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REVIEW

Agroecology: the key role of arbuscular mycorrhizas in ecosystem services

Silvio Gianinazzi · Armelle Gollotte ·
Marie-Noëlle Binet · Diederik van Tuinen ·
Dirk Redecker · Daniel Wipf

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Abstract The beneficial effects of arbuscular mycorrhizal (AM) fungi on plant performance and soil health are essential for the sustainable management of agricultural ecosystems. Nevertheless, since the ‘first green revolution’, less attention has been given to beneficial soil microorganisms in general and to AM fungi in particular. Human society benefits from a multitude of resources and processes from natural and managed ecosystems, to which AM make a crucial contribution. These resources and processes, which are called ecosystem services, include products like food and processes like nutrient transfer. Many people have been under the illusion that these ecosystem services are free, invulnerable and infinitely available; taken for granted as public benefits, they lack a formal market and are traditionally absent from society’s balance sheet. In 1997, a team of researchers from the USA, Argentina and the Netherlands put an average price tag of US $33 trillion a year on these fundamental ecosystem services. The present review highlights the key role that the AM symbiosis can play as an ecosystem service provider to guarantee plant productivity and quality in emerging systems of sustainable agriculture. The appropriate management of ecosystem services rendered by AM will impact on natural resource conservation and utilisation with an obvious net gain for human society.

Keywords Arbuscular mycorrhiza · Ecosystem services · Agroecology · Ecosystem sustainability

Introduction

Arbuscular mycorrhizas (AM) constitute a key functional group of soil biota that can greatly contribute to crop productivity and ecosystem sustainability in new plant production strategies. AM fungi, able to establish a symbiotic interaction with the root organs of 80% of plant families, not only improve the growth of plants through increased uptake of available soil phosphorus (P) and other non-labile mineral nutrients essential for plant growth, they have also ‘non-nutritional’ effects in stabilising soil aggregates, in preventing erosion, and in alleviating plant stress caused by biotic and abiotic factors (Smith and Read 2008). The beneficial effects of AM fungi on plant performance and soil health are essential for the sustainable management of agricultural ecosystems (Jeffries et al. 2003; Barrios 2007). Nevertheless, since the ‘first green revolution’, less attention has been given to beneficial soil microorganisms in general and to AM in particular.

Human society benefits from a multitude of resources and processes from natural and managed ecosystems, to which AM make a crucial contribution. These resources

S. Gianinazzi · M.-N. Binet · D. van Tuinen · D. Wipf (✉)
UMR INRA 1088/CNRS 5184/Université Bourgogne,
Plante-Microbe-Environnement, INRA-CMSE,
BP 86510, 21065 Dijon Cedex, France
e-mail: daniel.wipf@dijon.inra.fr

A. Gollotte
Welience Agro-Environnement, INRA,
17 rue Sully, BP 86510, 21065 Dijon Cedex, France

D. Redecker
UMR INRA 1229/Université Bourgogne,
Microbiologie du Sol et de l’Environnement, INRA-CMSE,
BP 86510, 21065 Dijon Cedex, France

Present Address:
A. Gollotte
Inoplant,
13 rue des Souhaits,
21110 Aiserey, France

and processes, which are called ecosystem services, include products like food and processes like nutrient transfer. Growing human needs and demands have led to an increase in resource demands imposed on ecosystems, greater global consumption of natural resources and a significant decline in ecosystem services. Many people have been under the illusion that these ecosystem services are free, invulnerable and infinitely available; taken for granted as public benefits, they lack a formal market and are traditionally absent from society's balance sheet. Since 1997, economists and ecologists have joined forces to estimate the annual value of the services that ecosystems provide (Costanza et al. 1997; Daily 1997; Boyd and Banzhaf 2007; Wallace 2007; Fisher and Turner 2008). Although most services lie outside the market and are difficult to calculate, minimum estimates equal or exceed global gross national product (Pimm 1997). In 1997, a team of researchers from the USA, Argentina and the Netherlands put an approximative price tag of US $33 trillion a year on these fundamental ecosystem services. This is nearly twice the value of the world's gross national product. In this study, two major ecosystem services, 'soil formation' and 'nutrient cycling', were respectively estimated to represent US $17.1 and 2.3 trillion (Costanza et al. 1997).

