Arbuscular mycorrhizal fungi act as biostimulants in horticultural crops

Youssef Rouphael[a*], Philipp Franken[b], Carolin Schneider[c], Dietmar Schwarz[d], Manuela Giovannetti[e], Monica Agnolucci[e], Stefania De Pascale[a], Paolo Bonini[f], Giuseppe Colla[g]

[a]*Department of Agricultural Sciences, University of Naples Federico II, Via Università 100, 80055 Portici, Italy*

[b]*Department of Plant Propagation, Leibniz-Institute of Vegetable and Ornamental Crops, Kühnhäuser Straße 101, 99090 Erfurt, Germany*

[c]*INOQ GmbH, Solkau 2, 29465 Schnega, Germany*

[d]*Leibniz Institute of Vegetable and Ornamental Crops, Theodor Echtermeyer Weg 1, 14979 Großbeeren, Germany*

[e]*Department of Agriculture, Food and Environment, University of Pisa, Via del Borghetto 80, 56124 Pisa, Italy*

[f]*Italpollina S.p.A., 37010 Rivoli Veronese, Italy*

[g]*Department of Agriculture, Forestry, Nature and Energy, University of Tuscia, 01100 Viterbo, Italy*

*Corresponding author. Fax: +39-(081) 7755129.

E-mail address: youssef.rouphael@unina.it (Y. Rouphael)

Abstract

In the coming years, more sustainable horticultural practices should be developed to guarantee greater yield and yield stability, in order to meet the increasing food global demand. An environmentally-friendly way to achieve the former objectives is represented by the biostimulant functions displayed by arbuscular mycorrhizal fungi (AMF). AMF support plant nutrition by absorbing and translocating mineral nutrients beyond the depletion zones of plant rhizosphere (biofertilisers) and induce changes in secondary metabolism leading to improved nutraceutical compounds. In addition, AMF interfere with the phytohormone balance of host plants, thereby influencing plant development (bioregulators) and inducing tolerance to soil and environmental stresses (bioprotector). Maximum benefits from AMF activity will be achieved by adopting beneficial farming practices (e.g. reduction of chemical fertilisers and biocides), by inoculating efficient AMF strains and also by the appropriate selection of plant host/fungus combinations. This review gives an up to date overview of the recent advances in the production of quality AMF inocula and in the biostimulant properties of AMF on plant health, nutrition and quality of horticultural crops (fruit trees, vegetables, flower crops and ornamentals). The agronomical, physiological and biochemical processes conferring tolerance to drought, salinity, nutrient deficiency, heavy metal contaminations and adverse soil pH in mycorrhizal plants are encompassed. In addition, the influence of bacterial interactions and farm management on AMF is discussed. Finally, the review identifies several future research areas relevant to AMF to exploit and improve the biostimulant effects of AMF in horticulture.

Keywords: abiotic stresses, biofertilisers, *Rhizophagus irregularis*, *Funneliformis mossae*, *Glomus* spp., horticulture, phytochemical compounds, sustainability.

Contents

1. Introduction

A primary issue for modern horticulture is facing two contradictory objectives, such as the need to produce food for the increasing world population and to minimise damage to the environment, which can in turn negatively impact horticulture (Duhamel and Vandenkoornhuyse, 2013). Meeting the former two goals represents a major sustainability challenge to the horticultural industry and scientists (Owen et al., 2015). In the last decade, several technological innovations were proposed in order to enhance the sustainability of production systems through a significant reduction of chemicals. A promising and effective tool would be the use of 'biostimulants'. The term biostimulants, often used in the plural form (Hamza and Suggars, 2001), refers to a group of compounds that act neither as fertilisers nor as pesticides, but have a positive impact on plant performance when applied in small quantities (du Jardin, 2012; Calvo et al., 2014). However, plant biostimulant is still a 'moving target' in the European Union, and its use in the scientific community is still nebulous (du Jardin, 2012). According to a general definition introduced by the European Biostimulants Industry Council (EBIC) in 2012, 'Plant biostimulants contain substance(s) and/or microorganisms whose function when applied to plants or to rhizosphere is to stimulate natural processes to enhance nutrient uptake, efficiency, tolerance to abiotic stress, and crop quality, with no direct action on pests' (www.biostimulants.eu). Among beneficial microorganisms, arbuscular mycorrhizal fungi (AMF) play a key role in plant performance and nutrition due to their capacity to improve plant mineral uptake (Smith and Read, 2008). AMF can only be grown in the presence of host plants (i.e. obligate symbionts; Owen et al., 2015), and are widely used in horticulture, in particular *Rhizophagus* (formerly known as *Glomus*) *intraradices* and *Funneliformis* (formerly known as *Glomus*) *mosseae* (Krüger et al., 2012). In fact, while the majority of inoculants presented on the market were mostly nitrogen-fixing bacteria products, it is expected that phosphorus-mobilising products including AMF will see an increase in demand (Transparency Market Research, 2014).

AMF symbiosis is particularly important for enhancing the uptake of the relatively immobile and insoluble phosphate ions in soil, due to interactions with soil bi- and trivalent cations, principally Ca^{2+}, Fe^{3+}, and Al^{3+} (Tinker and Nye, 2000; Fitter et al., 2011). The basis of this symbiosis is the capacity of AMF to develop a network of external hyphae capable of extending the surface area (up to 40 times) and also the explorable soil volume for nutrient uptake (Giovannetti et al., 2001), throughout the production of enzymes and/or excretions of organic substances (Marschner, 1998). AMF can secrete phosphatases to hydrolyse phosphate from organic P compounds (Koide and Kabir, 2000; Marschner, 2012), and thus improving crop productivity under low input conditions (i.e. phosphorus deficiency, Smith et al., 2011). The extraradical hyphae are also important to increase the uptake of ammonium, immobile micronutrients such as Cu and Zn and other soil-derived mineral cations (K^{+}, Ca^{2+}, Mg^{2+}, and Fe^{3+}) (Clark and Zeto, 2000; Smith and Read, 2008). AMF have been shown not only to improve plant nutrition (biofertilisers), but they also interfere with the phytohormone balance of the plant, thereby influencing plant development (bioregulators) and alleviating the effects of environmental stresses (bioprotector). This leads not only to increases in biomass and yield, but also to changes in various quality parameters (Antunes et al., 2012). The production of horticultural crops with high contents of phytochemicals (i.e. carotenoids, flavonoids and polyphenols) is a primary target that meets the demands of consumers and researchers due to their health-benefit effects (Rouphael et al., 2010a). In a recent review, Sbrana et al. (2014) reported that AMF symbiosis could induce changes in plant secondary metabolism leading to the enhanced biosynthesis of phytochemicals with health promoting properties. The same authors suggested that further research should investigate the mechanism(s) responsible for the increase in plant secondary metabolism through the selection of promising AMF taxa that are able to improve the nutraceutical value of horticultural products (Giovannetti et al., 2013).

In addition to the advantages mentioned above, AMF impart other important benefits such as tolerance to drought (Augé, 2001; Jayne and Quigley, 2014) and adverse soil chemical conditions in particular salinity (Evelin et al., 2009; Porcel et al., 2012), nutrient deficiency, heavy metal contamination (Garg and Chandel, 2010) and adverse soil pH conditions (Seguel et al., 2013; Rouphael et al., 2015).

Another promising tool and a meaningful approach for sustainable horticulture would be the co-inoculation with AMF and other microorganisms such as bacteria (i.e. PGPR) and beneficial fungi (i.e. *Trichoderma* spp.) (Xiang et al., 2012; Nadeem et al., 2014; Colla et al., 2015). The combined use of bacteria and AMF has been investigated in several studies but with contrasting results (Nadeem et al., 2014; Baum et al., 2015; Owen et al., 2015; Colla et al., 2015 and references cited therein). The synergetic/antagonistic effects of microbial inoculants were attributed to the nature and compatibility of the microbial strains used, as well as the interactions that take place between bacteria/fungi and plant species. Therefore, understanding which factors limit the performance of these bio inoculants will be very useful for improving the efficiency of this inoculum pool (Xiang et al., 2012; Nadeem et al., 2014).

Crop management involves a number of practices, which can influence AM symbiosis positively or negatively (See chapter 4; Gosling et al., 2006 and references cited therein). For instance, ploughing and high fertiliser application (i.e. P) can decrease AMF abundance and colonisation (Daniell et al., 2001; Avio et al., 2013; Lehmann et al., 2014). Other factors that may have detrimental effects on AMF symbiosis include the use of specific biocides and cropping with non-host plants (i.e. *Brassicaceae*, *Chenopodiaceae*) (Njeru et al., 2014). The later factor can be more deleterious to a highly mycorrhizal plants than phosphorus application or tillage (Gavito and Miller, 1998a).

Another important factor is the genotype of a crop. Different cultivars of tomato, for instance, can respond to mycorrhization either with positive growth responses or with an increase in shoot phosphate concentrations (Boldt et al., 2011). Also, the fungal strain which is selected and used for inoculation of the plants can play a role. In petunia, for example, three different fungal species showed generally positive effects, but only one was able to protect the plant against a pathogenic root fungus (Hayek et al., 2012). Particular effects of AM fungal inoculation should therefore be tested among different genotypes and environmental conditions.

In short, the maximum multiple benefits will be obtained using efficient AMF strains after the accurate selection of compatible species/genotype-fungus combinations, and through favourable management practices (Regvar et al., 2003).

The present review focuses on the recent advances of the biostimulant actions of AMF on plant health, nutrition and quality of horticultural crops (fruit trees, vegetables and ornamentals). The agronomical and physiological processes conferring tolerance to abiotic stresses in AMF plants as well as the influence of bacteria interaction and farm management will also be covered. The review will conclude by identifying several possibilities for future studies to improve the biostimulant.

2. Arbuscular mycorrhizal fungi

2.1. Taxonomy

AMF are formed between roots and a particular group of fungi, which are taxonomically separated from all other true fungi in the phylum *Glomeromycota* (Schüssler et al., 2001).

