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Progress and Challenges in Agricultural Applications of Arbuscular Mycorrhizal Fungi

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Arbuscular mycorrhiza is a widespread interaction between plant roots and mutualistic fungi that both promotes plant mineral nutrition and supports stability in many natural ecosystems. Given the demand in current agriculture for these ecosystem services, it appears desirable to further integrate this interaction in current management schemes. While two different approaches can be identified in this regard, a number of problems have limited the agricultural application of mycorrhiza to date. In this review, the sensitivity of arbuscular mycorrhizal fungi to certain agricultural management methods, the functional variability of arbuscular mycorrhizal fungi, and the variability of plant responsiveness will be discussed in particular. In addition we will focus on recent advances in the study of mycorrhiza in natural ecosystems, and illustrate how

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such knowledge might be used to further the integration of arbuscular mycorrhizal fungi in agricultural regimes, and so increase the sustainability and robustness of current practice.

Keywords agriculture, agroecosystems, anthropogenic impact, arbuscular mycorrhiza, biological diversity, community composition, ecosystem services, genetic variability, land use intensity, plant responsiveness

I. GROWING DEMAND AND LIMITING RESOURCES – PROBLEMS IN CURRENT AGRICULTURE

Crop domestication is a recent event, beginning only some 10,000 years ago. In this short time, we have remolded our crops, carried them great distances, and changed the nature of the soils they grow in. The Agricultural Revolution of the eighteenth century, and the Green Revolution of the twentieth,

saw adoption of high-input farming practices, and the selection of crops that benefit from the availability of fertilizers. The resources essential for these practices, however, such as, mineral nutrients, soil, or water, will become limiting in the near future. This applies in particular to mineral nutrients, where it is broadly recognized that current rates of application are neither economically viable, nor environmentally desirable. In this context, fertilizer use, and associated problems, in high-input areas (e.g. the United States, Europe, or China) (Guo *et al.*, 2010) can be distinguished from those in low-input areas (e.g. Africa, parts of South America; Vitousek *et al.*, 2009; Potter *et al.*, 2010). In both cases, fertilizer application is projected to decline due to increasing costs of mineral fertilizer; in the case of nitrogen due to energy costs; in the case of phosphates, due to a decrease in mineral availability (Cordell *et al.*, 2009; Gilbert, 2009). Where application rates are high, environmental damage presents a further argument for reducing use (see, e.g., Janzen *et al.*, 2003; Mishima *et al.*, 2010). The decreasing availability of further important resources, like soil or water, will lead to plant cultivation under increasingly suboptimal conditions (see, e.g., Rozema and Flowers, 2008). This trend will be aggravated by increasingly unfavorable climatic conditions as predicted by current climate change scenarios (Schmidhuber and Tubiello, 2007; Howden *et al.*, 2007; Battisti and Naylor, 2009), resulting ultimately in a clear increase of the impact of abiotic stress on plant production. At the same time, however, global demand in agricultural products is projected to markedly increase in the future, given an increase in world population and the currently developing demand for “biofuels.” Taken together, the factors detailed above indicate an increasing imbalance between the demand for agricultural products and the resources available for their production in the near future. The availability of mineral nutrients and an increase in abiotic (and possibly biotic) stress will become important limiting factors for plant production.

II. ECOLOGICAL IMPORTANCE AND AGRICULTURAL POTENTIAL OF ARBUSCULAR MYCORRHIZAL FUNGI (AMF)

The integration of key processes from natural ecosystems in agricultural management systems has been suggested as one approach to deal with the increasing agricultural problems. Natural processes often have evolved over long periods of time, and respective ecosystems in many cases are highly productive, resistant to pests, and retentive of nutrients (Ewel, 1999). Processes of particular potential with regard to plant stress resistance and the provision of mineral nutrients are connected to arbuscular mycorrhizas (AM), associations between plant roots and members from the small fungal phylum Glomeromycota (Schüßler, 2001; Schüßler *et al.*, 2001). Their key role in terrestrial ecosystems is substantiated by the evolutionary success of this group of organisms. In evolutionary terms, AMF are among the most ancient, and perhaps most unchanged organisms to be found today. According to fossil (Remy *et al.*, 1994; Redecker *et al.*, 2000) and phylogenetic evidence (Simon *et al.*, 1993; Heckman