Whilst some countries use tax systems to protect the environment by restraining levels of polluting activities (e.g. carbon tax) or to stimulate development of environmentally friendly policies (Ecological Tax Reform), Costa Rica is one of the first countries to make a national effort to protect ecosystem services (Pagiola 2007). In 1996, this country adopted a law (Forestry Law No. 7575) recognising four critical services provided by the nation's forests: carbon sequestration, hydrological services, biodiversity protection and scenic beauty. This law establishes a framework for payment for ecosystem services, set forth in a programme entitled PSA (Pagos por Servicios Ambientales) administered by the National Forestry Fund (FONAFIFO), in which landowners and all future purchasers of the land contract to provide against payment ecosystem services, for 20 years, via reforestation, sustainable management, preservation and regeneration activities.

The supply of agricultural products and ecosystem services are evidently essential to human existence and quality of life; however, recent agricultural practices that have greatly increased global food supply have had inadvertent, detrimental impacts on the environment and on ecosystem services. High-intensity agriculture has principally focused on productivity instead of integrating natural resource management into food production security; mechanisation, monocultures, and increased use of synthetic inputs (chemical fertilisers, pesticides) have degraded water quality, reduced arable lands and forest resources, and soil fertility (Foley et al. 2005). In consequence, novel and expedient methods are needed to manage Earth's ecosystem services, the loss of which will have important consequences for sustainable food production in the face of an increasing world population. Agriculture is the largest interface between humans and environment, thus reconciling crop production and environmental integrity, in other words sustainable crop production, is a major challenge for agriculture and future farmers (Robertson and Swinton 2005). This implies the need to develop crop management strategies that optimise soil fertility, biological diversity and crop robustness (Altieri 1995) by creating forms of agro-ecosystems that respect natural ecological processes and support productivity in the long term (Altieri 1999).

In this context, the ecosystem services rendered by soil biota in maintaining soil quality, plant health and soil resilience are extremely pertinent (Smith and Read 2008). In particular, soil microorganisms that form mutually beneficial relationships with plant roots have become a target of increasing interest in agricultural research and development because they offer a biological alternative to promote plant growth and reduce inputs in sustainable cropping systems (Hart and Trevors 2005). The ubiquity of AM fungi at the interface between soil and plant roots makes them a key functional group of soil biota which by their nutritional and non-nutritional activities profoundly influences ecosystem processes that contribute to the ecosystem services in agroecology. Our aims in this review are to highlight the key role that the AM symbiosis can play as an ecosystem service provider (for an overview see Table 1) to guarantee plant productivity and quality in emerging systems of sustainable agriculture. The appropriate management of ecosystem services rendered by AM will impact on natural resource conservation and utilisation with an obvious net gain for human society.

Services provided by arbuscular mycorrhiza in agrosystems

The evolutionary history of land plants is closely entwined with the evolution of AM fungi; earliest evidence for the existence of Glomeromycetes comes from spores and hyphae observed in Ordovician fossils, dating back some 460 million years ago (Redecker et al. 2000). At this time, land plants were at a very early evolutionary stage (Gensel 2008) and had most likely reached the morphological complexity of todays liverworts and hornworts. Arbuscule-like structures in plant fossils from the Devonian period (400 million years) indicate the probable presence of AM associations (Remy et al. 1994), although at this time plants had still not evolved roots as such, so that the existence of AM is older than that of true roots (Roth-Nebelsick and Konrad 2003). This early morphological

Table 1 Overview of the main roles that the AM symbiosis can play as an ecosystem service provider