Fossil and molecular phylogenetic data indicate that the first land plants already harboured AMF and would probably not have been able to enter the land without (Redecker et al., 2000). AMF are probably the most widespread plant symbionts and are formed by 80-90% of land plant species (Newman and Reddell 1987). This includes numerous important horticultural crops among the *Solanaceae* (e.g. tomato, eggplant or petunia), the *Alliaceae* (e.g. onion, garlic and leek), fruit trees (e.g. grapevine, citrus sp.), ornamentals and herbal plants (e.g. basil, thyme, rosemary). With a few exceptions, all AMF can form a mutualistic interaction with all mycorrhizal plants (Smith and Read, 2008). It is therefore not possible to recommend particular AM fungal strains for certain horticultural crops. However, because species of the genera *Gigaspora* and *Scutelleospora* may be harmful to the soil structure, most commercial inocula contain species of the genera *Rhizophagus* and *Funneliformis*. These species are present in almost all soils under a wide range of all climate zones (Smith and Read, 2008) and can, therefore, be applied in horticultural production in all geographical regions.

2.2. Life cycle and formation of AMF symbiosis

The life cycle of AM fungi starts with the asymbiotic phase by germination of the asexually formed chlamydospores in soil. This purely depends on physical factors such as temperature and humidity. As AM fungi are obligate biotrophs, they retract the cytoplasm without the presence of a plant and return to the dormant stage. Near plant roots, however, the pre-symbiotic phase starts with ramification of the primary germ tube (Giovannetti et al., 1993). This can be also induced by root exudates (Tamasloukht et al., 2000) or by particular metabolites like strigolactones (Akiyama et al., 2005). Upon physical contact with the root surface, the fungus builds up hyphopodia (appressoria) on the root surface. On the plant side, epidermal cells underlying hyphopodia undergo a particular mycorrhiza-specific process. They form the so-called pre-penetration apparatus, a transient intracellular structure which is used by the fungus to enter the root (Genre et al., 2005). Fungal hyphae colonise the roots first between or through cells with linear or simple coiled hyphae (Gianinazzi-Pearson and Gianinazzi, 1988). When reaching the inner cortex, the fungus changes the mode of colonisation and builds up highly branched hyphal tree-like structures in the apoplast of the plant cells, the name-giving arbuscules. Members of the *Glomineae* can also form lipid-rich vesicles as storage organs (Walker 1995). In parallel with root colonisation, the fungus explores the surrounding soil with its hyphae, where they can take up nutrients, interact with other microorganisms and colonise roots of neighbouring plants belonging to the same or different species. Hence, plants and their AM fungi are connected in a web of roots and hyphae (Read, 1998; Giovannetti et al., 2004) where they are able to exchange nutrients (Mikkelsen et al., 2008) or signals (Song et al. 2010). Finally, new chlamydospores are formed at the extraradicular mycelium and the life cycle is closed.

2.3. Production of inocula and quality aspects

Horticultural crops inoculated with AMF are becoming common practice, especially in intensive horticultural cropping systems due to the reduction of indigenous AMF populations in the soil. However, a high-quality inoculum is necessary for successful root colonisation with AMF, and should include: 1) blends of AMF (i.e. two or more mycorrhizal species are better than one); 2) high numbers of infective AMF propagules; 3) absence of plant pathogens and pests; 4) the presence of beneficial bacteria and additives which promote root mycorrhizal colonisation and activity; 5) dry solid inoculum (long shelf-life). Being obligate biotrophic organisms, AMF propagules can be produced on the roots of plants grown in an open field (e.g. ‘on-farm inoculum’; Douds et al. 2012) or in containers in greenhouses (Feldmann and

Schneider, 2008) (Fig. 1). Field propagation is the cheapest way to propagate AMF. Briefly, inoculated-host plants are cultivated in sandy soil, allowing the AMF to develop and propagate by themselves. Mycorrhizal roots and soil containing propagules are harvested at the end of the growing cycles, dried and used as inoculum. Despite the simplicity of this propagation method, there are several disadvantages like inconstant production, difficulty of spore harvest, and a high risk of inoculum contamination by pests, pathogens and weeds. Many of these problems could be solved by the soilless production of AMF inoculums in greenhouses using sterile substances, such as vermiculite, to grow host plants (Fig. 1). Moreover, commercial AMF inoculum from unsterile production can be a rich source of Plant Growth Promoting Microorganisms (PGPM) and mycorrhiza-helper-bacteria (Schneider and Döring, 2015, unpublished).

Among the mycorrhizal inocula found on the market, there is particular focus on products based on spores produced on the roots of plants under monoxenic conditions (*in vitro* culture system, Figure 1). Two main sterile *in vitro* systems were successfully developed for the production of mycorrhizal propagules monoxenically: 1) AMF are propagated on genetically modified Ri T-DNA roots by *Agrobacterium rhizogenes* (for review see Fortin et al., 2002; Declerck et al., 2005) and grown in the so-called Root Organ Culture (ROC) in Petri dishes; and 2) AMF are propagated on autotrophic plants, in which the shoot part develops outside the Petri dish either directly in the aerial environment (Voets et al., 2005) or in a sterile tube vertically connected to the dish (Dupré de Boulois et al., 2006). Both culture systems were adapted for large scale mycorrhizal inoculum production for commercial purposes, using small containers (Adholeya, 2003), airlift bioreactors or mist bioreactors (Jolicoeur et al., 1999; Fortin et al., 1996), container-based hydroponic culture systems or extended AM-P under a hydroponic system (Declerck et al., 2009). The *in vitro* culture system combines several advantages such as: 1) a pure and non-contaminated product (sterile conditions), 2) easy traceability and follow-up, 3) easy to concentrate, and 4) the potential to produce mycorrhizal propagules all year round. However, *in vitro* propagation is only applicable to *Rhizophagus irregularis,* and the short shelf life of inoculum, due to its liquid form, could also limit the commercial application. Furthermore, there are still very few long-term studies and direct comparisons of products from unsterile or sterile production systems, but negative impacts of sterile production methods have been reported (Calvet et al., 2013). Finally, several challenges are still arising, such as the urgent need for commercial products having a high concentration of infective propagules, and advanced inoculum forms (i.e. tablets, gel) to simplify the application in horticultural crops.

3. Functional significance of bacteria associated with AMF

The establishment and efficiency of AMF symbiosis may be affected by bacteria living associated with mycorrhizal roots, spores, sporocarps and extraradical hyphae. Bacteria associated with AMF show different functional abilities, particularly the promotion of spore germination and asymbiotic hyphal growth. Although spores of some AMF species germinate well in axenic culture, higher spore germination percentages and germling extent have been reported in the presence of soil and rhizosphere microorganisms. For example, *Streptomyces orientalis* promoted the spore germination of *F. mosseae* (Mugnier and Mosse, 1987), while different gram-positive bacteria, including *Paenibacillus* spp. and *Bacillus* spp., isolated from the mycorrhizosphere, stimulated AMF growth (Artursson and Jansson, 2003). Among the gram-positive bacteria, *Paenibacillus validus* was able to induce the production of fertile spores of *R. intraradices* Sy167 in dual culture, even in the absence of plant roots (Hildebrandt et al., 2006). Nevertheless, scant information is available on the mechanisms of bacterial activity on spore germination and hyphal growth. Some authors have reported that the germination of *G. margarita* spores was increased by the release of volatile compounds in axenic culture by field isolates of *Streptomyces* spp. (Tylka et al., 1991). Other authors showed that factors released by *Bacillus subtilis* and *Mesorhizobium mediterraneum* produced differential effects on *F. mosseae* and *G. rosea* spore germination and growth (Requena et al., 1999).

Recent findings showed that bacteria living intracellularly in AMF spores may play a role in spore germination and hyphal growth, as the intracellular symbiont *Burkholderia vietnamiensis* enhanced the germination frequency of *Gigaspora decipiens* spores (Levy et al., 2003). The discovery that intracellular unculturable symbionts - assigned to *Mollicutes*-related endobacteria (Mre) and to *Burkholderiaceae* - not only occur in the family *Gigasporaceae* (Bianciotto et al., 2000), but also across different lineages of AMF, confirming the importance of such entities in the AMF life cycle (Desirò et al., 2014; Agnolucci et al., 2015).

Several bacterial taxa live intimately associated with AMF spores, often embedded in the outer spore wall layers or in the microniches formed by the peridial hyphae interwoven around the spores of various *Glomus* species (Walley and Germida, 1996; Filippi et al., 1998). Such bacterial communities showed chitinolytic activity, which could play an essential and functional role in AMF spore germination (Ames et al., 1989). For example, chitinolytic bacteria represented 72% of all the chitinolytic microorganisms isolated from spore walls of *F. mosseae* (Filippi et al., 1998). Accordingly, recent culture-independent methods, such as PCR denaturing gradient gel electrophoresis (DGGE) analyses, detected bacterial taxa that are able to degrade biopolymers (*Cellvibrio*, *Chondromyces*, *Flexibacter*, *Lysobacter*, and *Pseudomonas*) in spore homogenates, suggesting that their ability to digest the outer walls of

AMF spores, mainly composed of chitin, may promote spore germination (Roesti et al., 2005; Long et al., 2008).

Mycorrhizospheric bacteria also showed plant growth-promoting properties, including indole acetic acid (IAA) production, nitrogen fixation, solubilisation of phosphate and phytates (Bharadwaj et al., 2008; Richardson et al., 2009). Such functional abilities are very important for the possible use of AMF and their associated bacteria as biofertilisers. Indeed, bacterial ability to solubilise mineral phosphate is an important functional trait. Phosphorus, a key element for plant growth, is poorly available, forming insoluble compounds with aluminium/iron and with calcium in acid and alkaline soil, respectively. Recent works have reported that phosphate-solubilising bacteria living in the hyphosphere of *R. irregularis* promote the mineralisation of soil phytate and plant phosphorus uptake (Zhang et al., 2014).

Additional functional activities of AMF-associated bacteria have been reported, such as the production of antibiotics providing protection against fungal plant pathogens (Citernesi et al., 1996; Li et al., 2007), the synthesis of bioactive compounds (Jansa et al., 2013) and the supply of nutrients and growth factors (Barea et al., 2002).

It is important to note that, as AMF are obligate plant symbionts, with soil-based hyphae and spores, the composition of bacterial communities living strictly associated with spores may vary depending on environmental variables. These may include specific spore wall composition and root exudates (Roesti et al., 2005), or culture substrates and host plant identity (Long et al., 2008). In a recent molecular work, the diversity of bacterial communities associated with the spores of six AMF isolates, belonging to different genera and species and maintained for several generations with the same host plant, under the same environmental conditions and with the same soil, has been investigated (Agnolucci et al., 2015). Results showed that such isolates displayed diverse bacterial community PCR-DGGE profiles, unrelated to their taxonomic position, suggesting that each isolate recruits different microbiota on its spores.

