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Utility of Arbuscular Mycorrhizal Fungi for Improved Production and Disease Mitigation in Organic and Hydroponic Greenhouse Crops

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Abstract

Arbuscular mycorrhizal (AM) fungi are considered to be enormously important in contemporary agriculture and horticulture for their ability to improve crop disease and fertility management in commercial field and greenhouse crop production. Recently, commercial greenhouse producers have begun using AM inoculum to increase yields and provide sustainable growing conditions in organic and hydroponic production systems. However, strong evidence in support of their effectiveness in hydroponic production is still lacking. Future research is expected to address benefits of the use of AM fungi in hydroponic greenhouse crops, such as defense against pathogen, herbivore attack and the effective management of photo-assimilates by plants, which are essential for fruit production. In order to increase our understanding of the usefulness of AM fungi in hydroponic greenhouses, large-scale trial and a cost-benefit evaluation of the process are needed. This article discusses the use of AM fungi for improving organic and hydroponic greenhouse crop production and disease control, considering that AM fungi inoculations in soil-based greenhouses and fields have proven to be very effective.

Keywords: AM fungi: Hydroponic; Greenhouse; Disease control; Fertility management; Biocontrol

Introduction

Over the past several decades, a strong interest has developed in the identification and culture of arbuscular mycorrhizal (AM) fungi for their application in agricultural production systems [1-3]. Apart from disease resistance, AM fungi are known to enhance plant growth through promoting increased uptake of phosphorous and other relatively immobile mineral nutrients, e.g., zinc and copper [3,4]. The benefits of AM fungal colonization include increased tolerance of roots to soil-borne pathogens [5] and drought stress, while modifying the stomatal behavior of host plants under water deficit conditions [6,7], and increased protection from salt stress [8]. Growth response to AM fungi depends on their species composition, host plant species, cultivar and growing conditions [9-11].

Hydroponic greenhouse production constitutes an important segment of modern greenhouse industries in developed countries. It provides several advantages to the growers by allowing soilless growing of the plants on perlite, coco coir or vermiculite substrates, which facilitate robust root development, efficient water and nutrient absorption, and avoidance of diseases caused by soil-borne pathogens. In addition, hydroponic systems provide a controlled environment, which helps insure a continuous supply of high quality crops for national and international markets. Successfully expanding greenhouse production will enable the agricultural industry to meet the food demands of an ever-increasing population the world over. The crop production quality and quantity in a hydroponic greenhouse is essentially dependent upon optimal crop root health and efficient nutrient management, in addition to lighting, pH, EC requirements, sanitization, effective disease management and suitable pollination conditions, where required. The available literature on commercial products containing AM fungi for production enhancement covers mostly their roles in field crops and some in organic soil-based greenhouses [12-16] highlights the various aspects of production. However, efforts to prove their utility in hydroponic greenhouses are now emerging because of the need for improved disease control and more efficient management of photo-assimilates, both of which will result in better production efficiency and enhanced profitability for growers [3]. Also, greenhouse growers traditionally inject extra CO_2 into the growing greenhouse environment, which is favourable for the plants. AM fungi are reported to assist in the management of surplus CO_2 in greenhouses [17,18]. The CO_2 enrichment and mycorrhizal effects help increase the photosynthetic activity of plants [17], while increased photosynthetic acclimatization effects following AM fungi application were observed in alfalfa [18]. AM fungi could be useful in hydroponic greenhouses where large-scale production of CO_2 through fossil fuel combustion for heating and their potential emission into the environment, can be managed and be quite useful in environmental stewardship while also enhancing crop yields and quality.

This article discusses the utility of AM fungi in vegetable crop organic and hydroponic greenhouse production systems. A significant amount of work on field and organic crops utilizing AM fungi have proven their effectiveness in vegetable crops. The current article also addresses the major benefits of AM fungal application in non-hydroponic greenhouses, such as disease mitigation and improved production, and envisages the idea of utilizing some of these benefits for hydroponic greenhouse crops by designing appropriate experimental trials and performing a cost-benefit analysis while conducting such trials.

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AM Fungi can Play a Significant Role in Crop Health Improvement

A compatible relationship established between AM fungi and host plants can lead to improved health of greenhouse crops. Also, the genotype of the cultivated crops shapes the species composition of AM fungal microflora leading to better prevention of disease outbreaks [19]. These ideas have been relatively unsupported in conventional agricultural systems, in favor of reliance upon the use of manufactured chemical pesticides for disease control. AM fungi coupled with rhizobacteria are proven to be very effective in disease and nutrition management [20,21]. Etesami and Alikhani have shown that co-inoculation of rhizosphere bacteria, such as *Pseudomonas putida* REN5 and *Pseudomonas fluorescens* with rice led to increased growth indices and N content compatible with full fertilizer rate equivalence [22]. They add that co–inoculation with these isolates decreased the application rate of N-fertilizer by up to 25% under *in vitro* and greenhouse conditions. Given the importance of AM fungi in agriculture, the current situation is changing, and a number of primary producers are using AM fungi inoculum to increase yields and improve production conditions, including pest management. AM fungi have also become the subject of hydroponic greenhouse experimentation, especially over the last decade [22-24].

