



Review

Health-Promoting Properties of Plant Products: The Role of Mycorrhizal Fungi and Associated Bacteria

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Abstract: The concept of food quality, traditionally based on nutritional and sensory properties, has recently acquired an additional meaning, referring to the health-promoting properties of plant products, that are ascribed to plant secondary metabolites called phytochemicals, primarily represented by polyphenolic compounds and glucosinolates. The diversity and content of phytochemicals in plant products are affected by different variables, such as plant genotype, agronomic factors, and arbuscular mycorrhizal fungi (AMF), which establish mycorrhizal symbioses with most crops, including cereals, legumes, vegetables, fruit trees, sunflower, cotton, and sugarcane. AMF and associated bacteria enhance plant growth and health, and affect the production of polyphenols and carotenoids, and the activity of antioxidant enzymes. The production of health-promoting phytochemicals was shown to be differentially modulated by different AMF isolates and bacterial strains, in several food plants, i.e., tomato, lettuce, strawberry, artichoke, maize, grapevine, sunflower. Here, we provide an overview of recent studies concerning the multiple roles played by AMF and associated bacteria in the modulation of the biosynthesis of plant secondary metabolites with health-promoting activity, and discuss the development of designed multifunctional consortia to be used in sustainable agriculture.

Keywords: arbuscular mycorrhizal symbiosis; biostimulants; mycorrhizosphere; AMF-associated bacteria; health-promoting food; phytochemicals

1. Introduction

The quality of plant products and their derived foods and ingredients represent the main aim to be pursued by sustainable agriculture, in the best interest of farmers, consumers, and producing countries. Recently, the concept of food quality, traditionally based on nutritional and sensory properties, has acquired an additional meaning, referring to the health-promoting properties of plant foods, an important societal issue, highly demanded by consumers. Thus, fruits, vegetables, legumes, grains, nuts, and seeds are currently valued not only for size, weight, external appearance, taste, and nutritional content, but also for their nutraceutical properties, i.e., their ability to promote human health by preventing diseases and decreasing the risk of mortality from cancer [1–3]. Such bioactive properties are mainly ascribed to plant secondary metabolites, called phytochemicals, that show antioxidant, antibacterial, and antiviral activities and the ability to protect against chronic diseases, encompassing also cardiovascular diseases (CVD), certain cancers, neurodegenerative diseases, and to

affect human metabolism, modulating detoxifying enzymes, hormone metabolism, and the immune system [4–8].

Phytochemicals are primarily represented by polyphenolic compounds, such as flavonoids, consisting of more than 5000 bioactive compounds reportedly active in the reduction of CVD risk and in chemoprotection, and by glucosinolates, encompassing about 130 molecules mainly found in Brassicaceae, plants considered as food protection agents, given the positive correlation between their consumption and cancer risk reduction [9–14].

The diversity and content of phytochemicals in plant products are affected by different variables, such as plant genotype, agronomic factors (management, soil mineral nutrients, drought, salinity, harvest season, agrochemicals), and the occurrence of root beneficial symbionts. Plant genotype has been widely studied in order to detect cultivars with increased concentrations in phytochemicals. A comprehensive set of data was provided by USDA National Food and Nutrient Analysis Program, which measured total antioxidant capacity (TAC) of over 100 different foods, including fruits, vegetables, and cereals. The analyses showed a large TAC variability, expressed as μmol of Trolox equivalents (TE)/g not only among different species of fruits—from 13.4 in apricots to 94.6 in cranberries—but also among varieties of the same species—from 26.7 in Golden Delicious to 42.7 in Red Delicious apples [15]. Such results stimulated researches and breeding programs aimed at selecting crops with enhanced concentrations of beneficial plant secondary metabolites. Agronomic factors have been increasingly investigated in order to detect and adopt the best managements and techniques to enhance health-promoting properties of crops. For example, a systematic literature review, performed on a data set of 343 peer-reviewed publications, revealed that organic crops, compared with non-organic ones, had higher concentrations of antioxidants, such as phenolic acids, flavanones, stilbenes, flavones, flavonols, and anthocyanins, and significantly lower levels of pesticide residues [16].