In conclusion, the emerging picture of mycorrizospheric interactions is one of a previously unimagined complexity, where different partners of a tripartite association - host plants, AMF and bacteria - may positively interact and provide new multifunctional benefits improving plant and fungal performances. For example, AMF associated bacteria may be transported along hyphae to the relevant soil volume explored (hyphosphere), where they may enhance nutrient availability (e.g. phosphate solubilizing, nitrogen fixing and chitinolytic bacteria) (Cruz and Ishii, 2011), control plant pathogens (e.g. siderophore and antibiotic producing bacteria) and promote plant growth (e.g. IAA producing bacteria). Further studies should be carried out in order to understand whether different compositions of AMF-associated bacterial communities may determine differential performances of AMF isolates, in terms of infectivity and efficiency. Successively, individual bacterial strains should be isolated from the best performing communities, in order to investigate their functional significance and select the best AMF/bacteria combinations to be utilised as biofertilisers and bioenhancers.

4. Influence of crop management practices on AMF

Efficient crop management is established to achieve horticultural produces with high yield and quality. In a previous review paper, Gosling et al. (2006) stated that ‘crop management involves a range of practices which can impact on the AMF association, both directly, by damaging or killing AMF, and indirectly, by creating conditions that are either favourable or unfavorable to AMF’. Compared with natural ecosystems, crop management has a negative impact on the AMF association. Agricultural soils are AMF impoverished, particularly in terms of numbers of species (Helgason et al., 1998; Menendez et al., 2001). These soils are often dominated by *Glomus* spp. (Oehl et al., 2003). The impact of various agricultural practices on soil biodiversity and AMF is still poorly understood (Verbruggen et al., 2010). A detailed review of their impact was published by Gosling et al. (2006). Here, we summarise the results, and add missing practices in horticultural crops and novel insights since then.

4.1. Practices benefiting AMF

Crop rotation has a strong impact on the population and activity of AMF. A low diversity of host plants seems to be related to a low diversity and the benefit of AMF. In its most extreme form, long periods of monoculture reduce soil quality in terms of microbial diversity and community structure (Hijri et al., 2006; Jiao et al., 2011). Although monoculture may not reduce the number of fungi, as found for watermelon compared with watermelon intercropped with pepper (Sheng et al., 2012), such data seem to be exceptional. Independent of the composition and length of rotations, most authors agree that they enhance both the density and diversity of AMF (Larkin, 2008; Vestberg et al., 2011). The more diverse the rotation, the better for AMF. Increasing crop diversity includes not only agricultural crops but also covers crops and weeds (Daisog et al., 2012; Njeru et al., 2015). Among the four cover crops compared, hairy vetch caused the highest AMF spore abundance. However, AMF species' richness and diversity were highest in fields with a mixture of seven cover crops analysed after a following tomato production (Njeru et al., 2015). Thus, the cropping history is also important for the promotion of AMF (An et al., 1993). Within the rotation, highly mycorrhizal-dependent crops seem to improve the density and diversity of AMF (Bharadwaj et al., 2007; McCain et al., 2011). In contrast, non-mycorrhizal hosts, such as *Brassicaceae*, may result in a reduced number of viable mycorrhizal propagules (Torres et al., 1995).

The use of organic fertilisers (e.g. manure, compost), and slow release mineral fertilisers (e.g. rock phosphate) do not seem to suppress AMF but may even stimulate them (Douds et al., 1997; Singh et al., 2011; Fernandez-Gomez et al., 2012; Cavagnaro, 2014). However, many authors emphasise a careful selection of organic amendments and no overuse (Ustuner et al., 2009). Moreover, the selection of organic amendments must take into consideration pesticide, heavy metals, humified organic matter, salinity, pH, soluble phosphorus and other inorganic nutrients.

Organic production is aimed at sustainable plant production that includes a diverse and active soil microbial community. Thus, organic horticulture *per se* is a benefit for AMF, as reported in many papers (Gosling et al., 2006; Galvan et al., 2009; Kelly and Bateman, 2010). Verbruggen et al. (2010) analysed whether organic farming improves AMF diversity and whether AMF communities from organically managed fields are more similar to those of species-rich natural grasslands or conventionally managed fields. The authors showed that the average number of AMF taxa was highest in grasslands (8.8), intermediate in organically managed fields (6.4) and lower in conventionally managed fields (3.9). These authors, thus, confirmed the hypothesis that higher AMF propagule numbers and diversity occurred in organic farming.

4.2. Practices impairing AMF

Within a rotation, bare fallow periods with a lack of host plants, non-mycorrhizal hosts, or crops with a weak colonisation, such as spinach (*Spinacea oleracea*) or pepper (*Capsicum annuum*), can have a significantly negative impact on AMF communities (Douds et al., 1997; Ryan and Graham, 2002; Njeru et al., 2015).

It is generally accepted that soil tillage strongly reduces AMF spore number and propagule sources and, thus, plant root colonisation by disrupting the mycorrhizal network (Galvez et al., 2001; Evans and Miller, 1988; Avio et al., 2013). However, exceptions are also possible here, particularly when the disturbance is low (Rasmann et al., 2009). Castillo et al. (2009) did not find a difference in AM diversity and intensity when comparing conventional tillage with no tillage treatments in six pepper or tomato production systems of small farmers.

Mycorrhization is possible and effective under irrigation (Baslam et al., 2012), even when treated wastewater was used (Vicente-Sanchez et al., 2014). However, the effectiveness of AMF in terms of root colonisation and impact on yield decreases with the enhancement and adaptation of the soil or substrate water status to high plant production (Kohler et al., 2009; Lazcano et al., 2014; Nedorost et al., 2014).

Comparable with the effect of irrigation on AMF is the effect of a sufficient and luxury nutrient supply to plants, particularly phosphorus. Although AMF can also be effective under an intensive fertigation, as shown for tomato (Fernandez et al., 2014), increased nutrient availability renders host plants unable to undergo symbiosis with AMF. This results in a lowered AM propagule density and AM colonisation (Naher et al., 2013). Thus, the application of higher soluble P concentrations hampers mycorrhizal formation (Bolan et al., 1984) and the mycorrhizal benefits can be annulled in some plants.

Horticultural crops are traditionally treated with large amounts of different fungicides in order to eliminate phytopathogenic fungi. However, most of these agents have detrimental effects on beneficial fungi, including AMF (Miller and Jackson, 1998; Carrenhoet al., 2000). Systemic fungicides, such as carbendazim and/or copper-based agents, such as copper-hydroxide, proved to have detrimental effects on AMF (Miller and Jackson, 1998; Xie Li et al., 2010). On the contrary, some fungicides such as metalaxyl and biological agents, stimulated root colonisation by *Glomus* species (Hwang et al., 1993; Udoet al., 2013). Hernandez-Dorrego et al. (2010) described the individual effects of 25 fungicides applied on leek foliage and soil. Fungicides containing prochloraz, mancozeb, iprodione, and tetramethylthiuram disulphide as well as fenarimole, and miclobutanil virtually eliminated or strongly inhibited mycorrhizal symbiosis. On the other hand, the colonisation was not affected by the soil treatment with fungicides containing chinosol, copper oxychloride, and propamocarb or after foliar application with fungicides containing fosethyl aluminium, ciprodinyl + fludioxonyl, fenhexamide, dimetomorph + folpet, and azoxytrobin. Results on other types of pesticides are even more confusing since their application can also have a transitory effect (Sarr et al., 2013).

Colonisation and sporulation of indigenous AMF may rapidly recover following inhibition after pesticide application (Deliopoulos et al., 2008; Ipsilantis et al., 2012). Different effects have also been reported depending on the hosts tested. Thus, the insecticide/acaricide ‘Phoxim’ was found to inhibit AM colonisation on carrot but not on green onion (Wang et al., 2011a, b). Indirect effects are explained for the use of antibiotics, such as streptomycin. They preferentially diminish bacteria and, thus, even enhance the abundance of AMF (Zhou et al., 2011). Herbicide application eliminating weeds diminishes plant diversity and, thus, the diversity and density of AMF. Therefore, if pesticide application is necessary, it is reasonable to suggest none or only the use of selected (biological) fungicides and other pesticides in low concentrations in order to reduce and avoid potential harmful effects on AMF.

An increasing number of scientists have investigated the use of AMF in soilless cultivation systems, although the beneficial and stimulatory effect of AMF on plant growth is disputed (Lee and George, 2005). The method would be particularly interesting for the mass production of inoculum (Ijdo et al., 2011). Horticultural plants of diverse families were tested, such as

Aliaceae, *Solanaceae*, *Cucurbitaceae*, as well as flower crops. As long as favourable organic substrates (e.g. coconut substrate) are used, the symbiosis may function and the conditions allow a successful colonisation of AMF (Lee and George, 2005). The more the system shifts to a hydroponics with less or inert substrate, the more difficult the colonisation becomes. In most cases, systems operate only when cultivated plants are pre-inoculated and the cultivation establishes all conditions that are beneficial for AMFs, as previously described (Hawkins and George, 1997). A low concentration of soluble P in the nutrient solution seems to be particularly important (Colla et al., 2008). Only Dugassa et al. (1995) reported a successful distribution of AMF in pure hydroponics using linseed (*Linum usitatissimum*). New infections arose since mycorrhizal donor plants were placed directly beside non-mycorrhizal plants.

Information on AMF symbiosis and grafted vegetables is rare. Kumar et al. (2015) reported that Maxifort used as a rootstock for tomato was easily inoculated and showed significantly better colonisation then self-grafted plants.

5. Effect of AMF on crop tolerance to abiotic stresses

5.1. Drought

AMF are known to present an effective and sustainable tool with which to enhance drought tolerance in horticultural crops, including fruit trees, vegetables and flowers (Asrar et al., 2012; Wu et al., 2013; Jayne and Quigley, 2014; Baum et al., 2015) (Table 1).