AM fungi are invariably required for good crop health in many agricultural production systems [25,26]. AM fungi can utilize 10-40% of the carbohydrates, predominantly sugars, which the plant produces by photosynthesis, while inhabiting the roots of the majority of plants. The long mycelia of these fungi enhance the plant's access to essential nutrients, such as phosphorus, nitrogen, potassium, zinc and copper, that would otherwise be available to the plant when only dissolved in water [27]. AM fungi achieve this by the formation of special structures called arbuscules [28], which, in turn, form through a complex interplay of strigolactones (SLs) and mycorrhizal factors [22,23]. The arbuscules are regarded as the functional site of nutrient exchange. An inadequate nutrient supply, which could cause reduced plant growth, can be alleviated to a great extent by the formation of arbuscules inside the cortex of plants [29]. Initially discovered as involved in the inhibition of axillary bud outgrowth, SLs incited a multitude of studies later showing that they also play a role in defining root architecture, secondary growth, hypocotyl elongation, and seed germination, mostly in interaction with other hormones. Their coordinated action with other hormones, such as auxins, cytokinins and gibberellins, which are known to drive growth, i.e., cell division leading to cellular proliferation (cytokinins), cell expansion (auxins) and elongation (gibberellins), chloroplast biosynthesis (cytokinins) etc., enables the plant to respond in an appropriate manner to environmental factors such as temperature, shading, day length, and nutrient availability [30].

Some important greenhouse crops that have been observed to display an increased tolerance to environmental stresses and diseases because of AM colonization are listed in Table 1. A literature survey of greenhouse research trials since 2002 where AM fungi have been employed for ensuring enhanced growth and yield of greenhouse grown vegetable crops are listed in Table 2. Presently, it is known that robust mycorrhizal growth leads to control of diseases due to a competition for space and nutrients in the soil and modification of root exudation, plant physiology and signaling [31], possibly preventing other pathogens from growing in the vicinity of the host plants. This may confer resistance to the invading disease-causing microbes. In addition, the secondary metabolites from a plant and fungal interactions play a crucial role in determining resistance to diseases in plants [21]. Possible mechanisms of action for plant secondary metabolites with antifungal effect could be mediated through induced systemic resistance and systemic acquired resistance processes [32]. Such secondary metabolites have been analyzed and found to

Crop Plant (Species)	AM Fungi	Substratum condition	Disease resistance against	References
Tomato (*Solanum lycopersicum* Mill.)	*Glomus mosseae*	Not shown	*Meloidogyne hapla* (N)	Cooper and Grandison [111]
Water melon *(Cucumis melo)*	*G. intraradices*	Not shown	*M. incognita* (N)	Heald et al. [5]
Tomato (*Solanum lycopersicum* Mill.)	*G. mosseae*	Not shown	*M. hapla* (N)	Reddy et al. [112]
Tomato (*Solanum lycopersicum* Mill.)	*G. mosseae*	Not shown	*Phytophthora parasitica* (F)	Pozo et al. [68]
Asparagus (*Asparagus officinalis*)	*Gigaspora margarita*, *G. fasciculatum* and *Glomus sp.*	Not shown	*Fusarium oxysporum* (F)	Matsubara et al. [113]
Tomato (*Solanum lycopersicum* Mill.)	*G. mosseae*	Not shown	*Meloidogyne incognita* (N)	Talavera et al. [114]
Asparagus (*Asparagus officinalis*)	*G. mossiae*	Not shown	*F. oxysporum* (F)	Matsubara et al. [115]
Tomato (*Solanum lycopersicum* Mill.)	*G. mosseae*	Not shown	*M. incognita* (N)	Diedhiou et al. [116]
Cucumber (*Cucumis sativus* L.)	*G. etunicatum*	Not shown	*F. oxysporum* (F)	Hao et al. [82]
Tomato (*Solanum lycopersicum* Mill.)	*G. monosporum and G. mosseae*	Hydroponic greenhouse	*F. oxysporum* f. sp. *radicis-lycopersici* (F)	Utkhede [63]
Pepper (*Capsicum annum* L.)	*G. mosseae*	Greenhouse	*Phytopthora* (F)	Ozgonen and Erkilic [117]
Melon (*Giotto melon* L.)	*Glomus spp.*	Seedling nursery on peat	*F. oxysporum* (F)	Martinez-Medina et al. [118]
Strawberry (*Fragaria × ananassa* Duch., 'Nohime')	*G. mosseae*	Greenhouse	*Fusarium oxysporum f. sp. fragariae* and *Colletotrichum gloeosporioides* (F)	Li et al. [119]
Pepper (*Capsicum annum* L.)	*G. mosseae* and *Trichoderma koningii*	Greenhouse soil based	*F. oxysporum* (F)	Oyetunji and Salami [120]
Onion (*Allium cepa*)	*G. aggregatum* and *T. harzianum*	Pot culture	*S. cepivorum* (F)	Leta and Selvaraj [121]
Cucumber (*Cucumis sativus* L.)	*G. intraradices*	Greenhouse Pot Culture	*Pythium delicense* (F)	Küçükyumuk et al. [122]
Tomato (*Solanum lycopersicum* Mill.)	*Funneliformis mosseae*	Pot culture	*Alternaria solani* (F)	Song et al. [66]