AM function	Ecosystem service(s) provided
Root morphology modification and development of a complex, ramifying mycelial network in soil	Increase plant/soil adherence and soil stability (binding action and improvement of soil structure)
Increasing mineral nutrient and water uptake by plants	Promote plant growth while reducing fertiliser requirement
Buffering effect against abiotic stresses	Increased plant resistance to drought, salinity, heavy metals pollution and mineral nutrient depletion
Secretion of 'glomalin' into the soil	Increased soil stability and water retention
Protecting against root pathogens	Increased plant resistance against biotic stresses while reducing phytochemical input (see Tables 2 and 3)
Modification of plant metabolism and physiology	Bioregulation of plant development and increase in plant quality for human health

integration of plant and fungal tissues is likely to be reflected in both partners by basic genomic and metabolic programmes which have persisted throughout the ages. However, plants have strongly diversified with evolution, reaching approximately 260,000 extant species, which in many cases can be assigned to defined ecological niches or habitats. In contrast, Glomeromycetes appear to have remained relatively unchanged over hundreds of millions of years, a situation that has been interpreted as morphological stasis (Croll and Sanders 2009), and no more than 200 morphospecies of these fungi are known today (Schüssler et al. 2001; http://www.amf-phylogeny.com). Most agricultural crop plants develop AM. As the existence of relatively high diversity of AM fungi and the use of intensive management practices in agricultural systems are often but not always incompatible (Hijri et al. 2006), the question arises as to the agroecological benefit of such diversity.

It can be hypothesised that a diverse community of AM fungi may offer a diverse pool of ecosystem services, but clearly more work is needed on diversity/function relationships in order to be able to answer this question. On the one hand, AM fungal species/isolates can show clear physiological diversity (Giovannetti and Gianinazzi-Pearson 1994; Munkvold et al. 2004) whilst, on the other, selection or breeding for plant varieties under high-nutrient conditions which ignore symbiotic activity can lead to the generation of plant genotypes which are less or non-receptive to mycorrhiza (Hetrick et al. 1993; Toth et al. 1990; Zhu et al. 2001). Similar lose of symbiotic activity due to selection has been observed for soya bean (Kiers et al. 2007). Such deleterious effects on symbiotic function, which are likely to go unnoticed in high-input agriculture, will be highly relevant under low-input conditions. In this context, efforts need to be made to elucidate the possible negative impact of breeding on AM function by comparing conventionally bred varieties with those adapted to low-input conditions (Hildermann et al. 2010). However, it should be underlined that no case is known where a host plant has completely lost its ability to form AM through regular selection or breeding activities. It has even been suggested that in the absence of a positive growth response of the host plant, the fungal symbionts may still be responsible for a large part of phosphate uptake in AM plants (Smith et al. 2009). Based on the finding that plant diversity influences AM fungal diversity (Johnson et al. 2003), evidence is accumulating that long-term monocropping may have a deleterious effect on AM fungal diversity although it may be difficult in each case to separate direct effects from accompanying factors of intensive agricultural management such as high-nutrient and pesticide input, soil disturbance (An et al. 1993; Oehl et al. 2003; Hijri et al. 2006).

In conclusion, the mycorrhizal symbiosis is an essential component of most plants and the challenge for agriculture today lies in the possibility to take advantage of the numerous ecosystem services of soil stabilisation, biofertilisation, bioprotection, bioregulation offered by this natural resource.

AM fungi increase soil stability

During development of AM, the fungal symbionts grow out from the mycorrhizal root to develop a complex, ramifying network into the surrounding soil which can reach up to 30 m of fungal hyphae per gramme of soil (Cavagnaro et al. 2005; Wilson et al. 2009). This network can make up to 50% of fungal mycelium in soil (Rillig et al. 2002) thereby representing a major part of the soil microbial biomass (Leake et al. 2004). This mycelial network can have a binding action on the soil and improve soil structure. In addition, the secretion by AM fungi of hydrophobic, 'sticky' proteinaceous substances, referred to as glomalin (Rillig et al. 2002), also contributes to soil stability and water retention (Bedini et al. 2009). The combination of an extensive hyphal network and the secretion of glomalin is considered to be an important element in helping to stabilise soil aggregates (Andrade et al. 1998; Rillig and Mummey 2006), thereby leading to increased soil structural stability and quality (Bedini et al. 2009; Caravaca et al. 2006).

Agronomic practices such as monoculture cropping, ploughing, or fertilisation have frequently been observed to have a negative impact on the amount as well as the diversity of AM fungi present in soils (Helgason et al. 1998; Oehl et al. 2005). A reduction in fungal biomass will result in a negative effect on soil stability and consequently increase the risk of soil erosion. This is not to be underestimated; in the UK, productivity loss due to soil erosion of agricultural soils has been estimated to 9.99 million €/year (Görlach et al. 2004). Since soil is a non-renewable resource on a human time-scale, the impact of erosion is often cumulative and in most instances irreversible.