AMF often induces modifications in the root architecture of plants, in particular root length, density, diameter, and number of lateral roots (Wu et al., 2013 and references cited therein). Better root system architecture in mycorrhizal plants allowed the extraradical hyphae to extend beyond depletion zones of plant rhizosphere making the uptake of water and low mobile nutrients (i.e. P, Zn and Cu) more efficient under a water-deficient environment (Smith and Smith, 2011). Wu and Zou (2009) studied trifoliate orange (*P. trifoliate* L. Raf.) seedlings and found that colonisation with *Glomus versiforme* increased the leaf mineral composition (N, P, K, Ca, Fe, Mn and Zn) under drought stress conditions, in comparison to non-inoculated plants. In pistachio cultivars (*Pistacia vera* 'Qazvini' and 'Badami-Riz-Zarand') grown under greenhouse conditions, plants inoculated with AMF (*F. mosseae* and *R. intraradices*) enhanced the uptake of low mobile minerals such as P and Zn and provided a more favourable leaf water status under different drought conditions (Bagheri et al., 2012). Many studies have shown that inoculation with AMF improved drought tolerance of citrus plants by lowering the osmotic potential through the net accumulations of inorganic and organic solutes, with the latter also potentially acting as osmoprotectants (Wu et al., 2013 and references cited therein). The effectiveness of AM symbiosis to improve drought tolerance was also observed in many vegetable crops. Open field tomato (*Solanum lycopersicum* L.) inoculated with AMF (*R. intraradices*) affected the agronomical and physiological responses of exposure under varying intensities of drought (Subramanian et al., 2006). The fruit yield of inoculated plants under severe, moderate and mild drought stress were significantly higher by 25%, 23%, and 16%, respectively, compared to non-inoculated plants. The authors concluded that the higher crop performance of inoculated plants was attributed to a better nutritional status (higher N and P) in conjunction with the maintenance of leaf water status. This effect on tomato was confirmed by Wang et al. (2014), who demonstrated that the colonisation of processing tomato 'Regal 87-5' plants by *F. mosseae* and *G. versiforme* could increase marketable yield by 20% and 32%, respectively, compared with those of non-inoculated plants under slight and heavy drought stress conditions. Also, greenhouse melon (*Cucumis melo* L. ' Zhongmi 3') plants inoculated with three *Glomus* species: *G. versiforme* and *R. intraradices* and, especially, *F. mosseae* showed higher tolerance to drought stress than non-inoculated plants, as indicated by plant heights, root lengths, biomass production and net photosynthetic rates (Huang et al., 2011). The authors suggested that the increase in drought tolerance and the better crop performance could be attributed to the production of antioxidant enzymes (SOD, POD, CAT) and the accumulation of soluble sugars by AM symbiosis. Davies et al. (2002) investigated the mechanisms underlying the alleviation of drought by a mixture of *Glomus* spp. from Mexico ZAC-19 (*G. albidium*, *G. claroides* and *G. diaphanum*) in Chile ancho pepper (*Capsicum annuum* L. San Luis). The authors found that ZAC-19 can potentially be incorporated into Chile pepper transplant systems to alleviate the detrimental effect of drought in open field production in Mexico, as indicated by the higher root-to-shoot ratio and leaf water potential. Similarly Davies et al. (1993) showed that drought promoted greater extraradical hyphae development of *G. deserticola* in bell pepper and consequently a higher water uptake, compared to non-mycorrhizal plants. AMF symbiosis improved lettuce (*Lactuca sativa* L. 'Romana') tolerance to drought stress and recovery by modifying plant physiology and the expression of plants genes (Aroca et al., 2008; Jahromi et al., 2008). Lettuce inoculated with the AMF *R. intraradices* presented higher root hydraulic conductivity and lower transpiration under drought stress, when compared to non-inoculated plants. The authors highlighted that plants inoculated with AMF were able to regulate their abscisic acid (ABA) concentrations in a better and faster way than non-inoculated plants, allowing a better balance between leaf transpiration and root water movement during drought stress and recovery (Aroca et al., 2008; Jahromi et al., 2008). Analysis of drought-stressed strawberries (*Fragaria* × *ananassa*) inoculated with a single treatment of either *F. mosseae* BEG25, *F. geosporus* BEG11 or a mixed inoculation of both species, indicated that single or combined inoculation with AMF enhanced growth, yield and water use efficiency (WUE) compared to non-mycorrhizal plants (Boyer et al., 2015). Inoculation with AMF has been reported to enhance WUE in watermelon

(Omirou et al., 2013). This suggests that AMF not only enhances water uptake, but also results in the host plant becoming more efficient in using water (Omirou et al., 2013). This could also be attributed to mechanisms that are able to increase transpiration and stomatal conductance (Augé, 2001), and increase nutrient availability (Smith et al., 2011).

Asrar et al. (2012) demonstrated that potted snapdragon (*Anthirhinum majus* 'Butterfly') plant inoculated with AMF *G. deserticola* can alleviate the deleterious effect of drought stress on flower quality (flower number and diameter). The better crop performance of inoculated snapdragon grown under drought stress conditions was attributed to the improvement in nutrients content (N, P, K, Ca and Mg), water relations, and chlorophyll content of the plants.

5.2. Salinity

Several reviews investigated the role of AMF in alleviating the adverse effect of salinity in agricultural and horticultural crops (Garg and Chandel 2010; Porcel et al., 2012; Baum et al., 2015). The former reviews reported that although salinity can negatively affect AMF growth (Juniper and Abbott, 2006), crop performance of mycorrhizal plants is improved under salinity stress (Table 2).

Khalil (2013) and Wu et al. (2010) reported that grapevine rootstocks (*Vitis vinifera* L., 'Dogridge', '1103' 'Paulsen' and 'Harmony') and citrus seedlings inoculated with *R. intraradices* (for grapevine), *F. mosseae* and *Paraglomus occultum* (for citrus) exhibited greater growth parameters (plant height, stem diameter, shoot and root biomass) compared to the non-inoculated plants. The higher crop performance in inoculated grapevine and citrus seedlings was attributed to a lower concentration of Na and Cl and the higher K, Mg concentration in leaf tissue and also to the higher K/Na ratio (Wu et al., 2010; Khalil, 2013). Similarly, Porras-Soriano et al. (2009) found that inoculating olive (*Olea europea* L.)

seedlings with three strains of AMF (*F. mosseae*, *R. intraradices* and *Claroideoglomus claroideum*) increased shoot and root biomass, nutrient uptake and tolerance to salinity, with *F. mosseae* being the most efficient fungi. These results indicate that an accurate selection of AM fungus is crucial for enhancing the effectiveness under specific environmental conditions. Moreover, the positive effect of *F. mosseae* on olive growth seems to be due to increased K uptake. Under salt conditions, K concentration was increased under salt conditions by 6.4-, 3.4- and 3.7-fold with *F. mosseae*, *R. intraradices* and *C. claroideum*, respectively. Potassium, plays a key role in the osmoregulation processes and the highest salinity tolerance of *F. mosseae*-colonised olive trees was concomitant with an enhanced K concentration in olive plants (Porras-Soriano et al., 2009). Sinclair et al. (2014) demonstrated that AMF species (*F. caledonius, F. mosseae and R. irregularis*) enhanced the growth of three strawberry cultivars (‘Albion’, ‘Charlotte’ and ‘Seascape’) grown under four salt concentrations (0-200 mM NaCl). Under severe salt conditions (100-200 mM), *R. irregularis* mitigated salt stress to a higher degree than the other two AMF species, indicating that fungal inoculants should be screened on a genotype- and condition-specific basis (Sinclair et al., 2014).

Abdel Latef and Chaoxing (2011) addressed the question of whether tomato (‘Zhongzha’105) with *F. mosseae* is able to increase its salt tolerance. The authors reported that mycorrhization alleviated salt-induced reduction of growth and fruit yield, and found that the concentration of P and K was higher and Na concentration was lower in AMF in non-AMF tomato grown under 0, 50, and 100 mM NaCl. They also suggested that AMF colonisation was accompanied by an enhancement of the ROS-scavenging enzymes, such as superoxide dismutase (SOD), catalase (CAT), peroxidase (POD) and ascorbate peroxidase (APX) in leaves of salt-affected and control treatment. The greater activity of antioxidant enzymes in plants inoculated with AMF compared to non-mycorrhizal plants was associated with the lower accumulation of lipid peroxidation indicating lower oxidative damage in the mycorrhized plants. Similarly, Hajiboland et al. (2010) demonstrated that improvement in tomato tolerance to salt stress ('Behta' and 'Piazar') inoculated with *R. intraradices* was related to a higher uptake of P, K, and Ca and to lower Na toxicity. Mycorrhization also improved the net photosynthesis by increasing stomatal conductance and by protecting PSII (Hajiboland et al., 2010). Increased sink strength of AMF roots has been suggested as a reason for the often observed mycorrhizal promotion of stomatal conductance (Augé, 2000). Moreover, Al-Karaki (2000) showed that the accumulation of P, Cu, Fe and Zn was higher in inoculated (*F. mosseae*) than in non-inoculated tomato plants under both control and medium salinity, whereas the Na concentration in the shoot was lower in mycorrhized plants, confirming one more time that plant tolerance to salt stress is improved by AMF colonisation.

Kaya et al. (2009) and Beltrano et al. (2013) found that mycorrhizal pepper ('11B 14' and 'California Wonder 300') inoculated with *Rhizophagus clarum* and *R. intraradices* respectively, maintained greater shoot biomass at different salinity concentrations compared to non-inoculated plants. The lowest crop performance in non-mycorrhizal plants in the two studies was attributed to higher Na and lower N, P, K concentrations in leaf tissue and also to the high leaf electrolyte leakage. However, the salt stress effect on pepper shoot biomass differs significantly between different fungus species (Turkmen et al., 2008). Colla et al. (2008) demonstrated that inoculation with AMF (*R. intraradices*) may help to overcome salinity stress in zucchini squash (*Cucurbita pepo* L. 'Tempra'), another important greenhouse vegetable. Improved nutritional (higher K and lower Na concentration in leaf tissue) and leaf water status may have assisted the plants to translocate minerals and assimilate to the sink, as well as alleviating the impacts of salinity on fruit production (Colla et al., 2008). Also, onion (*Allium cepa* L.) and basil (*Ocimum basilicum* L.) inoculated with AMF can alleviate deleterious effects of soil or water salinity on crop yield and growth (Cantrell and Linderman, 2001; Zuccarini and Okurowska, 2008).