Table 1: AM fungi application on important routinely grown vegetable greenhouse crops for disease resistance, showing that AM fungi has potential to control diseases in vegetable greenhouse crops.

Host-plant species	Inoculum composition	Yield increase	Plant nutrition improvements	Reference
Allium fistulosum	*Claroideoglomus etunicatum BEG168, Rhizophagus intraradices BEG141 and Funneliformis mosseae BEG167*	Shown	Shown	Guo et al. [123]
Cucumber (*Cucumis sativus)*	*Funneliformis mosseae, Rhizophagus intraradices and Diversispora epigaea*	Shown	Shown	Wang et al. [124]
Manihot esculenta	*Rhizophagus intraradices 11AG8903*	not measured	Not shown.	Carretero et al. [125]
Allium porrum	*Rhizophagus irregularis DAOM197198 and Diversispora epigaea DAOM196672*	not measured	Shown	Liu and Dalpé [126]
Plantago atrata, Pulsatilla slavica, and Senecio umbrosus	*Acaulospora bireticulata, Entrophospora baltica, Acaulospora paulinae, Claroideoglomus claroideum, Septoglomus constrictum, Diversispora trimurales, Ambispora gerdemannii, Archaeospora trappei Septoglomus constrictum, Septoglomus deserticola, Glomus macrocarpum, Scutellospora dipurpurescens, Acaulospora gedanensis, Acaulospora mellea, Funnelliformis caledonium and Claroideoglomus claroideum*	not measured	Shown	Zubek et al. [127]
Dioscorea spp.	*Funneliformis mosseae, Septoglomus deserticola, and Acaulospora laevis*	Shown	Shown	Dare et al. [128]
Allium fistulosum	*Claroideoglomus etunicatum and Diversispora epigea*	Shown	Shown	Shen et al. [129]
Allium spp.	*Rhizophagus intraradices*	not measured	not measured	Galván et al. [130]
Capsicum annuum	*Claroideoglomus etunicatum, Rhizophagus clarus, Rhizophagus intraradices, Funneliformis caledonium and Funneliformis mosseae*	not measured	Shown	Ortas et al. [131]
Solanum lycopersicum	*Claroideoglomus etunicatum BEN101, Claroideoglomus etunicatum BEN102, Claroideoglomus etunicatum BEN104, Claroideoglomus etunicatum BEN105, Glomus hoi BEN131, Glomus hoi BEN132, Glomus hoi BEN133, Claroideoglomus claroideum BEN143, Acaulospora scrobiculata BEN201, Acaulospora scrobiculata BEN202, Acaulospora spinosa BEN211, Acaulospora spinosa BEN212, Acaulospora spinosa BEN213, Acaulospora sp. BEN222, Acaulospora sp. BEN223, Kuklospora kentinensis BEN302, Kuklospora kentinensis BEN301, Funneliformis mosseae BEN111, Funneliformis mosseae BEN112, Sclerocystis sinuosa BEN122*	not measured	not measured	Affokpon et al. [132]
Solanum lycopersicum	*Funneliformis mosseae, Funneliformis caledonium, Septoglomus viscosum, Rhizophagus intraradices and Funneliformis coronatum*	Shown	Shown	Copetta et al. [133]
Allium sativum	*Rhizophagus fasciculatus and Funneliformis mosseae*	Shown	Shown	Patharajan and Raaman [134]
Piper longum	*Rhizophagus fasciculatus, Funneliformis mosseae, Glomeraceae* sp.*, Rhizophagus clarus, Claroideoglomus etunicatum and Diversispora epigaea*	Shown	Shown	Singh and Gogoi [135]
Capsicum annuum	*Rhizophagus irregularis DAOM197198*	not measured	Shown	Beltrano et al. [136]
Macadamia tetraphylla	*Glomeraceae sp., Acaulospora sp., Gigaspora sp. and Scutellospora sp.*	Shown	Shown	Yooyongwech et al. [137]
Prunus armeniaca	*Rhizophagus fasciculatus, Funneliformis mosseae, Glomus macrocarpum and Sclerocystis dussii*	not measured	Shown	Dutt et al. [138]
Solanum lycopersicum	*Claroideoglomus etunicatum KE118, Gigaspora gigantea VA105, Septoglomus deserticola FL912, Claroideoglomus claroideum ML108 and Funneliformis mosseae FR113*	Shown	not measured	Udo et al. [139]
Allium cepa	*Funneliformis caledonium BEG20, Funneliformis mosseae BEG12, Rhizophagus manihotis FL879, Rhizophagus irregularis BEG144, Paraglomus occultum WV224, Racocetra fulgida VA103B and Acaulospora spinosa NC501*	not measured	Shown	Gosling et al. [140]
Eriobotrya japonica	*Acaulospora laevis, Funneliformis mosseae and Funneliformis caledonium*	Measured	Shown	Zhang et al. [141]
Allium cepa	*Funneliformis mosseae BEG12, Rhizophagus manihotis FL879, Rhizophagus irregularis BEG144, Diversispora epigaea BEG47 and Acaulospora spinosa WV861A*	Shown	Shown	Taylor et al. [142]
Allium fistulosum	*Rhizophagus clarus CK001*	not measured	Shown	Sato et al. [143]
Cyclamen purpurascens	*Septoglomus constrictum*	Shown	Shown	Rydlová et al. [144]
Panicum turgidum	*Funneliformis mosseae, Rhizophagus intraradices and Claroideoglomus etunicatum*	Shown	Shown	Hashem et al. [145]
Solanum lycopersicum	*Funneliformis mosseae BEG12 and Rhizophagus irregularis BB-E*	Shown	Shown	Hart et al. [146]
Sorghum bicolor, Allium tuberosum, C. annuum and Daucus carota	*Scutellospora heterogama, Acaulospora longula, and Funneliformis mosseae*	not measured	Shown	Kim et al. [147]