et al., 2001; Schüßler, 2001; Schüßler *et al.*, 2001), the interaction dates back at least to the Ordovician period, when the very first land plants emerged. Nowadays about 80% of all plant species can become colonized by AMF; the interaction has been observed in all major terrestrial ecosystems (Öpik *et al.*, 2006). Central to the ecological role of the AM interaction is the transfer of nutrients between fungi and plant roots. AMF are obligate biotrophic organisms, completely dependent on photosynthetic carbohydrates provided by their hosts (Pfeffer *et al.*, 1999), and they may take up between 4 and 20% of the plant's total photosynthetic production (Smith and Read, 1997). In return, AMF provide a range of mineral nutrients, most notably phosphate, to their hosts. In certain cases, the major route of plant phosphate uptake is via AMF, even under conditions of sufficient phosphate availability in the immediate rhizosphere (Smith *et al.*, 2003). As a consequence of this exchange of nutrients, arbuscular mycorrhizal fungi (AMF) are important drivers of soil microbial communities, both because of their privileged access to plant carbon resources, and because of their extensive hyphal networks (Singh *et al.*, 2008; Bonfante and Anca, 2009). While AMF provide a large carbon reservoir for soil microbes due to hyphal exudates (Toljander *et al.*, 2007) and rapid cycling of large parts of their hyphal systems (Staddon *et al.*, 2003), more stable components of these fungi are responsible also for positive effects on soil aggregation, and on the accumulation of soil organic matter (Wilson *et al.*, 2009). Above-ground, AMF positively influence plant species diversity and affect species composition (van der Heijden *et al.*, 2006; Vogelsang *et al.*, 2006), mostly due to specific interactions of individual plant species and AMF strains.

On the single plant level, positive and negative growth effects of the AM interaction for the plant host have been described. In the past, negative growth effects have been interpreted to indicate excessive carbon loss by the plant referring to an interaction of more or less parasitic character (see, e.g., Grimoldi *et al.*, 2006). It has been shown recently, however, that negative growth effects may be due to other factors than excessive carbon drain (Facelli *et al.*, 2009; Grace *et al.*, 2009; Smith *et al.*, 2009). In addition, it has been suggested that the carbon invested by plants should not only be compared to the immediate return (of phosphate or other nutrients), but also to regard it as long-term investment by the plant, ensuring a continuous, stable supply of mineral nutrients (Landis and Fraser, 2008).

Colonization of plant roots by AMF not only affects plant mineral nutrition, but can have numerous other beneficial effects under stress conditions (Poza and Azcon-Aguilar, 2007; Miransari, 2010; Smith *et al.*, 2010), either by directly reducing the severity of a given stress factor, or by enabling colonized plants to better cope with stress. For example, it has been shown that AMF allow an increased accumulation of heavy metals in plant biomass under low concentrations of the toxic compounds with potential benefit for phytoremediation (Göhre and Paszkowski, 2006; Audet *et al.*, 2007). At higher metal concentrations, however, AMF work like filters, retaining heavy metals, and thereby protect their hosts (Audet *et al.*, 2007). Similar mechanisms have been suggested for the protective

effects of AMF against elevated levels of arsenic, (Smith *et al.*, 2010), atrazin (Huang *et al.*, 2007), and phenanthrene (Wu *et al.*, 2009). AMF also can protect plants against conditions of sub-optimal water potential (drought, flooding, salinity) by a number of different mechanisms (Fournies *et al.*, 2007; Miransari, 2010; Smith *et al.*, 2010). These include hydraulic conductance of fungal hyphae, and the induction of changes in host metabolism. AMF have also been shown to protect their hosts against flooding (Fournies *et al.*, 2007) or high soil temperature (Bunn *et al.*, 2009). Protective effects against biotic stress (pathogenic bacteria, fungi or nematodes) have been described consistently for below-ground interactions (Harrier and Watson, 2004; Pozo and Azcon-Aguilar, 2007; Singh and Vyas, 2009; Smith *et al.*, 2010), while above-ground effects may depend on the particular pathogen (Pozo and Azcon-Aguilar, 2007). Protective effects are explained by various mechanisms including improved mineral nutrition of AM plants, priming of plant defence reactions by AMF, and antagonistic effects on microorganisms (e.g., Singh and Vyas, 2009).

In summary, the traditional focus on nutrient exchange and growth responses for evaluating the “symbiotic efficiency” of a given AM interaction, appears to be too simplistic. In contrast, the physiological and ecosystem effects caused by AMF range from an increase in the nutrient uptake efficiency of plants and improvements in plant stress resistance to improvements in soil structure and soil microbiology (Gianinazzi *et al.*, 2010; Figure 1). Furthermore, the close association of AMF with various other soil microorganisms suggests that many of the ecosystem effects apparently caused by AMF derive from complex interactions with other microorganisms within the mycorrhizosphere established by these fungi (Singh *et al.*, 2008; Bonfante and Anca, 2009). Given the imminent problems facing global