AM fungi reduce the need for phosphate fertiliser inputs

Phosphate, which is an essential mineral nutrient for plant growth, is one of the three main mineral nutrients applied in agriculture. Rock phosphate sources are limited and on the basis of the presently known world phosphate reserves, most of the phosphate mines will be depleted in about 100 years (Herring and Fantel 1993; http://minerals.usgs.gov/minerals/pubs/mcs/2008/mcs2008.pdf). Although the consumption of triple-phosphate has been reduced in developed countries between 2000 and 2006 by 36%, reaching an annual amount of 0.3 million tonnes, whereas in the mean time it increased by 36% in the developing countries reaching an annual amount of 2.1 million tonnes (www.fertilizer.org/ifa/ifadata/search). Excess application of phosphate fertilisers is an important cause of water eutrophication, and therefore improvement of phosphate uptake efficiency by plants is a priority. Inorganic phosphate (Pi) has very limited diffusion capacities in soils and its rapid absorption from the soil solution by plant roots generates Pi depletion zones at the root surface resulting in a decline of directly absorbed Pi by the plant surface (Marschner and Dell 1994; Roose and Fowler 2004). The network of fungal mycelium connected to AM roots increases by several orders of magnitude the soil volume which can be explored by a plant so that a mycorrhizal root is more efficient in phosphate uptake than a non-mycorrhizal root (Smith and Read 2008). Under given field conditions, it has been estimated that a reduction of 80% of the recommended phosphate fertiliser could be supplemented by inoculation with AM fungi (Jakobsen 1995). It is evident that such reductions in phosphate application have important economical and environmental impacts.

AM fungi increase crop plant tolerance against abiotic stresses

Abiotic stresses cause extensive losses to agricultural productivity. Mineral depletion, drought, salinity, heavy metals or heat are serious problems in many parts of the world, in particular in arid and semi arid areas (Evelin et al. 2009). It is predicted that two thirds of cultivable land may disappear in Africa, a third in Asia and one fifth in South America by 2025 and that arable land area per inhabitant in the world will be reduced to 0.15 ha in 2050 (http://www.un.org/esa/sustdev/documents/agenda21/french/action12.htm). In the USA and Spain, one third of the country is undergoing desertification. The potential of AM fungi to enhance plant tolerance in abiotic stress conditions has long been recognised (Smith and Read 2008) and their manipulation in sustainable agricultural systems will be of tremendous importance for soil quality and crop productivity under severe edapho-climatic conditions (Lal 2009).

Amongst more recent examples of the use of beneficial soil microbes to improve crop tolerance against abiotic stress conditions, studies of the synergistic effect of co-inoculated bacteria and AM fungi from dry environments on plant growth under drought stress (Marulanda-Aguirre et al. 2008; Marulanda and Barea 2009) underlines the interest of manipulating autochthonous AM fungal isolates from dry soils for revegetation of degraded land sites to improve soil quality, and to fight desertification in Mediterranean ecosystems. For example an indigenous drought-tolerant strain of *Glomus intraradices* associated with a native bacterium reduced by 42% the water required for the production of *Retama sphaerocarpa* (Marulanda et al. 2006). AM fungi alleviate stress salinity in olive tree plantations in Spain or in arid North Africa where palm grove yields are considerably affected by drought and soil salinity (Bouamri et al. 2006; Porras-Soriano et al. 2009).

Another area where AM fungal inoculation has become a prospective tool for enhancing plant tolerance to environmental stress conditions is in the revegetation of naturally or industrially metal-contaminated soils. There are many examples in the literature to illustrate this role of the AM symbiosis, although the underlying mechanisms are not yet fully understood (Khade and Adholeyavan 2009). The occurrence of AM in Ni-hyperaccumulating plant species found naturally on metal-rich soils offers possibilities of using heavy metal-hyperaccumulating plants together with AM fungi for phytoremediation strategies (Turnau and Mesjasz-Przybylowicz 2003; Gamalero et al. 2009). Furthermore, many phosphate fertilisers are a major source of soil contamination by cadmium in agricultural systems

(Lugon-Moulin et al. 2006; Nziguheba and Smolders 2008) which again pleas for the reduction of crop reliance on phosphate fertilisers. AM fungi, through their mycelium network, not only improve Pi uptake by roots but they also have a buffering effect on the cadmium uptake, reducing the toxic effect of cadmium on plant growth (Rivera-Becerril et al. 2002; López-Millán et al. 2009).