Concerning leafy vegetables, Jahromi et al. (2008) demonstrated that the isolate DAOM 197198 of *R. intraradices* could be considered a potential AMF candidate because it stimulated the growth of lettuce under two concentrations of salinity. This effect was also associated with higher leaf relative water content and lower ABA in roots, indicating that AMF plants were less strained than non-mycorrhizal plants by salinity, thus they accumulated less ABA. In addition, under salinity, AM symbiosis enhanced the expression of LsPIP1; the latter gene is involved in the regulation of transcellular water flux. Such enhanced gene expression could contribute to regulating root water permeability to better tolerate the osmotic stress generated by salinity (Jahromi et al., 2008). In a recent study, Aroca et al. (2013) showed that AMF *R. irregularis* alleviated the deleterious effects of salt stress in lettuce ('Romana') by altering the hormonal profiles (i.e. higher production of strigolactone) and positively affecting plant physiology, thus allowing lettuce plants to grow better under adverse conditions. Vincente-Sánchez et al. (2014) also demonstrated that AMF (*G. iranicum* var. *tenuihypharum sp. nova*) was able to alleviate the negative effects of irrigation with high salinity reclaimed water on the physiological parameters (e.g. photosynthesis and stomatal conductance) in lettuce.

The positive effect of AMF application under salinity conditions was also observed in several ornamental species. For instance, Navvaro et al. (2012) and Gómez-Bellot et al. (2015) demonstrated the effectiveness of *R. intraradices* and *G. iranicum* var. *tenuihypharum sp. nova* to improve the growth and ornamental quality of carnation (*Dianthus caryophyllus* L. Kazan) and euonymus (*E. japonica* Thunb.) under saline stress, due to the ability of these strains to enhance the uptake of P, K, Ca, and Mg and at the same time to reduce the translocation of toxic ions (i.e. Na^+ and Cl^-) to the shoot. This might indicate that toxic ions might be retained in intraradical AM fungal hyphae or compartmentalised in the root cell vacuoles without moving into the root cell cytoplasm, which could be translocated to the shoots.

5.3. Nutrient deficiency

Several scientific papers have shown that plants inoculated with AMF were more efficient in the uptake and translocation of macro- and micronutrients to the shoot than non-inoculated plants (Table 3, Smith and Read, 2008). For instance, Koide et al. (2000) investigated the phosphorus use efficiency (PUE), ratio of plant dry mass to available P content in the soil) of mycorrhizal and non-mycorrhizal plants. A mycotrophic lettuce (*Lactuca stativa* L. 'Paris Island Cos') and non-mycotrophic beet (*Beta vulgaris* L. 'RedBall') species were grown in P-deficient soil and inoculated with *R. intraradices*. Plants inoculated with AMF decreased the PUE of lettuce, without affecting that of beet. The large increase in P concentration of lettuce caused by AMF inoculation was not matched by a similar increase in dry matter, leading to a decrease in PUE. Xu et al. (2014) demonstrated that the soil P concentration required for maximum growth of asparagus (*Asparagus officinalis* L.) could be lowered by AMF (*F. mosseae*) inoculation associated with improved phosphorus utilisation efficiency. In fact, the maximum asparagus growth was obtained at soil phosphorus of 59.3 mg kg^{-1} in inoculated compared to 67.9 mg kg^{-1} in non-inoculated plants, indicating that AMF improves P efficiency in particular under low soil P concentration. In agreement with this, Lynch et al. (1991) described increased effects of AM colonisation on bean plants in low soil P concentration. It is well established that AMF are particularly P efficient in P-deficient soils (Smith and Read, 2008) and this benefit appears to extend to other macronutrients, in particular N (Watts-

Williams and Cavagnaro, 2014). However, at higher soil P and N concentrations, AMF colonisation is lower, so the potential nutrient uptake of AMF may be reduced (Williams and Cavagnaro, 2014). Azcón et al. (2008) tested the impact of AMF on the percentage of N uptake from N fertilisation under different N soil concentrations. The authors showed that AMF resulted in higher N uptake from fertilisation in the presence of medium concentration of N (6 mM), whereas an opposite trend was observed with high amounts of N fertilisation (9 mM) (Miransari, 2011). Also potted tomato ('Darnika') plants inoculated with two AMF species (*F. mosseae* and *R. Intraradices*) showed higher marketable fresh yield mainly at lower level of fertilisation (half and quarter-strength nutrient solution) (Nedorost and Pokluda, 2012). Similarly, inoculation of pepper ('Demre Sivrisi') seedlings with different AMF species (*F. mosseae*, *R. intraradices*, *Claroideoglomus etunicatum*, *R. clarum*, *F. caledonium* and the mixture of these fungi) had positive effects on growth and quality of seedlings (Ortas et al., 2011). Inoculated pepper plants exhibited earlier flowering time, higher shoot, root biomass and leaf P, and Zn concentration as compared to non-inoculated control plants. Ortas et al. (2011) recommended that AMF species can be used to compensate for P and Zn deficiency under clay and lime soils, which cause P, Zn and Fe deficiency in several vegetable crops (Ortas, 2008). Also, in pepper, Abdel Latef (2011) indicated that *F. mosseae* was able to maintain efficient symbiosis with pepper ('Zhongjiao') in Cu-deficient soils (0 or 2 mM of $CuSO_4$). Under Cu-deficient conditions, inoculated pepper plants were able to improve not only growth but also pigment (chlorophyll and carotenoids) biosynthesis, mineral nutrition (P, K, Ca, and Mg), and osmolyte accumulation, suggesting that pepper plants inoculated with AMF could cope with low Cu availability in the root zone. Moreover, according to Bona et al. (2015), strawberry 'Selva' inoculated with a commercial AMF containing *R. intraradices*, *G. ageratum*, *G. viscosum, C. etunicatum*, and *C. claroideum* with 70% of the conventional fertilisation also had higher yield, fruit number, and larger size of the fruits than non-inoculated plants with conventional fertilisation (100%).

Xiao et al. (2014) studied the growth, magnesium concentration, and photosynthesis of two citrus cultivars ‘Newhall’ (*Citrus sinensis* Osbeck ‘Newhall’) navel orange and ‘Ponkan’ (*Citrus reticulate* Blanco ‘Ponkan’) under both Mg-poor (0 mg L^{-1}) and Mg-rich (24 mg L^{-1}) conditions in potted culture. Plant growth parameters, Mg concentration in various plant tissues and CO_2 assimilation rates of Mg-stressed plants in both cultivars, especially the ‘Newhall’ seedlings were enhanced by mycorrhizal inoculation (*G. versiforme*).

Several ornamental plants responded with growth and flowering promotion on AMF inoculation, especially under low fertiliser conditions. Pelargonium (*Pelargonium peltatum* ‘Balcon Imperial Compact’) plants inoculated with three different commercially inocula with two rates of compost addition (20% and 40%) increased the number of buds and flowers, as well as shoot P and K concentration, especially with a low dose of compost (20%), but no improvement in shoot biomass and N concentration (Perner et al., 2007). In line with the previous study, Gaur et al. (2000) demonstrated that inoculation with mixed indigenous AMF (*Gigaspora* and *Scutellospora spp*.) led to a marked improvement in both vegetative (dry biomass and shoot height) and reproductive (number of flowers) parameters of *Petunia hybrid*, *Callistephus chinesis* and *Impatiens Balsamina*. Gaur et al. (2000) also stated that inoculation with mixed AMF inocula should be adopted at nursery level for nutrient-deficient soil conditions, because it could be at least 30% cost economic when compared to conventional chemical fertilisers.

5.4. Heavy metals

AMF play a significant agricultural and ecological role in mitigating the detrimental effect of heavy metal (HM) contamination by immobilization of metals in the fungal biomass (Andrade and Silveira, 2008). Xavier and Boyetchko (2002) stated that 'AMF can alter plant productivity, because mycorrhiza can act as bioprotectants, biofertilisers or biodegraders'. Therefore, the benefits of AMF could be associated with metal tolerance as well as with metal plant nutrition (Garg and Chandel, 2010).

Several investigations proved that AMF attenuated heavy metals toxicity of diverse vegetable and ornamental crops (Table 4). Kapoor and Bhatnagar (2007) investigated the effect of AMF (*G. macrocarpum*) on plant growth and cadmium (Cd) uptake of potted celery (*Apium graveolens* L.) grown in soil with 0, 5, 10, 40 and 80 mg kg^{-1} Cd. The AMF alleviate the detrimental effect of Cd in particular at the highest level, on shoot and root biomass production. Mycorrhizal celery plants exposed to Cd were able to improve the uptake of Mg, leading to a higher chlorophyll concentration, higher production of photosynthate and consequently more biomass production (Giri et al., 2003). Another reason for decreased Cd concentration in inoculated celery may be attributed to the dilution effect due to the increased biomass and sequestration of Cd in the fungal structures within the cortical cells (Kaldrof et al., 1999). The role of AMF (*R. intraradices* BEG141) in enhancing Cd tolerance was also investigated in three genotypes of potted pea (*Pisum sativum* L.) cultivated in the presence of 2-3 mg kg^{-1} Cd (Rivera-Becerril et al., 2002). The authors demonstrated that pea inoculated with *R. intraradices* BEG141 attenuated the negative impact of Cd on growth parameters, since mycorrhizal roots act as a barrier against Cd transfer to the shoot (Rivera-Becerril et al., 2002; Andrade and Silveira, 2008). In agreement with the previous study, Lee and George (2005) indicated that Cd and nickel (Ni) were translocated to the shoot at much lower concentrations in inoculated (*F. mosseae* BEG107) cucumber plants compared to non-inoculated plants. The authors concluded that the successful growth of AMF cucumber plants on metal-rich substrates are stimulated when AMF hyphae can acquire high P concentrations (Lee and George, 2005).

Prasad et al. (2011) investigated the crop performance of basil grown at increasing concentrations of HMs (10 and 20 mg kg^{-1} Cr, 25 and 50 mg $kg^{-1}$of Cd, Ni, and Pb) inoculated with AMF (*R. intraradices*). Basil shoot dry mass was affected by an interaction between HMs and AMF inoculation. At low doses of HMs, AMF inoculation decreased the shoot yield of basil, while an opposite behaviour was recorded at elevated concentrations of HM in soil. Diaz et al. (1996) showed that HM uptake by AMF plants increases with low HM concentration, but it decrease under HM conditions. The protection behaviour of AMF under toxic HM concentrations was attributed to a possible binding of the metals in the extraradical hyphae or by limiting their translocation to shoots (Mozafar et al., 2002). The uptake/binding phenomena has been also observed in two recent studies on *Solanum nigrum* (Liu et al., 2015) and grafted tomato (Kumar et al., 2015). In the former experiment, *S. nigrum* inoculated with *G. versiforme* BGCGD01C increased Cd concentrations at low concentrations (25 or 50 mg kg^{-1}), but decreased Cd concentrations in shoot tissue at high Cd soil concentration (100 mg kg^{-1}). Kumar et al. (2015) also found that AMF inoculation (*R. irregularis*) was not able to alleviate the detrimental effect of Cd in the nutrient solution (25 µM) on the growth and productivity of grafted tomato because Cd could not be retained in intra-radical AMF or compartmentalised in the root cell vacuoles, leading to the translocation of Cd in the aerial parts. In a recent meta-analysis study on the dynamics of AMF symbiosis in HM phytoremediation, Audet and Charest (2007) demonstrated a transition role of the AM shifting from ‘enhanced uptake’ at low soil HM levels, to ‘metal binding’ at high soil HM levels.