Table 2: A brief survey of greenhouse trials conducted on the utility of AM fungi on different vegetable crops grown in soil and/or artificial media in the greenhouse over past ten years, demonstrating their utility in yield increase and plant nutrition acquisition. This survey shows that various greenhouse crops are amenable to yield increase through nutritional improvement by recruiting suitable AM fungi.

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be hormones, antifungal metabolites, as well as the metabolites of mutualistic interactions observed between plants [21,33]. The soil rhizosphere is a battlefield of microflora and microfauna communities in a tri-partite scheme consisting of beneficial microorganisms, pathogens and the plants that interact with pathogens and influence the outcome of pathogen infection [34]. Pérez-de-Luque et al. have demonstrated that interactions between roots, mycorrhizal fungi and plant growth-promoting rhizobacteria (PGPRs) synergistically effect growth and systemic disease resistance in plants [35]. This enhanced defensive capacity in response to infection by arbuscular mycorrhizal fungi is known as 'mycorrhiza-induced resistance' (MIR). This interaction provides systemic protection against a wide range of pathogens and shares characteristics with systemic acquired resistance (SAR) after pathogen infection and induced systemic resistance (ISR) following root colonization by non-pathogenic rhizobacteria [36]. AM fungi can suppress plant pests and diseases through induction of systemic resistance [37-39]. Research over the last decade has shown that engineering the arable soil microbiome through the use of selected genotypes has had positive effects on the soil biotic environment and is conducive to plant health [2,40,41].

It is commonly assumed that fungal stimulation of the plant immune system is solely responsible for MIR. MIR is a cumulative effect of direct plant responses to mycorrhizal infection and indirect immune responses to ISR-eliciting rhizobacteria in the mycorrhizosphere [42]. PGPRs induce various mechanisms that can affect plant growth. These mechanisms include nitrogen fixation, phosphorus and zinc solubilization [43]. In non-limiting conditions of light, water and mineral nutrients, cytokinins secreted by PGPR are known to drive plant growth by expediting the processing of metabolites through the various plant cell cycle checkpoints, resulting in production of more cells [43].

Soil is the seat of interactions between bacteria and fungi, which establishes a communication network to keep microhabitats in balance. Prominent mediator molecules of these interactions are inorganic and organic microbial volatile compounds (mVOCs) and about 300 bacteria and fungi are known as VOC producers and approximately 800 mVOCs were compiled in DOVE-MO (database of volatiles emitted by microorganisms) [44]. PGPRs are also known to secrete phytohormones, such as cytokinins, and could be cultured and developed as a biofertilizer [43]. Plant-originated cytokinins, already known for promoting cell division, nutrient mobilization and leaf longevity [45] are considered to mediate plant immunity through salicylic acid (SA) signaling [46]. During pathogen attacks, plants trigger a hypersensitive response by the activation of cytokinin biosynthetic gene ipt, which rapidly kills cells near the infection site and deprives the pathogen of nutrients, thus preventing its spread [47]. The study by Novák et al. has elucidated a diverse set of processes that link ipt activation to necrotic lesion formation, while evaluating the potential of cytokinins as signals and/or mediators in plant defence against pathogens [47]. Cytokinins are known to recruit a downstream subset of signaling components, which regulate processes such as cell proliferation and the defense response [48]. Currently, several lines of investigation are needed to elucidate a clearer picture of cytokinin-induced defense responses to a variety of plant pathogens [50]. It is believed that microorganisms contain over 30 growth-promoting compounds from the cytokinin group along with 100 gibberellic acids and other groups of hormones [49] which could possibly be very important to help plants withstand environmental stresses, including pathogen-based stressors. Some investigations have also established cytokinin and/or auxin associations of fungal pathogens of plants [50]. However, more research with respect to cytokinins, auxins and fungal phytopathogens needs to be carried out to completely understand the mechanism involved in this interaction. Plant-associated bacteria provide another set of benefits by initiating biofilm formation and biosurfactant activity, which are enormously important in the biocontrol of disease-causing pathogens. Furthermore, this relationship should prompt the study of 'green' chemicals, such as bacteria-mediated biosurfactants and their application in biocontrol of pathogens [49].