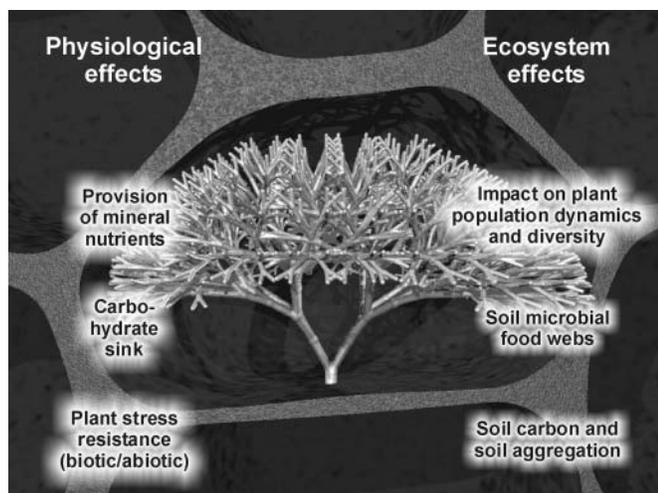


FIG. 1. Physiological and ecosystem effects of the AM interaction from a plant perspective. The background shows a model of the symbiotic interface of the interaction, a highly branched fungal structure (the “arbuscule”) within a colonized root cortical cell. This interface is the main location for symbiotic nutrient exchange.

agriculture, there is an obvious interest in integrating the AM interaction in agricultural management. The reasons for the limited success of such approaches so far (see, e.g., Manoharachary, 2007) will be discussed in the following sections.

III. APPROACHES AND CHALLENGES FOR AGRICULTURAL APPLICATIONS OF AMF

The adoption of natural processes for agricultural management is not without problems, and one might well ask whether processes established over millions of years under natural conditions can really be adapted for human purposes in agroecosystems. The main differences between natural ecosystems and agroecosystems are in nutrient cycling and biological diversity; the high input of mineral nutrients necessary to maintain productivity in most current agroecosystems is, as already mentioned, not sustainable. The integration of AMF into agricultural management may be one approach to deal with this problem. The poor biological diversity of current agroecosystems, on the other hand, might be an important hurdle for the successful integration of these organisms. In general, there are two different approaches to the integration of a biological process in human production of agricultural products: to adapt the process as far as possible to current agroecosystems (the “reductionist” approach), or to adapt agroecosystems to fit the process in question (the “holistic” approach). Although these two approaches might be combined in practice, for the sake of clarity we will discuss them separately in this review (Figure 2). In the reductionist approach AMF are regarded as a means to increase plant performance under given circumstances of low biological diversity. Such an approach ultimately results in the application of specialized fungal inocula adapted to the given condition and to the target organism. The holistic approach, in contrast, claims that ecosystem services provided by AMF are dependent on the diversity of respective communities. In consequence, the

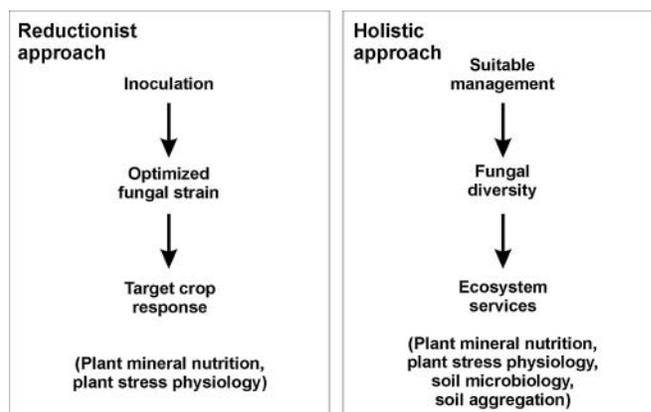


FIG. 2. Different approaches for agronomic application of AMF. While the reductionist approach relies on the inoculation of optimized fungal strains (adapted to specific conditions and the target crop under cultivation), the holistic approach aims at maximizing fungal diversity for ensuring AMF-dependent ecosystem services.

holistic approach aims rather at conserving and restoring native AMF diversity than at introducing specialized fungal inocula. Ultimately, this is only possible by increasing the biological diversity of the complete system, i.e., by completely redesigning the whole production process.

To discuss the integration of AMF in agricultural management systems in more detail, we have identified three particular issues which will be explored in the following chapters: 1) sensitivity of AMF to a variety of agricultural practices, 2) functional diversity of AMF, and 3) variation in plant responsiveness to AMF.

A. Impact of Agricultural Management on Community Composition of AMF

The composition of the AMF community is strongly affected by agricultural management. A clear negative correlation between land use intensity and the diversity of AMF communities has been demonstrated on a global scale (Öpik *et al.*, 2006), in studies in Central Europe (König *et al.*, 2010; Oehl *et al.*, 2010), in the Netherlands (Verbruggen *et al.*, 2010), under Mediterranean climate conditions (Lumini *et al.*, 2010), in humid, temperate rainforests from Iran (Bakhshipour *et al.*, 2009), under dry and under humid subtropical climate conditions (Franca *et al.*, 2007; Tchabi *et al.*, 2008), and under tropical climate conditions (Moeskops *et al.*, 2010), to name only the most recent publications. Overall, the negative correlation between AMF diversity and anthropogenic soil disturbance is consistent enough that AMF diversity (or root colonization levels) has been proposed as a measure for soil quality (Baar, 2010). The large number of reports is contrasted by only a few analyses which indicate no connection between the diversity of AMF and land use intensity (Börstler *et al.*, 2006; Galvan *et al.*, 2009), although in the case of a Thuringian meadow community studied by Börstler *et al.*, there was an impact of land use intensity on AMF species composition, if not on diversity. A number of studies (e.g., Moeskops *et al.*, 2010, and Verbruggen *et al.*, 2010) have suggested that organic farming decreases AMF diversity less than conventional farming, but, nevertheless, a reduction in diversity was observed compared with areas not used for agricultural production. In addition to this general negative correlation between land use intensity and AMF diversity, a negative impact of land use intensity on functional traits of AMF has been discussed (Verbruggen and Kiers, 2010).