Liu et al. (2011) found that AMF inocula (*R. intraradices* BGC USA05, *G. constrictum* BGC USA02, and *R. mosseae* BGC NM04A) can improve the capability of reactive oxygen species (ROS) scavenging by enhancing the activities of the antioxidant enzymes (CAT, SOD, POD) and reducing Cd translocation to marigold shoots (*Tagetes erecta* L.) under Cd stress conditions (50 mg kg^{-1}). The shoot and root biomass of the inoculated marigold plants were significantly higher by 15-47% and 48-130%, respectively, compared to those recorded in non-inoculated plants. Also, in ornamental plants, Gonazález-Chávez and Carillo-González (2013) demonstrated that AMF inoculation (*F. mosseae*) had positive effects on leaf number, and shoot and root biomass of chrysanthemum (*Chrysanthemum maximum* 'Shasta'), cultivated in hydroponics at higher concentrations of mine residues. Inoculated chrysanthemum plants accumulated less Pb and Cu in the above ground biomass (e.g. flowers) than non-mycorrhizal plants, whereas the exclusion effect was not observed for Zn, indicating that Zn translocation and accumulation may depend on fungus-plant interactions, levels and types of metal (Leyval et al., 1995). Co-inoculation with a mixture of *G. mosseae* and *G. intraradices* suppress the detrimental effects of Cd (0-60 mg kg^{-1}) and Pb (0-300 mg kg^{-1}) on the crop performance of statice (*Limonium sinuatum*). The results of the previous studies suggested that marigold, chrysanthemum and statice are potential ornamental candidates in polluted sites, mainly inoculated with AMF.

5.5. Adverse soil pH

Rufyikiri et al. (2000) investigated the tolerance to Al toxicity in response to inoculation with *R. intraradices* (MUCL 41833) in potted banana (*Musa acuminata* colla 'AAA Giant Cavendish' subgroup) plants. Forty days after inoculation with AMF, the inoculated plants grown under 78 and 180 μM Al exhibited the highest shoot biomass compared to the non-inoculated plants, and the better performance of inoculated banana plants was attributed to the capacity of *R. intraradices* to reduce the Al concentration in both shoots and roots. Nevertheless, a recent research of Rouphael et al. (2015) demonstrated the role of AMF (*R. irregularis* and *F. mosseae*) in alleviating the detrimental effects of acidity (nutrient solution pH of 3.5) and aluminium toxicity (pH 3.5 + 1mM Al) in zucchini squash. The inoculated plants under both acidity and Al-stress conditions had higher total biomass and marketable yield than non-inoculated zucchini squash. The authors demonstrated that the better crop performance of inoculated plants under adverse pH conditions were related to the improved nutritional status of in particular mono- and bivalent cations (K, Ca, and Mg), which are commonly deficient in acidic soils (Clark, 1997), to the low Al translocation to the shoot and to the capacity of maintaining cell membrane stability and integrity (Rouphael et al., 2015). Concerning the enhancement of alkalinity tolerance by AMF inoculation, Cardarelli et al. (2010) and Rouphael et al. (2010b) found substantial differences in the morphological, physiological and biochemical responses of inoculated (*R. intraradices*) and non-inoculated zucchini squash and cucumber, supplied with nutrient solutions at two pH values (6.0 or 8.1). In both studies, AMF inoculation mitigates the detrimental effect of alkalinity on yield and yield components by maintaining higher chlorophyll content and the net assimilation rate of CO_2, and also by improving the nutritional status (higher P, K, Mn, Zn and especially Fe concentration) in leaf tissue. The higher translocation and accumulation of Fe in inoculated compared to non-inoculated zucchini squash and cucumber was the main mechanism reducing the deleterious effect of iron deficiency due to alkalinity on crop productivity (Cardarelli et al., 2010; Rouphael et al., 2010).

Cartmill et al. (2007, 2008) investigated the ability of a mixed *Glomus* species isolate ZAC-19 (*G. albidum*, *C. claroideum*, and *G. diaphanum*) to enhance the tolerance of sensitive

(*Rosa multiflora* 'Burr') and moderately tolerant (vinca [*catharantus roseus* (l.) G. Don) ornamental plants to high alkalinity in irrigation water. Cartmill et al. (2007) concluded that inoculation with ZAC19 improved *Rosa multiflora* tolerance to bicarbonate-induced alkalinity in irrigation water (0, 2.5, 5, and 10 mM of HCO_3^-), through improved chlorophyll biosynthesis, and nutrient uptake and translocation (e.g. P and Fe), as well as low iron reductase and soluble alkaline and phosphate activities. Similarly, Cartmill et al. (2008), using the same mixed *Glomus* species, demonstrated that AMF inoculation enhanced plant growth parameters of vinca at high HCO_3^- concentration (7.5 and 10 mM), in particular leaf area, which permitted the increase in photosynthesis rate. The authors highlighted that the tolerance of AMF-inoculated vinca plants to high alkalinity in irrigation water was associated with an increase in P uptake and translocation and to the ability of the AMF plants to maintain the detoxifying activity through increased antioxidant activity.

6. Effect of AMF on nutraceutical value of horticultural products

Recent findings showed that AMF symbioses are able to modify host plant primary and secondary metabolism, stimulating the production of phytochemicals in the roots and shoots of mycorrhizal plants (Sbrana et al., 2014). Such physiological changes may be ascribed to a transient activation of host defence reactions in colonised roots and the accumulation of antioxidant compounds, such as the yellow pigment mycorradicin, which is produced in the roots of mycorrhizal gramineous plants (Strack and Fester, 2006). Indeed, the higher content of mineral nutrients may modulate the production of plant secondary metabolites; for example increasing ascorbic acid, flavonoids, rosmarinic and cichoric acid levels (Larose et al., 2002; Schliemann et al., 2008). Moreover, the basic metabolism of root cells, such as plastid biosynthetic pathways and the Krebs cycle, is altered by arbuscule colonisation, with increases in amino acids, fatty acids and apocarotenoids (Lohse et al., 2005).

In experimental conditions, plants inoculated with AMF produced important biochemical changes leading to apocarotenoid, phenolic acids, carotenoids, and polyphenols accumulation (Walter et al., 2000), to alterations in the activity of superoxide dismutase (SOD) in roots and shoots of different plant species (Ruiz-Lozano et al., 1996; Fester et al., 2005) and of different antioxidant enzymes in the shoots of lavender, rice, and three Mediterranean shrubs (Alguacil et al., 2003; Marulanda et al., 2007;Ruiz-Sànchez et al., 2010). Accordingly, levels of transcripts encoding the key shikimate pathway enzyme phenylalanine-ammonia-lyase were also enhanced by the AMF species *F. mosseae* and *G. versiforme* inoculated in *Oryza sativa* and *Medicago truncatula* roots, respectively (Blilou et al., 2000), while transcripts encoding chalcone synthase increased in *M. truncatula* roots colonised by *G. versiforme* (Harrison and Dixon, 1993) and *R. intraradices* (Bonanomi et al., 2001).

Several horticultural and aromatic plants were assessed for the production of phytochemicals in response to AMF. One of the most extensively investigated is *Ocimum basilicum* (sweet basil), which showed higher accumulation of antioxidant compounds, such as rosmarinic acid and caffeic acid, and of essential oils in shoots and leaves, when inoculated with different *Glomus* species (Copetta et al., 2006; Touissant et al., 2007; Rasouli-Sadaghiani et al., 2010). The concentration of essential oils was increased also in *Foeniculum vulgare* seeds produced by plants inoculated with *R. fasciculatum*, compared with non-mycorrhizal controls (+62.5%). Similar results were obtained in mycorrhizal *Echinacea purpurea*, which produced higher concentrations of phytochemicals with therapeutic value, such as pigments, caffeic acid derivatives, alkylamides and terpenes, when inoculated with the AMF species *R. intraradices* and *Gigaspora margarita* (up to 30 times) (Gualandi, 2010). The medicinal plant

Hypericum perforatum produced higher shoot levels of the anthraquinone derivatives hypericin and pseudohypericin when inoculated with *R. intraradices* and with a multispecies inoculum (Zubek et al., 2012). However, different AMF species may show differential performances: for example, *R. clarum* increased root concentration of thymol derivatives in *Inula ensifolia*, more than *R. intraradices* (Zubek et al., 2010).

Thus far, the production of phytochemicals in plant fresh foods commonly used for human nutrition, as affected by mycorrhizal symbiosis, has been investigated in a limited number of plant species. For example, mycorrhizal lettuce leaves showed higher contents of anthocyanins, carotenoids and phenolics than controls (Baslam et al., 2011), while in strawberry fruit, *R. intraradices* colonisation increased the content of the anthocyanidin cyanidin-3-glucoside (Castellanos-Morales et al., 2010). It is interesting to note that the double inoculation of *Glomus* spp. and two plant growth-promoting bacterial strains belonging to the genus *Pseudomonas* were able to enhance the production of the two main forms of anthocyanins in strawberry fruit, pelargonidin malonyl glucoside and pelargonidin 3-rutinosidein (Lingua et al., 2013).