In addition to flavonoids and strigolactones present in the root exudates of plants, the AM fungi also release signal molecules, identified as lipochito-oligosaccharides or Myc factors, which stimulate root growth and branching [51]. Host plants and microbes are capable of producing a wide range of volatile organic compounds, consisting of volatile plant hormones, such as ethylene, methyl jasmonate, and methyl salicylate, which function as airborne signals in mediating plant communication, thus playing a significant role in biocontrol. The symbiosis between fungi and plants is known to establish a molecular dialogue, which benefits the host plants by the activation of antioxidant, phenyl propanoid or carotenoid pathways [52]. AM fungi are preferentially selected by biologically active compounds, which are released by the host plant exudates (Figure 1) [53].

AM Fungi and their Impacts on Greenhouse Horticultural Crops

Bedding plants

Bedding plants are a group of rapidly growing ornamental plants that are typically placed into flower beds that create colorful displays

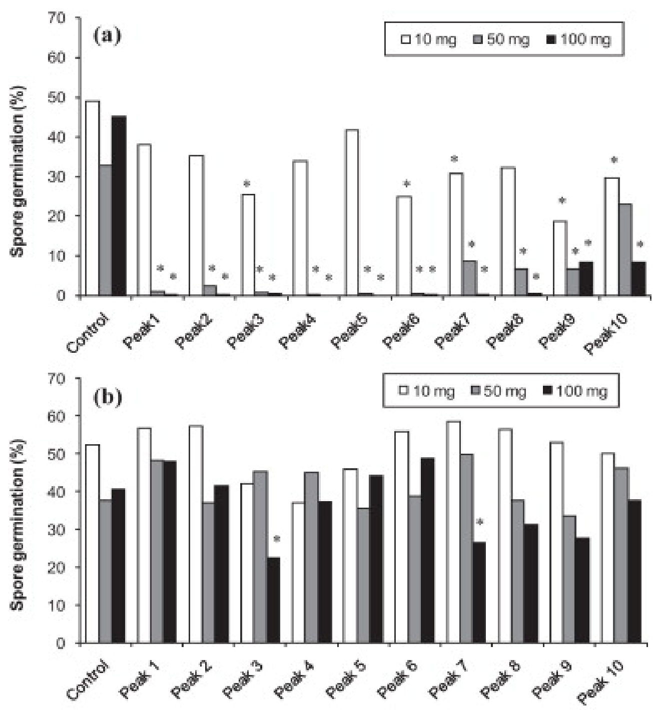

Figure 1: Percentage of inhibition of spore germination by the fractions of plant root extracts analysed through HPLC using 25% MeOH for solubilizing them, in two isolates of AM fungi (a) *G. etunicatum* and (b) *G. rosea*. Stars indicate a statistically significant difference from the control (Student's t test, $P<0.05$) (adapted from Ellouze et al. [53], with author's permission).

during spring, summer or winter depending on their geographical location. Generally, these plants consist of annuals, biennials or tender perennials. Bedding plants can be grown in soil-based and peat-based media. Alternative production systems, such as soilless culture and where AM fungi have been used to benefit the plants, have been used less frequently. Ethylene, a colorless and odorless gas, is responsible for preventing flowering, shortening internode length, increasing branching, initiating fruit ripening, triggering leaf and flower senescence and abscission, causing leaf chlorosis (yellowing), and improving adventitious rooting [54]. Some crops are relatively insensitive to ethylene while others are very sensitive. Mycorrhizal colonization in a soilless medium (peat-based) significantly increased flower vase-life and decreased flower ethylene production of a bedding plant named Maryland White. Cultivar-specific ethylene production due to AM fungal activity in bedding plants has been reported [55]. For example, in snapdragon cultivars, the reduction in ethylene production caused by mycorrhizal colonization was highly variable based on cultivar selection. Koide and Besmer showed that an increase in fertilizer P concentration together with AM fungal colonization resulted in increased ethylene production [55]. In another study, the AM fungus *Glomus constrictum* Trappe was observed to increase growth, flower pigments and phosphorous content of marigold (*Tagetes erecta*) plants, grown under different levels of drought stress. Plant growth, phosphorous uptake, and plant productivity of AM fungi-treated plants were improved under drought stress levels [56]. Furthermore, their study showed that the total pigments of mycorrhizal plants grown under well-watered conditions were 60% higher, thus reinforcing the utility of AM fungi in bedding plants. Heidari and Nazarideljou [57] showed a significant and positive symbiosis between *Glomus mosseae* and zinnia plants, which led to improved flower quality. In another study, Heidari et al. analyzed the positive and significant effects of AM fungi on morpho-physiological traits under different irrigation regimes compared to the control treatment (without AM fungi) [58]. Increased drought stress was responsible for improved flower morphology, pigmentation and plant physiology.

