmann & Boyle, 1999). Host species may release carbon into the mycelium which may support formation of mycorrhizae with other hosts. In effect, host plants provide energy that serves, directly or indirectly, to subsidize formation of mycorrhizae with newly germinating hosts (Moora & Zobel, 1996; Smith & Read, 1997). This subsidy allows these seedlings to receive nutrients or other mycorrhizal benefits while minimizing the energetic costs of mycorrhizal establishment to seedlings. For example, weed communities in several cropping systems have recently been shown to enhance mycorrhizal colonization and growth of subsequent crops (Feldmann & Boyle, 1999; Kabir & Koide, 2000). However, this effect will be beneficial only if growth of the species that receives the subsidy is desirable. A counter-example is provided by a recent demonstration of a substantial carbon subsidy to an invasive rangeland weed (*Centaurea maculatalam*) via mycelial connections to desirable rangeland grasses (Marler *et al.*, 1999).

It is also possible that AMF may have negative effects on agro-ecological functioning of weed communities, simply by increasing abundance of problematic host weeds. A variety of such weeds appear to be host species, such as *Ambrosia artemisiifolia* L., *Avena fatua* L., *Abutilon theophrasti*, or *Setaria lutescens* (Crowell & Boerner, 1988; Koide & Li, 1991; Koide & Lu, 1992; Koide *et al.*, 1994). The challenge is to determine the balance of beneficial and negative effects of AMF on agro-ecological functions of weed communities.

The use of AMF to shape weed agro-ecological functioning of weed communities may offer a novel avenue of weed management. As demonstrated above, AMF are clearly capable of powerfully inhibiting growth of certain non-host weed species. If this effect is common, then AMF might serve as a broad-spectrum, self-sustaining biocontrol agent wherever agronomic management can maintain populations of effective AMF. Similarly, if mutually-beneficial interactions between AMF and ecologically useful host weeds are commonplace, then AMF may help to maintain these species in weed communities.

Research directions

First the mycorrhizal responsiveness of agricultural weeds is poorly known. Present notions of the host/non-host status of weeds are generally based on field surveys of root colonization (Newman & Reddell, 1987; Boyetchko, 1996), but such indications of colonization do not resolve parasitic or antagonistic interactions from mutualisms (Francis & Read, 1995). Mycorrhizal responsiveness has been determined in terms of AMF effects on germination, growth and reproduction for only a few major weed species, most of which are AMF hosts. Therefore, further examination of mycorrhizal responsiveness of weeds is needed, focusing upon AMF effects on weed germination, growth, stress tolerance, and interspecific interactions with other plants, herbivores and pathogens. Particularly needed are characterizations of AMF effects on these aspects of plant function in weeds from putative non-host families. Additional important questions include the specificity of interactions between particular weed species and particular AMF taxa, and geographic and ecotypic variation in AMF:weed interactions. Such specificity and variation are to be expected – genetic variation affecting the plant:AMF relationship is well documented both within and among plant and AMF species (Koide *et al.*, 1988; Bryla & Koide, 1990; Hetrick *et al.*, 1993; Sanders *et al.*, 1996; Smith & Read, 1997; Van der Heijden *et al.*, 1998a).

Second, to assess the impacts of AMF on weed communities, manipulative field experiments are needed in which some perturbation technique is used to suppress AMF fungi. Applications of broad-spectrum fungicides have been used for this purpose in other plant communities (see Gange *et al.*, 1993; Newsham *et al.*, 1995a; Hartnett & Wilson, 1999). Other perturbation techniques – e.g. tillage that disrupts the soil mycelial network – might also be suitable (Johnson *et al.*, 1997). All available perturbation techniques, including fungicides (Pedersen & Sylvia, 1997) and soil fumigation, have multiple agro-ecological effects and require careful interpretation. Methodological improvements are needed to improve our ability to resolve effects on AMF from other effects of perturbation. Ideally, a series of studies should be conducted on weed communities that provide model systems in several different cropping systems.