Among vegetables, two crops in particular, globe artichoke and tomato, are currently considered functional foods (even "nutraceutical foods" or "pharmafoods"), since their consumption may play a key role in promoting human health. Artichoke, utilised by the pharmaceutical industry for its high contents in chlorogenic acid, cynarine, and luteolin, represents a rich source of phytochemicals, including polyphenols and inulin (Raccuia and Melilli, 2004; Ceccarelli et al., 2010a). When inoculated in a microcosm with two AMF species, artichoke leaves increased total polyphenolic content (TPC) and antioxidant activity, expressed as antiradical power (ARP) by 50% and 33%, respectively, compared with the controls; flower heads, the edible part of globe artichoke, followed the same trend, even 2 years after transplanting in the field, showing ARP increases of 52% and 32% in the first and second year, respectively (Ceccarelli et al., 2010b). Tomato is a source of several beneficial phytochemicals, such as lycopene, ascorbic acid, vitamin E, flavonoids, and phenolics. Mycorrhizal tomato fruit showed significantly higher concentrations of glucose, fructose, malate and nitrate when inoculated with a mixed AMF-rhizobacterial inoculum (Copetta et al., 2011). Investigations of antioxidant, oestrogenic/anti-oestrogenic and genotoxic activities of tomato fruit produced by mycorrhizal plants revealed that inoculation with the AMF species *R. intraradices* increased fruit P and Zn contents by 60% and 28%, respectively, and lycopene content by 18.5% (Giovannetti et al., 2012). Moreover, the high anti-oestrogenic power displayed by the extracts (both hydrophilic and lipophilic fractions) of mycorrhizal tomatoes, strongly inhibited 17-b-estradiol-human oestrogen receptor binding. These findings showed that tomato fruit produced by mycorrhizal plants may possibly antagonise the oestrogen-like activity of xenobiotics to which humans are exposed through the food chain (Giovannetti et al., 2012).

7. Conclusions and prospects

The use of arbuscular mycorrhizal symbionts as a biostimulant in horticultural crops has greatly increased in the last two decades, mostly due to their ability to secure production and yield stability in an environmentally sustainable way. Throughout the review, we have examined the promising biostimulant effects of AMF to enhance the root system and thus, macro and micronutrients uptake via increased nutrient transport and/or solubilisation. Maximum benefits will be only achieved by adopting beneficial farm management practices (e.g. the use of organic fertilisers or the exclusion of some biocides), by inoculation with efficient AMF strains and also by an accurate selection of plant host/fungus combinations.

Inoculation with selected AMF can boost plant secondary metabolism leading to improved nutraceutical compounds and can also confer tolerance to drought and adverse chemical soil conditions. Another important aspect is the evaluation of the capability of AMF in improving crop productivity under field conditions. However, most of the studies reported in the scientific literature were conducted under controlled conditions (growth chamber or greenhouses, sterile substrate), and the response of AMF may vary significantly in the natural environment, since a number biotic and abiotic stresses can interact with these fungi and may affect their performance.

Finally scientists, horticulturists and industries need to collaborate to integrate this modernised agricultural practice as an effective and sustainable tool for improving yield and product quality of horticultural crops. Future researches should be focused on: 1) understanding the AMF strains/crop species/environments interaction in order to select the best combinations; 2) the development of high quality inocula having an high concentration of infective propagules, long shelf life and 'easy to use' formulations; 3) the identification of the combination of bacteria/AMF strains that interact synergistically to maximise the benefits; 4) assessing the efficiency of AMF inoculation under field conditions, and multiple stress factors; and 5) identifying the molecular mechanisms behind the enhancement of health-promoting phytochemicals in horticultural products induced by AMF inoculation.

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Legends to the figures

Fig.1. Arbuscular mycorrhizal fungal inocula can be produced on-farm, *ex vitro* in greenhouses or climate chambers or *in vitro* on plants, in root organ cultures (ROCs) or in biofermentors. Required conditions, advantages and disadvantages of the three technologies are summarised.

Table 1

Effects of inoculation with AMF on the agronomical, physiological and biochemical performance of horticultural crops under drought conditions.

Horticultural species	Mycorrhizal species	Growing conditions	Crop performance and stress tolerance	Reference
Poncirus trifoliata	*G. versiforme*	Greenhouse	Inoculation increased fresh, dry weight and leaf area of seedlings under drought stress due to improved uptake of P, K and Ca.	Wu and Zou (2009)
Pista chiavera	*F. mosseae* and *R. intraradices*	Greenhouse	Inoculated pistachio plants had higher P, K, Zn and Mn leaf concentrations than non inoculated plants.	Bagheri et al. (2012)
Solanum lycopersicum	*R. intraradices*	Open field	The marketable fresh yield of inoculated plants was higher by 12-25% depending on the severity of drought than non inoculated plants due to higher uptake of N and P in shoots and roots.	Subramanian et al.(2006)
Solanum lycopersicum	*F. mosseae, G. versiforme*	Greenhouse	Colonization of tomato plants by AMF increased growth responses and yield by 19-32% compared to non inoculated plants under various water stress conditions.	Wang et al. (2014)
Cucumis melo	*F. mosseae, G. versiforme, R. intraradices*	Greenhouse	AMF plants in particular those inoculated with *G. mosseae* showed higher tolerance to drought as indicated by their enhanced growth parameters, antioxidant activities, soluble sugars contents, net phostosynthetic rate and photosynthetic water use efficiency.	Huang et al., 2012
Capsicum annuum	*Glomus* mix (*G. albidium*, *G. claroides* and *G. diaphanum*)	Greenhouse	Pepper plants inoculated with the *Glomus* mix ZAC-19 enhanced drought tolerance, as indicated by higher leaf water potential and higher root-to-shoot ratio in comparison to non inoculated plants.	Davies et al. (2002)
Lactuca sativa	*R. Intraradices*	Growth chamber	Inoculating plants were able to enhance tolerance to drought stress through a higher values of root hydraulic activity, reduced transpiration, faster and better regulation of abscisic acid in comparison to non inoculated plants.	Aroca et al. (2008)
Fragaria × *ananassa*	*F. mosseae, F. geosporus and mixed inoculation*	Greenhouse	Inoculation with one or two fungal species increased strawberry growth, yield, SPAD index and water use efficiency (WUE) under water stress conditions.	Boyer et al. (2015)

Anthirhinum majus	*G. deserticola*	Greenhouse	Inoculating plants produced plants with higher flower yield, shoot and root dry matter. The drought tolerance of mycorrhizal plants was attributed to the improvement of water relations, chlorophyll and macronutrients content (N, P, K, Ca, and Mg).	Asrar et al. (2012)

Table 2

Effects of inoculation with AMF on the agronomical, physiological and biochemical performance of horticultural crops under saline conditions.

Horticultural species	Mycorrhizal species	Growing conditions	Crop performance and stress tolerance	Reference
Vitis spp. rootstocks	*R. Intraradices*	Open field	Inoculated plants were able to maintain higher concentrations of leaf P and K, and lower leaf Na and Cl accumulation leading to higher growth parameters.	Khalil (2013)
Citrus tangerine	*F. mosseae, Paraglomus occultum*	Greenhouse	The salt tolerance of citrus seedlings was enhanced by associated AMF with better plant growth, root morphology, photosynthesis and nutritional status (higher leaf K, Mg and K/Na ratio and lower Na).	Wu et al. (2010)
Olea europea	*F. mosseae, R. intraradices, Claroideoglomus claroideum*	Greenhouse/Open field	Mycorrhizal plants showed the lowest biomass production reduction (-34%) under salinity in comparison to control plants (-78%), with *G. mosseae* being the most efficient. The stress tolerance was due to increased K acquisition.	Porras-Soriano et al. (2009)
Fragaria × ananassa	*F. caledonius, F. mosseae, R. irregularis, F. mosseae + R. irregularis*	Greenhouse	The mixture of two AMF increased growth parameters to a higher degree than the single species at low salinity (0-50 mM), whereas at higher salinity (100-200 mM) *R. irregularis* mitigated salt stress better than the remaining species.	Sinclair et al. (2014)
Solanum lycopersicum	*F. mosseae*	Greenhouse	Mycorrhization alleviated salt induced reduction of fruit yield due to the lower accumulation of Na, higher leaf concentration of P, K, higher enhancement of activity of SOD, CAT, POD and APX.	Abdel Latif and Chaoxing (2011)
Solanum lycopersicum	*R. intraradices*	Growth chamber	Inoculating plants produced more biomass than the control under stress. Mycorrhization were able to lower H_2O_2 and lipid peroxidation in shoots indicating lower oxidative damage in colonized plants.	Hajiboland et al. (2010)
Capsicum annuum	*R. clarum*	Greenhouse	Inoculation improved pepper key growth parameters under salt stress and reduced cell membrane leakage.	Kaya et al. (2009)

Cucurbita pepo	*R. intraradices*	Greenhouse	Crop inoculation alleviated the detrimental effect of salinity on growth and productivity due to improved nutritional (higher K and lower Na in leaf tissue) and leaf water status.	Colla et al. (2008)
Lactuca sativa	*R. intraradices*	Laboratory/greenhouse	Inoculation enhanced the expression of the gene LsPIP1, responsible of root water permeability regulation, thus tolerating the osmotic stress generated by salt stress.	Jahromi et al. (2008)
Lactuca sativa	*R. irregularis*	Greenhouse	Inoculating plants were able to alleviate the negative effects of salinity by altering hormonal throughout an increase in strigolactone production.	Aroca et al. (2013)
Dianthus caryophyllus	*R. intraradices*	Greenhouse	Inoculation with AMF may ameliorate the negative effects of salinity on ornamental value (flower size and color) due to increased of N, P, and Ca and the reduction of toxic ions (Na and Cl).	Navarro et al. (2012)
Euonymus japonica	*Glomus iranicum var. tenuihypharum*	Greenhouse	Inoculation increased plant growth parameters under reclaimed wastewater by increasing the P, Ca and K concentration in leaves.	Gómez-Bellot et al. (2015)

Table 3

Effects of inoculation with AMF on the agronomical, physiological and biochemical performance of horticultural crops under nutrient deficiency conditions.