AM fungal utility in hydroponic greenhouses

Hydroponic greenhouses utilize nutrient recirculation systems to reduce environmental pollution resulting from the discharge of unused fertilizer solutions. However, this can increase the risk of attack by root pathogens because inoculum is distributed by the re-circulating nutrient solution. Presence of mycorrhizal fungi may reduce diseases caused by pathogens [59], while promoting plant growth, yield and quality [60]. Understanding individual vegetable crop-specific cases based on available information would address the gaps in awareness of the utility of AM fungi in hydroponic greenhouses and allow us to manage them through devising ingenious research strategies. The crops considered for such studies were as follows:

Tomato: A popular vegetable, tomato is known to be rich in beneficial anti-oxidant compounds for human health. Horticultural practices employing AM fungi are expected to influence the concentration of these secondary metabolites through increased nutrient and water absorption by plants. An experiment, performed under glasshouse conditions by Ulrichs et al., examined whether organically grown 'Vitella F1' tomatoes differed in their fruit content of lycopene, β-carotene and total phenols from that found in conventionally grown tomatoes [61]. In their study, tomato plants inoculated with AM fungi (*Glomus* sp.) showed higher lycopene content in fruits, increased β-carotene and total phenolic contents with an increased root fresh weight. Tahat et al., studied the ability of AM fungi to colonize tomato (*Lycopersicum esculentum*. Mill) roots under glasshouse conditions while using *Glomus mosseae*, *Scutellospora* sp. and *Gigaspora margarita* in their study [62]. They showed that AM fungi colonized tomato roots from *G. mosseae* (80%) to *G. margarita* (20%).

The tomato crop is mostly vulnerable to root and crown rot in hydroponic greenhouses, primarily due to infections with *Fusarium*, *Pythium* and *Phytophthora*. Limited research has been conducted on the potential of AM fungi to control these diseases on tomatoes grown hydroponically in commercial greenhouses (Table 1). Research trials on tomato plants treated with *G. monosporum* and *G. mosseae* reduced *Fusarium oxysporum* f. sp. *radicis-lycopersici* (FORL) infection on tomatoes, while producing significantly higher fruit yields and fruit numbers [63,64]. Several explanations have been given to the mechanisms elucidating the pathogen resistance developed in tomatoes due to AM fungal inoculation. Al-Raddad, proposed that AM fungi-inoculated plants had increased disease resistance possibly due to morphological alterations, such as thickening of the cell walls by lignification [64], while Dehne and Schoenbeck observed that tomato plants inoculated with AM fungi became more resistant due to increased lignin synthesis around the stele region [65]. They assumed that lignification was caused by increased phenol synthesis by the tomato plants. Furthermore, hydrolytic enzymes, such as β-1, 3-glucanase, chitinase, phenylalanine ammonia-lyase (PAL) and lipoxygenase (LOX) in tomato leaves were attributed to be playing a vital role in plant development, morphogenesis, plant microbe signaling and antifungal activities upon AM fungi pre-inoculation followed by pathogen inoculation [66]. Two additional basic b-1, 3- glycanase isoforms were also reported by Pozo et al. on tomato plant roots pre-inoculated with *G. mosseae* and post-infected with *Phytophthora parasitica* [67]. While explaining the possible mechanism of disease resistance due to AM fungi application in tomatoes, Caron et al. found that increased phosphorous concentration was not responsible for inducing this resistance [68].

Scientific studies describing field trials on tomato, eggplant and pepper seedlings employing *Glomus* spp., including *G. fasciculatum, G. monosporum* and *G. mosseae* inoculations, were performed by Dasgan et al. [69]. They used *G. fasciculatum* in a hydroponic greenhouse system to determine its effects on tomato growth, yield, fruit properties, nutrient uptake and substrate ion accumulation of plants. A significant increase in the fruit yield and improved fruit size was found with mycorrhizal inoculation due to an effective use of photo assimilates by these tomato plants, which was essential for fruit production. Their conclusion that mycorrhizal inoculations were useful in alleviating deleterious effects of re-cycling soilless systems for tomato crop production was very important from a grower's stand-point, since they have to re-circulate the soilless systems (nutrient solution). Furthermore, mycorrhiza created a superior nutritional status by increasing the amounts of ascorbic acid and soluble sugars by solubilizing the P in the tomato plants [70]. In a greenhouse experiment, AM fungal inoculation with BIOCULT mycorrhiza granules (consisting of both *G. etunicatum* and *G. intraradices*) made on 'Rodade' tomatoes, exhibited superior transplant performance due to their higher shoot fresh weight, high shoot/root ratio, higher root biomass and higher root growth rate [71]. In a recent report Ziane et al. envisaged the importance of AM fungi in facilitating optimal fertilizer utilization in order to achieve satisfactory growth and yield of a tomato crop [72]. Additionally, they suggested that the application of AM fungi could compensate for the reduction in chemical fertilizers, thus offering a more sustainable farming system that was respectful of the environment. The role of Plant Growth-