AM fungi protect plants against biotic stresses

To limit the spread of pests causing great yield losses in cultivated crops, conventional agriculture has been using large quantities of pesticides as well as plant breeding programmes in order to obtain disease-resistant plants. However, pesticides are often only partially effective against soil-borne diseases. Moreover, they are detrimental to human health and to the environment and as a consequence an ever-increasing number of pesticides is being taken off the market. In addition, disease resistance obtained by plant breeding programmes is often due to single plant genes, which can be rapidly overcome by evolutionary biodiversity in pathogenic agents. Complementary approaches have therefore to be developed to ensure durable tolerance of plants to pathogens.

Numerous studies have demonstrated the beneficial effect of AM fungi in increasing plant tolerance to biotic stress caused by soil-borne pathogens interacting with many plant species. This has been consistently shown for a number of pathogenic fungi or Oomycetes such as *Fusarium*, *Rhizoctonia*, *Verticillium*, *Thievalopsis*, *Aphanomyces*, *Phytophthora* and *Pythium*, as well as nematodes from the genera *Heterodera*, *Meloidogyne*, *Pratylenchus* and *Radopholus* (reviewed in Harrier and Watson 2004; Whipps 2004; Hao et al. 2009). Most of the research has been carried out under very controlled conditions at early stages of plant growth but a few studies conducted in the field or in the greenhouse under real production conditions confirm these results (Bødker et al. 2002; Newsham et al. 1995; Torres-Barragan et al. 1996; Utkhede 2006). It would be too difficult to present here all the papers published on this topic. Instead we have chosen to illustrate this by results obtained for tomato which is one of the most widely grown vegetables in the world, and which is susceptible to many insects, bacteria and nematodes causing significant reduction in fruit yield (34%) under current production practices (Engindeniz 2006). Although this plant is not highly responsive to AM fungi in terms of plant growth (Smith et al. 2009), it clearly benefits from mycorrhization when challenged by root pathogens such as *Fusarium oxysporum* f. sp. *radicis-lycopersici*, *Rhizoctonia solani*, *Phythophthora parasitica* or *Meloidogyne incognita* (Table 2). In this case, root colonisation by AM fungi can largely reduce root infection and disease severity caused by the pathogens, resulting in increases in plant fresh weight (up to 198%) and fruit yield (14.3%) as compared with pathogen-infected non-mycorrhizal plants (Table 2). This clearly justifies the comparison of mycorrhiza to a ‘health insurance’ for plants (Gianinazzi and Gianinazzi-Pearson 1988). Variation, however, exists in the efficiency of bioprotection between AM fungal species or isolates (Martinez-Medina et al. 2009; Pozo et al. 2002; Thygesen et al. 2004; Utkhede 2006). Nonetheless, even where there is no immediate positive effect on plant growth and yield (Table 2), a reduction in disease development can be beneficial for decreasing pathogen populations in the soil and this may have a positive impact on following crops.

Overall, the greater tolerance of mycorrhizal plants against root pathogens provides bioprotection as an ecosystemic service for sustainable agriculture since it can be active against a wide spectrum of pathogens and could complement innovative multiple allele quantitative resistance obtained by plant breeding.

AM enhance plant quality for human health

Mineral content and secondary metabolites of crops used as food or medicinal remedies can be beneficial in preventing diseases such as cancer, cardiovascular and neurodegenerative diseases or microbial infection (Cummings and Kovacic 2009; Seeram 2008). For example, zinc deficiency alters the immune and gastrointestinal systems, blood cell development, thyroid hormone metabolism as well as pancreas, liver and brain activity, and can increase risks of diabetes, coronary artery disease and cancer (Cummings and Kovacic 2009). Approximatively 30% of the world’s soils are Zn deficient, particularly in tropical areas (Cavagnaro 2008) and this leads to reduced yields and Zn content in crop products, resulting in inadequate dietary Zn intake for many human populations and a negative impact on human health. Several studies have reported that AM can increase Zn uptake by plants even under field conditions (Cavagnaro 2008). For example, the Zn content in shoots and fruits of field-grown wild-type mycorrhizal tomato plants was found to be up to 50% higher than in a mutant with reduced mycorrhizal colonisation (*rmc*) (Cavagnaro et al. 2006).