A number of factors have been suggested to underlie the negative correlation of land use intensity and AMF diversity, most notably the low diversity of plant hosts under agricultural conditions and soil disturbance by tilling or fertilizer application. In native ecosystems (Johnson *et al.*, 2003; Wolf *et al.*, 2003; Johnson *et al.*, 2005a;), as well as in disturbed environments (König *et al.*, 2010), it has been demonstrated that AMF diversity is closely correlated with host diversity, that different plant species support different fungal strains (Gollotte *et al.*, 2004), and that even the identity of neighboring plants has an impact on the fungal strains

colonizing a given plant (Mummey *et al.*, 2005). Recently, it has been suggested that ecological grouping of a given plant is the main factor determining preferences towards given AMF strains (Öpik *et al.*, 2009; König *et al.*, 2010). Under agricultural conditions, the situation is exacerbated, when non-host plants are cultivated on a given field, be it as the main crop (Vestberg *et al.*, 2005; Castillo *et al.*, 2008) or as cover crop (Mathimaran *et al.*, 2005). In addition to host diversity, soil disturbance, by tilling or fertilizer application (Li *et al.*, 2009; König *et al.*, 2010) and shifting soil pH have been shown to also strongly impact the AMF community (Dumbrell *et al.*, 2010). A negative impact of tillage on AMF diversity has been demonstrated in field experiments in Southern Chile (Borie *et al.*, 2006; Castillo *et al.*, 2006), Mexico (Algualcil *et al.*, 2008) and Central Europe (Jansa *et al.*, 2002; Jansa *et al.*, 2003). There is a long record of publications showing negative impacts of fertilizer amendment on AMF communities, both in natural environments as well as in agricultural settings. In forest soils in the Los Angeles area Egerton-Warburton *et al.*, showed in 2001 that an increase in soil nitrogen levels due to anthropogenic atmospheric NO_x was correlated with a considerable decrease in AMF spore numbers and species diversity. A comprehensive study in grassland ecosystems at five different locations across North America found a negative impact on AM structures following nitrogen fertilization at low soil N:P values, and a positive impact at high soil N:P values (Johnson *et al.*, 2003). These observations were interpreted to indicate that plant nutrient status determines carbon allocation to AM structures, with external nitrogen improving the potential for mycorrhiza formation at insufficient soil P (high soil N:P) values. A similar positive effect of additional mineral nutrients for root colonization by AMF was observed by Johnson *et al.*, in 2005b, when grassland plots were fertilized by lime, nitrogen and a combination of both factors. In an agricultural setting a clear negative effect of fertilizer amendment on mycorrhizal diversity has been described by Wang *et al.*, in 2009.

The decrease in AMF diversity and abundance in agricultural land is interpreted in terms that AMF strains particularly sensitive to external conditions are eliminated while strains able to cope with low host diversity and a high degree of soil disturbance are more successful. Such differences in sensitivity result in the occurrence of generalist and specialist AMF strains; respective patterns of distribution can be observed on a global scale (Öpik *et al.*, 2006), as well as in more localized analyses (Oehl *et al.*, 2010). In the case of one particular successful generalist strain (*Glomus mosseae*) it has been shown by Rosendahl *et al.* (2009) that this strain experienced a recent population expansion which appears to be connected to the development of agriculture. In addition, it has been shown that agricultural management in general (Rosendahl *et al.*, 2008), or soil phosphate levels and host plant availability in particular, not only affect the balance of AMF strains within a given community but also the balance of AMF genotypes within a given fungal strain (Ehinger *et al.*, 2009).