Promoting Microorganisms (PGPM), which includes AM fungi, has been demonstrated in hydroponically grown soybean where an efficient production enhancement was achieved through an increase in photosynthetic activity [73]. N uptake by AM fungi in tomatoes has been proven to confer a competitive advantage and to fine tune the growth-defense balance for the host in N-depleted root environments [74].

Cucumber: AM fungi have been found to be equally useful for cucumbers, another important crop for greenhouse vegetable markets. In this crop, they enhance the efficiency of nutrient acquisition and overall growth rate in order to permit more efficient sequence cropping throughout the year [75]. AM fungal symbiosis with cucumber plants helped in taking up nutrient, salts and water from the soil (in a soil-based container system) and made them available to the plant partner [75,76], while the fungus obtained the essential carbohydrates produced during photosynthesis from the plants [77]. This increased the ecological and the physiological fitness of the plant [78] and increased growth, health and crop yield in cucumbers [79,80]. AM fungi also enhanced tolerance against soil-borne diseases [81-85], pests and nematodes [86,87], and also increased drought tolerance and reduced water consumption [88]. Recently, AM fungi have been known to enhance silicon-based plant defenses against root herbivores through interactions involving multiple mechanisms that require further research [89]. However, there is absence of effective symbiotic fungi in commercially available growth substrates, which often limit plant growth and yield in commercial greenhouses. There is also a lack of published information on the value of AM fungi in greenhouse cucumber production (Table 2), which is surprising in view of the importance of this crop to the greenhouse vegetable industry and to our knowledge of the growth-enhancing effects of AM fungi in general. The efficacy of AM fungi to enhance growth of greenhouse cucumber from seeding through fruit production needs to be considered. Trimble and Knowles, investigated greenhouse cucumber growth following infection by three species of AM fungi under varying levels of P nutrition [90]. They specifically analyzed the allocation of soluble carbohydrates and N within plants due to the presence of AM fungi. Their findings suggested that plant phosphorous status guides the efficiency with which plants take up and assimilate nitrogen (N) [91] and is also key to the partitioning of carbohydrates [92-94].

Lettuce, eggplant and pepper: The association of lettuce with AM fungi benefited plant growth and increased the content of copper, iron, anthocyanins, carotenoids and, to a lesser extent, phenolics in mycorrhizal compared to non-mycorrhizal plants, which are potentially beneficial for human health [52,95,96]. The parameters for measuring the effects of AM fungi on plant growth, plant height, shoot fresh weight, total yield, fruit size and length of leaf blade were used, and the shoot fresh weight of eggplant was found to increase up to 47%, 28% and 29% by inoculating with *G. mosseae*, *G. monosporum* and *G. fasciculatum*, respectively, while total yield per plant was increased up to 60%, 43% and 7%, respectively [64]. The most effective fungus was *G. mosseae*, which improved plant growth of the three inoculated crops (lettuce, eggplant and pepper) in the experiments conducted by Al-Raddad [64], although *G. fasciculatum* was the most efficient isolate in colonizing roots of eggplant and peppers. Douds et al. found that AM fungal inoculation of eggplant crops significantly increased the yield of fruit [97]. They recommend that the routine use of AM fungal inoculum could increase the yield of eggplant with minimal changes to the grower's normal practices.

Major challenges in the use of AM fungal inoculants

Over the past few decades, companies throughout the world have manufactured and commercialized AM fungal inoculants using either a single AM species or mixtures of species that may include PGPR or other symbiotic and/or biocontrol fungi [98]. Industrial manufacturing of AM fungi as crop inoculants is a relatively new undertaking and, despite the practical demonstrations of their efficiency (Table 2), their adoption by crop producers has been slow, most likely due to concerns over the cost, quality and efficiency of marketed products. One of the main issues with the use of commercial AM fungi inoculants in agriculture is related to their performance under specific local conditions. Native AM fungi species are often considered to be mutualistic [99-102]. Faye et al. have evaluated the need to pre-evaluate commercial mycorrhizal inoculants on a selected crop and regional soil types before launching large-scale field use [103]. AM fungi-containing products are rarely used in commercial agriculture because of: (a) difficulties in producing AM fungal inoculum in large quantities, (b) their beneficial effects, and (c) uncertainties about possible negative impacts of added AM fungi to the resident AM fungi populations [104].