One of the most important factors modulating the production of phytochemicals is represented by the establishment of mycorrhizal symbioses between plant roots and an ecologically and economically significant group of soil-beneficial fungi belonging to Glomeromycota (<http://taxonomicon.taxonomy.nl/Reference.aspx?id=10727>, accessed 13 November 2020), arbuscular mycorrhizal (AM) fungi (AMF), which play a major role in crop production, as they reduce the need of chemical fertilizers and pesticides while increasing soil health and biological fertility. AMF associate with the root systems of about 80% of land plant species, including the most important temperate and tropical agricultural crops, such as rice, corn, barley, wheat, legumes, vegetables, fruit trees, encompassing grapevine and olive, and other economically valuable plants like sunflower, cassava, cotton, sugarcane, tobacco, coffee, tea, cocoa, rubber, oil palm. Only few plants do not establish mycorrhizal symbioses, including Chenopodiaceae, Brassicaceae, Caryophyllaceae, Polygonaceae, Juncaceae, Proteaceae, and *Lupinus* within Fabaceae [17]. AM fungal symbionts enhance plant growth and production, absorbing and translocating soil mineral nutrients—mainly P, N, S, K, Ca, Fe, Cu, and Zn—to plant host roots, in exchange for carbon, and positively affect also crop tolerance of biotic and abiotic stresses [17]. Furthermore, a vast community of bacteria live in close association with AMF mycelium and spores—mycorrhizospheric bacteria—playing important roles in plant growth promotion and health [18]. The potential synergistic interactions between such microbiota and AMF has boosted research into their targeted management, opening new avenues for the development of designed multifunctional consortia to be used in sustainable agriculture [19].

A large body of investigations showed that AMF may affect the production of plant secondary metabolites, by modifying terpenoid metabolism and shikimate pathway, enhancing isoprenoids, polyketides, and polyphenols biosynthesis. They also increase the content of polyphenols and carotenoids, and the activity of antioxidant enzymes, mevalonate, malonyl-CoA, and shikimate pathways, enhancing isoprenoids, polyketides, and polyphenols biosynthesis [20,21]. Here, we provide an overview of recent studies concerning the multiple roles played by AMF and associated bacteria in the modulation of the biosynthesis of plant secondary metabolites with health-promoting activity.

We also discuss the best research strategies for their utilization in sustainable agriculture for the production of plant foods with high nutritional and nutraceutical value (Figure 1).

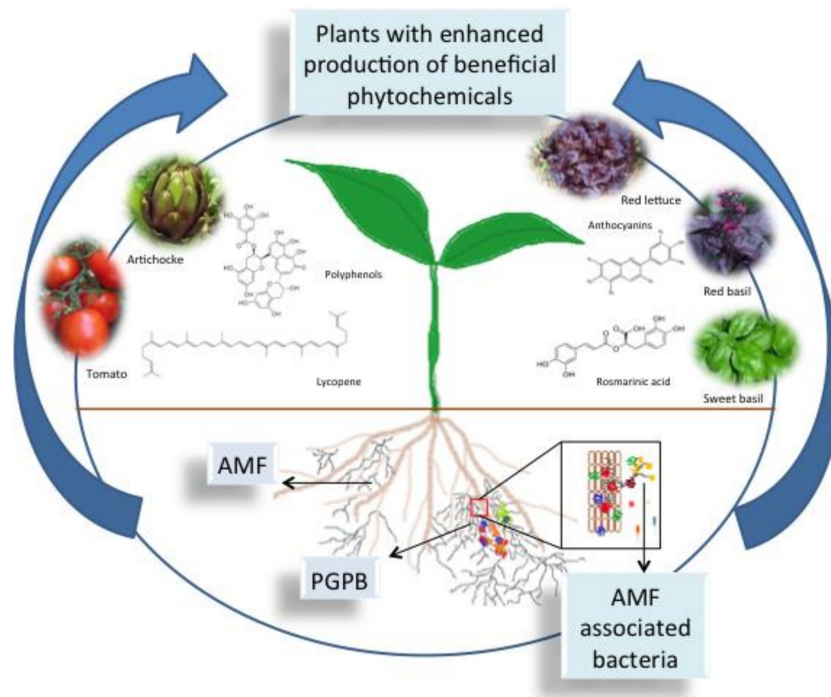


Figure 1. Schematic drawing representing the effects of different beneficial soil microbial communities on plant production of health-promoting phytochemicals. AMF, arbuscular mycorrhizal fungi; PGPB, plant growth promoting bacteria.