Horticultural species	Mycorrhizal species	Growing conditions	Crop performance and stress tolerance	Reference
Citrus sinensis and *C. reticulate*	*G. versiforme*	Greenhouse	Inoculation two citrus cultivars with *G. versiforme* has the potential to increase plant growth parameters, photosynthesis and Mg concentration in plant tissues under low magnesium conditions.	Xiao et al. (2014)
Asparagus officinalis	*F. mosseae*	Greenhouse	The soil P concentration required for maximum yield growth of asparagus seedlings could be lowered by inoculation with *F. mosseae*, associated with increased phosphorus utilization efficiency.	Xu et al., 2014
Solanum lycopersicum	*F. mosseae, R. intraradices*	Open field/Pot experiment	Inoculation increased the marketable fresh yield of tomato in particular at low fertilization regimes.	Nedorost andPokluda (2012)
Capsicum annuum	*R. clarum, Claroideoglomus etunicatum, R. intraradices, G. etunicatum, F mosseae,* and mixture	Greenhouse	Inoculating plants were able to increase the uptake of P and Zn content compared to the control. Thus AM species can be used to compensate P and Zn deficiency under nutrient tress conditions.	Kaya et al. (2011)
Capsicum annuum	*F. mosseae*	Greenhouse	Under Cu-deficient conditions inoculation enhanced plant growth, pigment biosynthesis and uptake of the macronutrients, P, K, Ca and Mg.	Abdel Latef (2011)
Petunia hybrid, Callistephus chinensis, Impatiens balsamina	*G. Gigaspora* and *Scutellospora spp.*	Greenhouse	Inoculation with mixed indigenous AMF improve both vegetative and reproductive parameters of the three ornamentals. With inoculation, the expenses of phosphorus fertilization could be reduced to70%.	Gaur et al. (2000)

Table 4

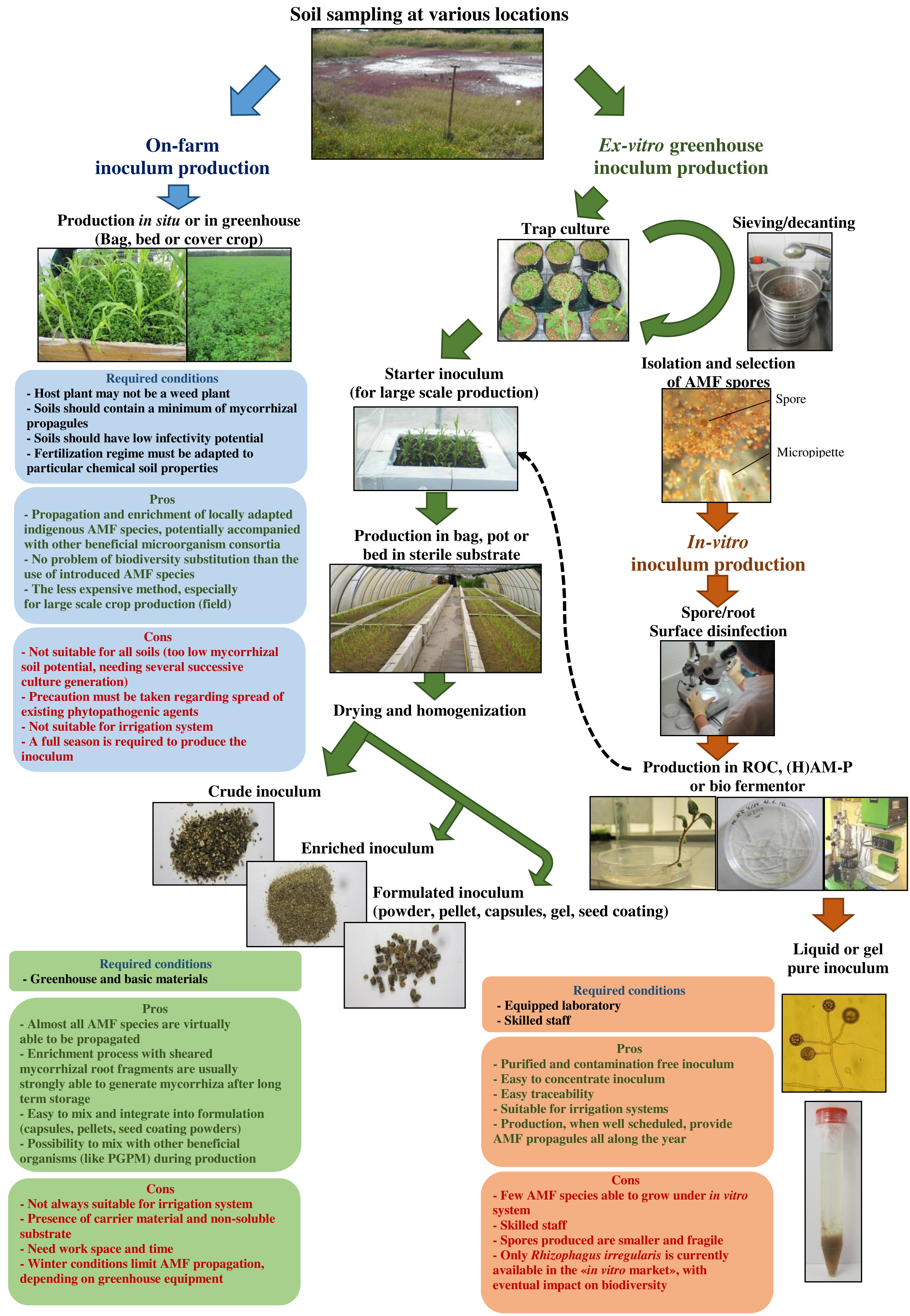
Effects of inoculation with AMF on the agronomical, physiological and biochemical performance of horticultural crops under heavy metal pollutants

Horticultural species	Mycorrhizal species	Growing conditions	Crop performance and stress tolerance	Reference
Apium graveolens	*G. macrocarpum*	Open field/Pot experiment	AMF enhanced the biomass production under Cd stress conditions. Overall, higher chlorophyll concentration and production of photosynthate was observed in inoculated plants.	Kapoor and Bhatnagar (2007)
Pisum sativum	*R. intraradices*	Growth chamber	The inoculated plants mitigate the negative effect of Cd on growth parameters since mycorrhizal roots acts as barrier against heavy metal translocation to the shoot.	Rivera-Becerril (2002)
Grafted *Solanum lycopersicum*	*R. irregularis*	Greenhouse	AMF inoculation was not able to alleviate the detrimental effect of Cd (25 μM)on yield because Cd could not be retained in intra-radical AM fungi, leading to translocation of Cd in the aerial parts.	Kumar et al. (2015)
Ocimum basilicum	*R. intraradices*	Greenhouse	AMF inoculation enhanced heavy metal concentration (Cd, Pb and Ni) in shoots thus decreasing yield, whereas at high soil dose inoculation reduced metal concentration in shoot with beneficial effect on yield.	Prasad et al. (2011)
Tagetes erecta	*R. intraradices*	Greenhouse	Inoculation enhanced the activities of antioxidant enzymes CAT, SOD, POD and reduced translocation of Cd to shoots leading to a higher biomass production.	Liu et al. (2011)
Chrysanthemum maximum	*F. mosseae*	Greenhouse	Inoculated plants accumulated less Pb and Cu in the shoot whereas no exclusion effect was recorded for Zn.	González-Chávez and Carillo-González (2013)

Table 5

Effects of inoculation with AMF on the agronomical, physiological and biochemical performance of horticultural crops under adverse soil pH conditions.

Horticultural species	Mycorrhizal species	Growing conditions	Crop performance and stress tolerance	Reference
Musa acuminata	*R. intraradices*	Growth chamber	The higher crop performance of inoculated plants under Al stress was attributed to the reduced Al concentration in shoots and roots.	Rufyikiri et al. (2000)
Cucurbita pepo	*R. irregularis and F. mosseae*	Greenhouse	Inoculation increased growth and productivity of zucchini squash under acidity and Al toxicity by improving nutritional status (K, Ca, Mg), low Al concentration in shoot and maintaining cell membrane integrity.	Rouphael et al. (2015)
Cucurbita pepo	*R. intraradices*	Greenhouse	The higher crop performance in inoculated plants was related to the capacity of maintaining higher SPAD index, net CO_2 and to a better nutritional status (high P, K, Fe, Zn and Mn) under alkaline conditions.	Cardarelli et al. (2010)
Cucumis sativus	*R. intraradices*	Greenhouse	Inoculating plants were able to maintain growth and yield under alkalinity conditions. The AMF improved the photosynthesis and the nutritional status (high P, K, Mg, Fe, Zn and Mn, and low Na) in response to bicarbonate.	Rouphael et al. (2010)
Rosa multiflora	ZAC-19: *G. albidum, C. claroideum and G. diaphanum*	Greenhouse	Inoculation with ZAC-19 mitigate the detrimental effect of bicarbonate in irrigation water on rose through an improve in nutrient uptake (P and Fe), low iron and phosphate activities.	Cartmill et al. (2007)
Catharantus roseus	ZAC-19: *G. albidum, C. claroideum and G. diaphanum*	Greenhouse	Effectiveness of inoculated vinca plants to high alkalinity was associated to an increase in P uptake and to maintain the detoxifying activity through increased antioxidant activity	Cartmill et al. (2008)


Soil sampling at various locations
On-farm
inoculum production
Production in situ or in greenhouse
(Bag, bed or cover crop)
Required conditions
- Host plant may not be a weed plant
- Soils should contain a minimum of mycorrhizal propagules
- Soils should have low infectivity potential
- Fertilization regime must be adapted to particular chemical soil properties
Pros
- Propagation and enrichment of locally adapted indigenous AMF species, potentially accompanied with other beneficial microorganism consortia
- No problem of biodiversity substitution than the use of introduced AMF species
- The less expensive method, especially for large scale crop production (field)
Cons
- Not suitable for all soils (too low mycorrhizal soil potential, needing several successive culture generation)
- Precaution must be taken regarding spread of existing phytopathogenic agents
- Not suitable for irrigation system
- A full season is required to produce the inoculum
Ex-vitro greenhouse
inoculum production
Trap culture
Sieving/decanting
Isolation and selection
of AMF spores
Spore
Micropipette
Starter inoculum
(for large scale production)
Production in bag, pot or
bed in sterile substrate
Drying and homogenization
Crude inoculum
Enriched inoculum
Formulated inoculum
(powder, pellet, capsules, gel, seed coating)
Required conditions
- Greenhouse and basic materials
Pros
- Almost all AMF species are virtually able to be propagated
- Enrichment process with sheared mycorrhizal root fragments are usually strongly able to generate mycorrhiza after long term storage
- Easy to mix and integrate into formulation (capsules, pellets, seed coating powders)
- Possibility to mix with other beneficial organisms (like PGPM) during production
Cons
- Not always suitable for irrigation system
- Presence of carrier material and non-soluble substrate
- Need work space and time
- Winter conditions limit AMF propagation, depending on greenhouse equipment
In-vitro
inoculum production
Spore/root
Surface disinfection
Production in ROC, (H)AM-P
or bio fermentor
Liquid or gel
pure inoculum
Required conditions
- Equipped laboratory
- Skilled staff
Pros
- Purified and contamination free inoculum
- Easy to concentrate inoculum
- Easy traceability
- Suitable for irrigation systems
- Production, when well scheduled, provide AMF propagules all along the year
Cons
- Few AMF species able to grow under in vitro system
- Skilled staff
- Spores produced are smaller and fragile
- Only Rhizophagus irregularis is currently available in the «in vitro market», with eventual impact on biodiversity