In order to improve the use of commercial inoculants, 12 AM fungi were evaluated in greenhouse by Robinson Boyer et al. [104]. They propagated the commercial mycorrhizal inoculants in a trap pot culture under sterilized sand to evaluate mycorrhizal potential for maize (*Zea mays* L.) root colonization, while comparing them with an indigenous soil inoculum. Their findings revealed that three inoculants significantly increased root colonization levels compared with the soil inoculum. Thirteen fungal strains were subjected to extraction in their studies from the pot culture survey, which also included five undeclared species and four declared species, which did not produce spores. In their second experiment, commercial products were inoculated into soil to assess their impact on maize growth and yield. Their major finding was that inoculants increased root colonization levels and also increased the shoot biomass of maize plants albeit slightly. This information should allow researchers to experiment with the methodologies for hydroponic greenhouse crops, where pre-AM fungal-colonized substrates can be used effectively and by mitigating the challenges of competition by the indigenous soil inoculum. Additionally, the application of AM fungi in hydroponic greenhouse crops will possibly help reduce challenges such as economic concerns envisioned by commercial vegetable growers, which may be encountered in pre-evaluating commercial mycorrhizal inoculants on selected crops and in regional soils before launching large-scale field use. A study using AM fungi and synthetic fertilisers on sunflower plants showed a greater plant height, stem diameter and leaf chlorophyll content, whereas there was increased mycorrhizal hyphal and arbuscular growth when AM fungi and organic fertilizers were used together [105]. Abobaker et al. demonstrated clearly that AM fungi had beneficial effects on plant growth albeit without also having significant use of organic fertilizers [105].

Potential gains from using AM fungi on greenhouse crops

Berruti et al. have reviewed the amount of work carried out thus far on the use of AM fungi in greenhouses vs. in open field areas. They suggested that 65% of the experiments carried out up to 2015 were in greenhouses, while 24% were in open-field conditions [106]. They found that fungal colonization gain in inoculated plants, compared to non-inoculated controls, was significantly more frequent in the greenhouses than in open-fields. They tentatively attributed this to the pre-existing AM fungal propagules in the field plots, while control pots in greenhouses with sterilized substrates were free of AM fungal propagules or were highly reduced in AM fungal diversity. Interestingly, it was observed that the root biomass benefitted more from inoculation in field conditions than in greenhouses [106]. This was probably due to the fact that containerized roots stopped growing because of constraints imposed by pot boundaries at a certain point in time during cultivation. In addition, the containerized inoculated plants were more likely to rely massively on fungal-mediated uptake [107] and reached a maximum level of exploration of the substrate sooner than non-inoculated plants, without increasing the root biomass. However, they advocated that the effectiveness of AM fungal inoculation on shoot biomass, yield, and plant nutrition did not seem to be equally successful in greenhouse and open-field conditions [106]. Here, it seemed important to supplement containerized or hydroponic, pre-grown, AM fungal substrates with lower amounts of exogenous nutrients (fertilizers containing N and P) as has been done by researchers to increase the nutritional quality of the vegetable crops [107,108].

Conclusion

Mycorrhizal fungi have been shown to be capable of making nutrients available to plants and providing a better transplant performance by offering higher shoot fresh weight, high shoot/root ratio, higher root biomass and higher root growth rate. In addition, protection from diseases caused by root pathogens is a major benefit that AM fungi could offer in both containerized and hydroponic production systems. Once AM fungi colonize the plants, they remain with the root systems and can be transferred into other soil/substrate locations and plantings on the infested roots. Future multi-location experimental trials on the application of AM fungi in hydroponic greenhouse systems utilizing the various types of production systems discussed in this article could promote more widespread and successful use of this technology. Furthermore, cost-benefit analyses of this technology would increase awareness among the potential end-users of the benefits of AM fungal inocula. The successful colonization of AM fungi in hydroponically grown vegetable crops has met with both success and failure. However, the information discussed in this article could assist scientists in gaining insight on the potential utility of AM fungi and to help them to plan and interpret the results of scientific trials on vegetable crops grown in hydroponic greenhouses.

Urbanization may lead to an upsurge in human population to over 5 billion by 2030 [109]. Popularizing hydroponic greenhouse production through disease and nutrient management experimental trials could contribute to vegetable crop production in a significant way. These endeavors could further be assisted with developing technologies such as rooftop plant production systems, which allow growers to grow food crops and ornamental plants using hydroponic greenhouses [108]. Scientific studies have revealed that AM fungi have proven their utility as a sustainable alternative to the use of conventional chemical fertilizers in urban farming, especially green roof manuring [97]. The concepts derived through trials on the lines discussed in the current article could help commercial greenhouse growers to better meet the needs of a rapidly growing population of urban consumers.

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