While the reduction in AMF diversity under agricultural management is not a real problem for the reductionist approach, the holistic approach in the view of most authors essentially relies on conserving AMF diversity. As a consequence, in this approach, agricultural practices have to be modified as far as possible to reach this aim (see, e.g., Jeffries *et al.*, 2003; Cardoso and Kuyper, 2006; Gosling *et al.*, 2006; Watt *et al.*, 2006; Shennan, 2008; Verbruggen and Kiers, 2010). It is important to note in this context, that even agricultural practices of organic farming, as an example for agricultural management intended to reduce anthropogenic impact as far as possible, are not ideal for maintaining AMF diversity (see, e.g., Verbruggen *et al.*, 2010). Negative aspects of organic farming include the addition of organic fertilizer and the use of tillage. The most important point, however, might be the monoculture of crop plants, in some cases even of crop plants not suitable for fungal colonization like rapeseed or sugar beet. Management of biological diversity of agroecosystems might be a crucial point for restoring or maintaining a high diversity of AMF communities in the holistic approach in general. In contrast, in the case of the reductionist approach the negative impact of agricultural practices on fungal performance can be alleviated by using fungal inocula with low sensitivity for such practices. A number of such fungal strains have been described in recent years (see, e.g., Rosendahl *et al.*, 2009) and might be used as the basis for further breeding approaches (Angelard *et al.*, 2010). Nevertheless, even such relatively resistant strains, are likely to be negatively affected by conditions such as the presence of large quantities of mineral fertilizer or the unavailability of host plants for prolonged periods.

B. Functional Variability of AMF Strains and Genotypes

A number of studies have observed variation in host performance following colonization by different strains of AMF (Lerat *et al.*, 2003; Li *et al.*, 2008; Pringle and Bever, 2008; Fedderman *et al.*, 2010). This differential impact of AMF on plant growth also applies to the community level, with the observation that different AMF communities may exert different growth effects with regard to a given host plant (Uibopuu *et al.*, 2009). Given that the plant growth response to AM colonization appears to be the result of a complex interplay of various processes (most notably provision of AMF derived phosphate, decrease of root phosphate uptake, fungal carbon drain), differences in any of these might lead to variation in the outcome of the symbiosis. Functional variability may affect all these processes, since it has been reported that AMF may differ in the amount of carbon allocated to them (Lerat *et al.*, 2003), in the amount of mineral nutrients they provide (Ravnskov *et al.*, 1995; Smith *et al.*, 2004; Jansa *et al.*, 2005; Wenke, 2008), and in the degree to which they trigger a reduction in AMF-independent phosphate uptake by the host (Smith *et al.*, 2004). In addition, AMF strains have been shown to differ in structural and biochemical properties of their extraradical and intraradical hyphal systems (Hart and Reader, 2002). Cavagnaro *et al.*, (2005) have shown that different fungal strains react differently to a patchy phosphate distribution in the

soil, and in 2006 Avio *et al.*, presented a system for the evaluation of structural properties of extraradical hyphal systems and demonstrated differences in these systems for different fungal strains colonizing *Medicago truncatula*. Functional variability is not only observed in AM nutrient balance, however, but also in the protective effects of AM fungi with regard to biotic or abiotic stress. In an experiment set up by Sikes *et al.* (2009), the degree of bioprotection of *Allium cepa* and *Setaria* against *Fusarium oxysporum* was dependent on the AMF strain employed, while at the community level, it has been demonstrated that bioprotection capacity correlates with AMF community richness (Maherali and Klironomos, 2007). Furthermore, AMF strains have been shown to differ in their ability to protect their host roots from toxic alumina concentrations (Kelly *et al.*, 2005) and in their positive impact on soil aggregate stability (Piotrowski *et al.*, 2004).

In addition to functional variation among strains, there is also a considerable degree of genetic and functional diversity within strains (Sanders, 2004). A high degree of genetic diversity has been documented for the widespread strain *Glomus intraradices* (e.g., Koch *et al.*, 2004; Börstler *et al.*, 2010). In addition, Croll and Sanders have observed in 2009 that in the field there is the possibility of genetic recombination, for at least some genetic variants. Functional variation in *Glomus intraradices* corresponding to the genetic variation just detailed has been documented by Koch *et al.* (2006) and Croll *et al.* (2008). Extending the work on hyphal properties of different AMF strains cited above (Hart and Reader, 2002; Avio *et al.*, 2006), Munkvold *et al.*, demonstrated in 2004 that within-strain functional variation is greatest in the extent and architecture of the hyphal system, while the uptake of phosphate by a given hyphal element appeared to be less variable.

The high degree of plasticity and variability of AMF has different implications for the holistic and reductionist approach. In the reductionist approach variability was initially regarded as a major hurdle for the application of AMF (Hart and Trevors, 2005). This variability of AMF, on the other hand, has been used successfully to select fungal strains suitable for specific agricultural applications; strains providing positive growth effects to the host plants soybean and red clover (Sturmer, 2004), sweet potato (Gai *et al.*, 2006) and yam (Tchabi *et al.*, 2010) have been selected. Lately, such approaches have been further improved by segregating and recombining nucleotypes of individual fungal strains in order to obtain strains conferring a strong positive growth effect (Angelard *et al.*, 2010). While it remains to be demonstrated that such strains can be established and persist in a given environment (Hart and Trevors, 2005), this strategy opens a clear perspective for the reductionist approach (Sanders, 2010).