It is also becoming evident that the AM symbiosis can stimulate the synthesis of plant secondary metabolites, which are important for increased plant tolerance to abiotic and biotic stresses or beneficial to human health through their antioxidant activity (Seeram 2008). These bioactive compounds include organosulfides, polyphenols (phenolic

Table 2 Disease reduction and effect on plant growth induced by AM fungi in tomato plants infected by pathogenic fungi, Oomycetes or nematodes

Pathogenic agent	AM fungus	Growth conditions	Disease reduction	Effect on plant growth or yield	Reference
Fusarium oxysporum f. sp. *radicis-lycopersici*	*Glomus intraradices* (commercial inoculum)	Greenhouse 7 weeks, transplanting in infested field	Disease incidence, −10 to −34%	No effect on fruit yield	Datnoff et al. 1995
	G. intraradices OM/95	Growth chamber, 8 weeks	Disease severity, −12%	Root fresh weight, +48%	Akkopru and Demir 2005
	Glomus monosporum *Glomus mosseae*	Greenhouse 28 weeks, near-commercial conditions	Percentage of infected plants, −30%	Fruit yield, +14.3%	Utkhede 2006
Meloidogyne incognita	*G. mosseae* BEG12	Greenhouse, 12 weeks	Number of juveniles, −85% Number of females, −75%	No significant effect on plant growth	Talavera et al. 2001
	Glomus coronatum	Greenhouse, 15 weeks	Gall index, −42%	No significant effect on plant growth	Diedhiou et al. 2003
Phytophthora parasitica	*G. mosseae* BEG12	Growth chamber, 9 weeks	Number of root necroses, −50%	Shoot weight, +121%	Cordier et al. 1996
Rhizoctonia solani	*G. mosseae* BEG12	Growth chamber, 28 days	Percentage of root infection, −87%	Shoot weight, + 198%	Berta et al. 2005

acids, anthocyanins, flavonoids), phytosterols, stilbenes, vitamins, lignans and terpenoids including carotenoids (Hooper and Cassidy 2006; Kirby and Keasling 2009; Stan et al. 2008). Although it is well-known that AM fungi can stimulate synthesis of phenolic compounds (phenolic acids, flavonoids) and activate the carotenoid pathway in roots (Harrison and Dixon 1993, 1994; Morandi 1996; Schliemann et al. 2008; Strack and Fester 2006), only a few analyses have targeted final crop products (leaves, roots or fruits) of mycorrhizal plants used in food or in medicinal remedies (Table 3). Nonetheless, these studies indicate that activation of plant secondary metabolism in response to AM fungi can result in increases in essential oil concentration of plant tissues or in the content of individual molecules. The reported data also show that even under field conditions AM fungi can enhance leaf, fruit or bulb accumulation of many molecules with medicinal interest (Table 3). For example, the 95% increase in artemisinin concentration in leaves of mycorrhizal *Artemisia annua* (Chaudhary et al. 2008) is of both medical and economical interest since artemisinin, which is highly priced, is considered as the best treatment for uncomplicated malaria when used as part of a combination therapy (Kirby and Keasling 2009).

It is however important to note that the beneficial impact of AM fungi on plant mineral and secondary metabolite contents depends not only on AM fungal species or isolates, but also on plant genotype and fertilisation regime (Chaudhary et al. 2008; Gianinazzi et al. 2008; Khaosaad et al. 2006; Perner et al. 2008; Sailo and Bagyaraj 2005; Toussaint et al. 2007), which again underlines the need to develop crop management strategies using appropriate plant/AM fungal combinations and culture practices for the production of mycorrhizal plants with nutritional quality.