Third, if direct evidence confirms the importance of AMF effects on weeds in conservation tillage systems, then pertinent questions will arise about the community and evolutionary ecology of weed:AMF interactions. Recent work suggests that diversified AMF communities have the strongest effects on plant communities (Van Der Heijden *et al.*, 1998b; Klironomos, 1999). Studies are needed to determine if this is true of AMF:weed interactions. If so, then a process of community assembly will be required to develop diverse AMF communities from the depauperate communities that are apparently present in many high-input agro-ecosystems (Ellis *et al.*, 1992; Helgason *et al.*, 1998). Important issues may include the temporal dynamics of AMF diversity and effects on community assembly of environmental factors, disturbance events, and landscape-level factors, such as availability of AMF propagules to colonize fields.

Development of AMF communities that beneficially affect weed communities may involve evolutionary change in AMF or weed species. Relevant evolutionary changes may include increased capacity for mutualism by plant or fungus and adaptation to edaphic and disturbance factors. Conversely, cropping systems that include factors that are inimical to the AMF:plant mutualism, such as situations with high synthetic fertility inputs, appear to select for AMF species or genotypes that provide substantially reduced benefits to crops (Johnson, 1993; Johnson *et al.*, 1997; Scullion *et al.*, 1998; Feldmann & Boyle, 1999). It is conceivable that antagonistic behaviour

towards non-host weeds, or other AMF behaviours that affect the agro-ecological functioning of weed communities, might also be degraded by whatever processes of selection occur in these cropping systems. As noted above, it is clear that abundant genetic variation affecting AMF:plant interactions is available for evolutionary mechanisms to act upon. Molecular methods for characterizing AMF variation (e.g. Helgason *et al.*, 1998) are likely to be indispensable to resolving this variation and characterizing the evolutionary processes that act upon it.

Lastly, many events in agricultural ecosystems that are harmful to AMF can be regarded as disturbances to AMF communities. Events that may have such an effect include crop harvest, grazing, tillage, rotation to non-host crops, application of biocides, large nutrient inputs, seasonal extremes of environmental factors, and fallow periods. In several plant communities, there are indications of mechanisms that serve to maintain AMF communities in settings where frequent or strong disturbance occurs (Perry *et al.*, 1990). Among these are the so-called 'biological legacies' identified by Perry (1995): structures that provide protection for AMF from harmful disturbances. For example, in forest systems, large fallen trees appear to provide physical protection for AMF that are essential to forest regeneration after extensive logging or fire. Analogous provisions may be needed to maintain effective AMF communities in the disturbance regime of an agro-ecosystem. For example, 'zone' tillage, in which tillage is confined to 20–30-cm bands in which crop seeds are sown, may serve to preserve AMF mycelial networks. Host weeds and self-sowing cover crops may also function as biological legacies in cropping systems (Perez-Moreno & Ferrera-Cerrato, 1997; Feldmann & Boyle, 1999; Fontenla *et al.*, 1999; Kabir & Koide, 2000).

Conclusions

In our view, there are two fundamental goals of weed management. The first goal is effective control of weed species that cause major yield losses or other serious problems. The second goal is to maximize the agro-ecological benefits provided by the weed community of an agro-ecosystem. In some cases, these goals may conflict, requiring a careful weighing of costs and benefits of weeds present in a given cropping system. In recent decades, weed control efforts have focused on the first goal, perhaps in support of a predominant management objective of high crop yield. Now, the range of management objectives in agronomy is broadening. Increasing the efficiency of input use, maintaining soil and water resources, and reducing environmental impacts of farming are global imperatives. In response, management actions have shifted in pursuit of these goals, in addition to that of high yield. For example, farmers are seeking to enhance levels of soil quality and beneficial biodiversity in agro-ecosystems, and to reduce levels of off-farm movement of soil sediment and agrochemicals. Present evidence permits the hypotheses that certain weed species can play beneficial roles by helping to achieve these objectives, and that AMF:weed interactions may be critically important to realizing these beneficial roles of weeds. We recommend an expanded research effort to test these hypotheses. Through this effort, weed science will help to answer a fundamentally important scientific question: how can biological diversity be used to increase the productivity and sustainability of farming (CAST, 1999)?

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