While the reductionist approach ultimately aims to reduce fungal variability as far as possible, the holistic approach tries to maximize fungal diversity to obtain a fungal community able to provide the whole range of AMF ecosystem services under a variety of biotic or abiotic stress conditions. Given the wide

range of ecosystem services, and given the complex interactions of AMF with other soil microorganisms, it appears likely that maintaining (or restoring) the diversity of AMF at a given stand is indeed necessary for this aim, although fungal diversity may not necessarily correlate with desired fungal functional traits (Verbruggen and Kiers, 2010). The non-additive effects of combining individual fungal strains (Jansa *et al.*, 2005; Gustafson and Casper, 2006), as well as the observations of Maherali and Klironomos (2007) that bioprotection capacity correlates with AMF community richness support this reasoning, however. Nevertheless, more experimental evidence for this central hypothesis of the holistic approach is required.

C. Variation of Plant Responsiveness

It has been widely reported that there is significant genetic variation among crop varieties in their ability to profit from mycorrhizal association (Koide *et al.*, 1988; Hetrick *et al.*, 1992; Kaeppler *et al.*, 2000; Zhu *et al.*, 2001; Helgason *et al.*, 2002; Reynolds *et al.*, 2006). On this basis, a breeding program can be envisaged to generate crop lines that maximize benefit from AMF, or conversely to select against material that exhibits an especially poor response. Indeed, there is evidence that, in natural environments, plant responsiveness to AM colonization is subject to selective pressure as demonstrated by observations that local plant genotypes and AMF strains often result in the best symbiotic performance (Klironomos, 2003; Al Agely and Sylvia, 2008), while, conversely, *Hypericum perforatum* exhibits reduced responsiveness to AMF in North American ecosystems, where it constitutes an invasive species (Seifert *et al.*, 2009). For plant breeders, however, the challenge remains to devise a sound framework for comparing lines, and, in particular, to avoid confusion between an enhanced ability to profit from association with AMF and a reduced ability to grow without them (Janos, 2007; Sawers *et al.*, 2008, 2010). To clarify this situation, Janos (2007) has distinguished mycorrhizal responsiveness (i.e., the difference in plant growth of mycorrhizal and non-mycorrhizal plants at a given phosphate concentration) from mycorrhizal dependence (i.e., the minimal concentration of phosphate required for a given level of plant performance in the absence of AMF). It should be emphasized, however, that dependence remains a component of responsiveness, and that differences in dependence can change responsiveness; i.e., genetic variation that impacts the performance of non-colonized plants can change the level of responsiveness with no effect on mycorrhizal associations per se (Janos, 2007; Sawers *et al.*, 2008, 2010). This point is well illustrated by consideration of highly dependent plants. For example, maize mutants with disrupted root morphology grow exceptionally poorly when nutrients are limiting but can approach wild-type performance when colonized by AMF (Paszkowski and Boller, 2002). Clearly, although showing high responsiveness, such mutants are not useful to a breeding program. To avoid these and other complications, Sawers *et al.* (2010) have suggested replacing the analysis of responsiveness by the examination of the

covariance of non-colonized and colonized plant performance in comparative studies (Sawers *et al.*, 2008, 2010).

In a number of cases it has been possible to correlate variation in plant responsiveness with specific ecological, anatomical, or physiological features. Negative correlations between plant responsiveness and the extent of plant root systems or root hairs have been discussed for a long time (see, e.g., Tawaraya, 2003). Along these lines Hoeksema *et al.* show in a recent review of the relevant literature (2010) that groups such as non-N-fixing forbs or C4-grasses are more responsive to AMF than N-fixing forbs or C3-grasses. These observations, however, can be considered in light of the impact on plant dependence. For example, the ability to form stolons is correlated with responsiveness, due to a reduction in plant dependency (Sudova, 2009). Successional status has also been correlated with responsiveness, although no clear global patterns have emerged; in tropical rainforests, seedlings from species early in succession are better supported by AMF when compared to species late in succession (Zangaro *et al.*, 2007); in montane ecosystems, however, there is an opposite effect, with a positive impact of AMF predominantly on late successional plant species (Rowe *et al.*, 2007).

In addition to variation in plant responsiveness among ecological groups, differences have been observed among varieties of given plant species. While research on corn and soybean cultivars (Khalil *et al.*, 1994) and wheat genotypes (Hetrick *et al.*, 1996) dates back to the 1990s, such studies have multiplied in recent years, targeting a variety of agriculturally or horticulturally important plant species (grapevine: Linderman and Davis, 2001; tomato: Labour *et al.*, 2003; marigold: Linderman and Davis, 2004; pepper: Sensoy *et al.*, 2007; maize: Hao *et al.*, 2008; Miyauchi *et al.*, 2008; soybean: Khalil *et al.*, 1999; rice: Gao *et al.*, 2007; Hajiboland *et al.*, 2009). As demonstrated by Hetrick *et al.* in 1995, who worked on wheat genotypes carrying specific chromosomal insertions, it appears possible to identify plant genetic factors responsible for this variation in future research.