Necessary resources for future management of AM ecosystem services

In the context of fingerprinting AM fungal activity in situ, international culture collections such as INVAM (http://invam.caf.wvu.edu), IBG (http://www.kent.ac.uk/bio/beg/) or GINCO (http://emma.agro.ucl.ac.be/ginco-bel/) which hold well-defined isolates could help considerably by acting as a germplasm reference reservoir for managing the contribution of mycorrhizal fungi to ecosystem services. The activity of these collections could expand and evolve towards providing innovative on-request services aimed at (a) preserving commercial fungal lines, (b) assessing inoculum quality for industrials and producers (quality label) (Gianinazzi et al. 1989), (c) exploiting molecular technologies to elaborate molecular probes to identify (barcoding) or monitor AM fungi and (d) providing technical

Table 3 Effect of AM fungi on secondary metabolism in leaves, roots or fruits/tubers of different crops used as food or for medicinal purposes

Plant	AM fungus	Growth conditions	Increase in secondary metabolism	Reference
Allium cepa	Commercial inoculum containing *Glomus mosseae, Glomus intraradices, Glomus claroideum, and Glomus microaggregatum*	Greenhouse experiment, 14 weeks	Quercetin-4′-O'monoglucoside concentration in bulbs, 52% Antioxidant activity in bulbs, 36%	Perner et al. 2008
	G. intraradices BEG141	Field experiment, up to harvest	Methyl cysteine sulfoxide concentration in bulbs, 106%	Gianinazzi et al. 2008
	G. mosseae BEG12		Isoalliine concentration in bulbs, up to 48%	
Anethum graveolens	*Glomus macrocarpum, Glomus fasciculatum*	Field experiment, 15 weeks	Essential oil concentration in fruits, 90%	Kapoor et al. 2002a
			Limonene concentration in fruits, 77%	
			Dihydrocarvone concentration in fruits, 110%	
			Carvone concentration in fruits, 117%	
Artemisia annua	*G. macrocarpum, G. fasciculatum*	Field experiment, 12 weeks	Essential oil concentration in leaves, 66% Artemisinin concentration in leaves, up to 95%	Chaudhary et al. 2008
Coleus forskohlii	*Acaulospora laevis*	Greenhouse experiment, 150 days	Forskolin concentration in roots, up to 147%	Sailo and Bagyaraj 2005
	Gigaspora margarita, G. bagyarajii, G. etunicatum, G. fasciculatum *G. intraradices, Glomus leptotichum*			
	G. macrocarpum			
	G. monosporum, G. mosseae			
	Scutellospora calospora			
Coriandrum sativum	*G. macrocarpum, G. fasciculatum*	Greenhouse experiment, up to fruit harvest	Essential oil concentration in fruits, up to 43%	Kapoor et al. 2002b
			α-pinene concentration in fruits, up to 697%	
			β-pinene concentration in fruits, up to 48%	
			p-cymene concentration in fruits, up to 280%	
			δ-linalool concentration in fruits, up to 9%	
			Geraniol concentration in fruits, up to 408%	
			β-caryophyllene concentration in fruits, up to 54%	
Echinacea purpurea	*G. intraradices* DAOM181602	Greenhouse experiment, 13 weeks	Total phenolics concentration in shoots, 67%	Araim et al. 2009
Foeniculum vulgare	*G. macrocarpum, G. fasciculatum*	Field experiment, 15 weeks	Essential oil concentration in fruits, 78%	Kapoor et al. 2004
			Methyl chavicol concentration in fruits, 6%	
			cis-anethol concentration in fruits, 211%	
			trans-anethol concentration in fruits, 7%	
Ipomoea batatas	*G. intraradices* BEG141	Field experiment, up to harvest	β-carotene in tuber, up to 25%	Farmer et al. 2007
	G. mosseae BEG167		β-carotene in tuber, up to 40%	
Ocimum basilicum	*Gigaspora rosea* BEG9	Growth room, 63 days	Essential oil concentration in leaves, 50%	Copetta et al. 2006
			Rosmarinic acid concentration in leaves, 50%	

Table 3 (continued)

Plant	AM fungus	Growth conditions	Increase in secondary metabolism	Reference
			α-terpineol concentration in leaves, 63%	
	Glomus caledonium BEG162	Greenhouse experiment, 7 weeks	Caffeic acid concentration in shoots, 50%	Toussaint et al. 2007
	G. intraradices (commercial inoculum)	Greenhouse experiment, 16 weeks	Anthocyanin concentration in leaves, 35%	Lee and Scagel 2009
Origanum vulgare	*G. mosseae* BEG12	Greenhouse experiment, 12 weeks	Essential oil concentration in leaves, up to 50%	Khaosaad et al. 2006
Trachyspermum ammi	*G. macrocarpum, G. fasciculatum*	Field experiment, 15 weeks	Essential oil concentration in fruits, 70%	Kapoor et al. 2002a
			Para-cymene concentration in fruits, 26%	
			Thymol concentration in fruits, 51%	
Vitis vinifera	*A. laevis*, *Acaulospora scrobiculata*, *Entrophospora colombiana*, *Gigaspora gigantea*, *Glomus manihotis*, *Scutellospora heterogama*	Greenhouse experiment, 60 days	Carotenoid concentration in leaves, up to 31% Total phenolic concentration in leaves, up to 900%	Krishna et al. 2005

information and training for industrials and users (http://www2.dijon.inra.fr/pme/index.htm).

AM fungi vary in their ability to provide ecological services and suitable tools have to be defined in order to fully evaluate their contribution. Molecular tools have considerably improved the possibility to identify and monitor AM fungi in ecosystems but a quick and reliable test for evaluating their functionality is still lacking. The alkaline phosphatase test has represented a first attempt towards this goal (Tisserant et al. 1993).

Concluding comments

With the development of industrial agriculture, field labour and chemical input have «substituted» ecosystem services but the high amounts of energy and chemical products needed to support this production system have reached a limit (IAASTD report 2008). If the risk of large, costly,or irreversible changes is to be reduced or avoided, future (modern) agriculture should be based on the implementation of ecological management practices that deliberately maintain resilience of ecosystem services. This means integrating the development of crop management strategies that optimise the impact of beneficial microbes, like AM fungi, on plant production. Present-day industrial agricultural practices place several constraints on the use of services provided by mycorrhiza; however in order to manipulate AM fungi and to achieve their efficient use for long-term agricultural stability and productivity, we have to increase our knowledge on the impact of different production strategies on both the diversity of AM fungal communities and its relation to production quantity and quality. Future work has to focus on the:

- reduction of (a) tillage which disrupts the mycelial network and reduces AM fungal diversity, (b) bare fallows which impact on AM fungal diversity by the absence of host-plants, (c) chemical fertiliser usage which decreases AM fungal root colonisation, (d) the use of non-mycorrhizal crops in rotation which decreases the abundance of AM fungi through allelopathic effects, (e) biocide and soil fumigant treatments toxic to AM fungal communities;
- development of production strategies, which mimic natural processes via (a) the use of organic fertilisers promoting AM fungal colonisation and effectiveness, (b) the promotion of ley farming periods to increase AM fungal potential and diversity, (c) the diversification of crop rotations with limited use of non-mycorrhizal crops in order to increase AM fungal populations and diversity, (d) the inoculation with mixed AM fungal inocula to overcome detrimental effects of management practices on AM fungal populations.

A key point in the application of such management methods is a change in breeding strategies from the selection of plants adapted to high fertiliser and biocide usage to the selection of plants with increased capacities to exploit AM fungal attributes

The large-scale exploitation of AM fungi into plant production systems has so far been hampered by (a) the use of selected crop varieties that are recalcitrant to mycorrhizal fungi, (b) the decreased implementation of crop rotation systems and (c) excessive chemical inputs. Additional barriers to rationally exploiting beneficial soil microbes like AM fungi as ecosystem services range from economical, technical and cultural aspects to legislative policy. The development of the mycorrhiza inoculum producing industry is faced with these different problems, which limits its contribution to the development of AM fungi as ecological services in agricultural soils. Nevertheless, considerable progress has been made in the last decade towards the use of AM fungi, particularly for the production of high value crops such as ornamentals or fruit trees. Furthermore, recent knowledge on the optimization of the role of AM fungi in the production of health-related biomolecules by fruits or vegetables having pharmaceutical properties is opening a new window for the mycorrhizal industry.

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