Plant breeding usually selects for fast-growing varieties with a high capacity to take up available mineral nutrients. In accordance with this selection pressure, agricultural plants have been described to be considerably less responsive to AMF when compared to uncultivated plants (Tawaraya, 2003). In the case of wheat it has also been shown that older varieties with a lower uptake capacity of phosphate were more responsive to AMF than younger varieties with a higher endogenous uptake capacity (Zhu *et al.*, 2001). In the case of maize varieties, however, modern hybrids were colonized more extensively than old landraces (An *et al.*, 2010), and genotypes adapted to low phosphate environments were less responsive to AMF than genotypes adapted to high phosphate environments (Wright *et al.*, 2005). Wright *et al.*, proposed in 2005 to use genotypes from high phosphate environments with a high responsiveness for AMF as a starting point for future breeding approaches, while Sawers *et al.* suggested in 2008 to rather focus on highly responsive genotypes with a low dependency. In a similar way, Newton *et al.* (2010)

included mycorrhizal responsiveness as a potentially positive trait of old cereal landraces to be reintroduced into modern varieties. As an alternative, or rather complementary approach, the use of molecular tools addressing signal transduction processes in the AM interaction for breeding purposes has been proposed (Rengel, 2002; Wissuwa *et al.*, 2009).

IV. HOLISTIC OR REDUCTIONIST – A QUESTION OF DIVERSITY

Summarizing the previous chapters, it can be stated that variability, both on the plant as well as on the fungal side, is a central feature of the AM interaction. In natural ecosystems communities of the two partners, of more or less diversity, are optimally adapted to each other. Inclusion of AMF in agroecosystems may require either selection of plant and fungal partners with suitable features from the variability available for use in conventional agroecosystems (reductionist approach) or reliance on synergistic effects of AMF communities of high diversity (holistic approach). In this latter case agroecosystems have to be reshaped, possibly progressively over a number of seasons, to allow for such highly diverse AMF communities.

Following the reductionist approach, it appears questionable whether the use of single AMF strains really is able to provide the whole range of ecosystem services attributed to AMF in natural ecosystems. Nevertheless, it is fair to say that given the recent success in selecting AMF strains with desired features (Angelard *et al.*, 2010) and given the steady advances in inoculum production (Ijdo *et al.* 2010) important steps towards successful agricultural applications have been taken. This success is particularly crucial, since the high variation of fungal strains has been regarded as a major challenge to application (Hart and Trevors, 2005), and since poor quality of commercial inocula has been identified as a further obstacle (Tarbell and Koske, 2007). While there is still a trade-off in inoculum production between inoculum price and purity, the dynamics of the field reviewed by Ijdo *et al.* (2010) is remarkable and gives hope for further improvements. The two main remaining issues with the reductionist approach, however, are uncertainties regarding establishment and effectiveness of artificial fungal inocula under field conditions. In spite of technological improvements, i.e., the application of T-RFLP for the analysis of AMF diversity (Mummey and Rillig, 2007), the analysis of establishment and persistence of artificial inoculum under agricultural conditions remains challenging. The proposition made by Piotrowsky and Rillig in 2008 to complement work on AMF persistence with the analysis of AMF succession in general, is a valuable but even more ambitious aim. Using the T-RFLP methodology in greenhouse experiments, Antunes *et al.* (2009) did not find evidence for the establishment of AMF inocula in native fungal communities. Field experiments using less reliable methods only provided partial evidence for such establishment. Girvan *et al.* (2004) used primers specific for ribosomal sequences of Glomales in general, and could demonstrate an increased presence of such

fungi after respective inoculation experiments in winter wheat cultivation. Farmer *et al.* (2007) used more specific primer pairs but, nevertheless, apparently detected other strains in addition to that used as inoculum. Their results indicate partial establishment of the fungal strains used for inoculation of sweet potato plants six weeks after inoculation. Regarding the effectiveness of fungal inocula, which if detected might give at least some indication for a successful establishment, clearly skeptical reviews as, e.g., from Ryan and Graham (2002), are contrasted by more optimistic perspectives. Lekberg and Koide (2005) summarized their meta-analysis of literature data by concluding that AM inoculation and shortened fallow is able to increase plant biomass under low phosphorus conditions and low levels of indigenous AMF. This statement agrees with the conclusion from Ryan and Graham, who had identified high soil phosphate levels as a major hurdle for the effectiveness of AMF in production agriculture. These conclusions seem to limit the application of AMF to low-input systems. Nevertheless, there is still room for improvements both in terms of plant responsiveness as well as in terms of fungal effectiveness (see Sanders, 2010), which might give the option of applying AMF inocula under high-input conditions. In addition, as mentioned earlier, other benefits of the AMF-interaction, different from pure growth effects might prove equally important in the long term. This appears to be particularly important for the establishment of the reductionist approach, since, in terms of nutrient efficiency, application of AMF will have to compete with current efforts to increase root capacities for the uptake of mineral nutrients directly (Hammond *et al.*, 2004). Such benefits, not connected to nutrient uptake, might also motivate the application of AMF inocula under high-input conditions, given that it becomes possible to obtain sufficient colonization levels under such conditions.

In the development of the holistic approach, management targets have shifted from advancing “beneficial” AMF strains and repressing “parasitic” ones (see, e.g., Kiers *et al.*, 2002) to the aim of establishing maximum AMF diversity (Jeffries *et al.*, 2003; Cardoso and Kuyper, 2006; Gosling *et al.*, 2006; Watt *et al.*, 2006; Shennan, 2008). In many cases, this target is discussed in the wider perspective of improving soil microbial communities or rhizosphere communities in general (Johansson *et al.*, 2004; Shennan, 2008). Efforts to obtain high AMF diversity are motivated by the possibility that there are ecosystem functions of AMF relevant to agriculture, which depend on AMF diversity, and which are not provided by individual fungal strains. Such a possibility is indicated by the observation of synergistic effects provided by combining fungal strains (Jansa *et al.*, 2005; Gustafson and Casper, 2006) as exemplified by the observations of Maherali and Klironomos (2007) who demonstrated a connection between AM community richness and bioprotective effects. When looking at the wide range of AMF ecosystem services and their interactions with other soil organisms, it appears in fact questionable whether one isolated strain will be able to provide all relevant ecosystem services. Given this emphasis on fungal diversity, further demonstration

of actual beneficial effects of such diversity in an agricultural setting, however, remains an urgent and demanding task. A number of alternative management strategies have the potential to promote diversity AMF in agricultural systems (Lichtfouse *et al.*, 2010), either by reducing disturbance by fertilization and tillage, or by increasing biological diversity. Such alternatives comprise multispecies plant cropping systems (Malézieux *et al.*, 2009), cultivation of perennial grains (Glover *et al.*, 2010), conservation agriculture and conservation tillage (Hobbs *et al.*, 2010), coppiced biomass plantations (Rooney *et al.*, 2009), low-input agriculture on marginal lands (Tilman *et al.*, 2006; Fargione *et al.*, 2008; Debolt *et al.*, 2009; Blanco-Canqui, 2010) and organic agriculture in general (Smukler *et al.*, 2008). In addition approaches like the on-farm production of native inocula (Douds *et al.*, 2010) and the use of leguminous shrubs and trees as symbiotic islands under arid condition (Herrera *et al.*, 1993; Camargo-Ricalde and Dhillion, 2003) may have beneficial effects for AMF communities. Further interesting options that are being investigated include the synergistic effects of AMF and earthworms (Zarea *et al.*, 2009), and possible positive effects of AMF for weed management (Jordan *et al.*, 2000; Jordan and Huerd, 2008; Cameron, 2010; Rinaudo *et al.*, 2010). AMF are an important component in almost all natural ecosystems (from the arctic to tropical rainforests) improving nutrient cycling and soil structure and increasing ecosystem stability. Therefore, while the management systems summarized above may be beneficial for the establishment of diverse AMF communities, such communities may be equally important for the success of these management systems. Since it has already been proposed to use AMF diversity and root colonization levels as a metrics for soil quality (Baar, 2010), such measurement might be similarly useful to monitor the progress of the management systems in question. Large-scale, cost-effective monitoring of AMF communities, however, is one of the major technical challenges, which remain to be solved, for a rational application of AMF in agriculture.

V. CONCLUSIONS

Current agricultural trends provide a strong momentum for establishing agricultural applications of AMF. In this context, AMF can be used under conventional as well as under alternative agricultural regimes, as discussed in terms of the reductionist and the holistic approach. In this review, challenges to AMF application connected to AMF sensitivity, AMF functional variability, and to variability in plant responsiveness have been discussed. Major research efforts will be necessary to cope with these challenges. As demonstrated by recent success in selecting appropriate AMF strains, however, such challenges may turn out to provide unexpected possibilities. Despite impressive advances, it appears unclear for the time being whether the reductionist approach will really be able to cope with the complexity of soil microbial interactions in agricultural fields, and whether it will be possible to improve on current biotechnological efforts aimed towards directly improving root nutrient

uptake efficiency. On the other hand, it appears that the holistic approach may give more immediate returns, and it is important to stress that AMF should be regarded as essential components of alternative agricultural approaches, such as, conservation tillage, low-input agriculture or organic agriculture. Indeed, AMF may, in part, be crucial for the success of such production systems. Improvements in the management of AMF under such conditions might therefore directly translate into improvements of performance of these production systems. One particularly important general point, with regard to both the holistic and the reductionist approach, is the further refinement and application of techniques for detecting and following AMF strains or communities in the field. While we are certainly still far from applying methods of precision agriculture to soil microbes (as envisioned by Welbaum *et al.*, 2004), progress in this area might be essential for the future of agricultural applications of AMF.

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