2. Arbuscular Mycorrhizal Fungi and Associated Bacteria

AMF are obligately biotrophic symbionts whose life cycle cannot be completed in the absence of the host plant. They are named after the intracellular structures, arbuscules, formed by fungal hyphal branching in root cortical cells, where nutrient exchanges between the two partners of the symbiosis occur: AMF obtain plant-derived carbon (up to 20% of total photosynthates), while releasing mineral nutrients, mainly P, absorbed and transferred from the soil to the host by the extraradical mycelium (ERM) [17]. ERM consists of a large interconnected mycelial network spreading from mycorrhizal roots into the surrounding soil and is the essential element of the symbiosis, representing an efficient absorbing system, given the high surface-to-volume ratio of the hyphae where diverse mineral nutrient transporter genes are expressed [22–24]. Currently, AMF are classified within 11 families—*Acaulosporaceae*, *Ambisporaceae*, *Archaeosporaceae*, *Claroidoglomeraceae*, *Diversisporaceae*, *Gigasporaceae*, *Glomeraceae*, *Pacisporaceae*, *Paraglomeraceae*, *Pervetustaceae*, and *Sacculosporaceae*. They encompass more than 300 species, described on the basis of morphological characteristics of the spores produced by ERM (shape, color, size, spore wall, subtending hypha structure, mode of spore germination, spore ontogeny, root colonization pattern) and/or molecular data (http://www.amf-phylogeny.com/amphylo_species.html, accessed 13 November 2020). However, a higher number of environmental sequences (virtual taxa, <https://maajiam.botany.ut.ee/?action=about>) have been obtained by ecological studies carried out using molecular tools. A great diversity is shown by AMF, not only among species, but also among isolates of the same species. In particular, they may differ by the ability to establish a rapid and extensive root colonization, that is affected by spore dormancy and germination rate, the production of lengthy hyphal germlings and a large number of infection structures (appressoria), and by the rate of intraradical colonization and arbuscule formation. AMF differs also for efficiency, i.e., their ability to increase plant performance, that is affected by ERM

structure, viability and ability to uptake soil mineral nutrients and transfer them to the host plant. Moreover, differential efficiency has been reported among AMF also with regard to the modulation of plant secondary metabolism and the production of health-promoting compounds [21,25].

A third partner of mycorrhizal symbioses is represented by the microbiota associated with AMF spores, sporocarps, and extraradical hyphae. The early ultrastructural studies showed the occurrence of bacteria between spore wall layers and sporocarps peridial hyphae [26–28], while molecular investigations lead to the identification of taxa living in close association with AMF spores, belonging to the orders *Actinomycetales*, *Bacillales*, *Burkholderiales*, *Pseudomonadales*, *Rhizobiales* [29–32]. On the other hand, culture-dependent approaches, allowing the isolation of the cultivable bacteria, revealed their functional significance. Some bacterial taxa, defined “mycorrhizal helper,” enhanced mycorrhizal activity by promoting spore germination, germlings hyphal growth, mycorrhizal establishment, and ERM development [33–35], other taxa showed potential roles as plant growth promoting bacteria (PGPB) by solubilizing phosphate, mineralizing phytate, fixing nitrogen and producing indole acetic acid, siderophores, and antibiotics [32,36–41]. In addition to such properties, AMF-associated bacteria were shown to modulate plant biosynthesis of beneficial phytochemicals, suggesting a potential synergy with AMF in the production of health-promoting compounds [18].

3. The Production of Beneficial Phytochemicals as Affected by AMF

The early works on the differential accumulation of phytochemicals in mycorrhizal plants reported data obtained from roots of species belonging to the family Gramineae, Liliopsida, and Rosopsida, which produced a yellow pigment, named mycorradicin, identified as the core structure of glycosylated cyclohexenone derivatives [42]. A blumenol C-glycoside was first found in mycorrhizal maize roots [43] and other blumenols were recently detected in roots and shoots of mycorrhizal plants belonging to different species (*Nicotiana attenuata*, *Solanum lycopersicum*, *Solanum tuberosum*, *Hordeum vulgare*, *Triticum aestivum*, *Medicago truncatula*, and *Brachypodium distachyon*) [44]. Other works revealed that colonized root cells underwent diverse cytological and metabolic changes, from the modulation of plastid biosynthetic pathways and Krebs cycle to increases in the production of fatty acids, apocarotenoids, amino acids, flavonoids, such as quercetin, acacetin and rhamnetin, isoprenoids, polyketides and polyphenols [45–52]. The modification in the activity of antioxidant enzymes, including superoxide dismutase, both in roots and shoots of different plants, suggested a positive role of AMF in the protection from oxidative damages caused by biotic and abiotic stresses [53–57]. Accordingly, the increased expression of defense genes encoding phenylalanine ammonia-lyase in *Oryza sativa* and *Medicago truncatula* roots and chalcone synthase in *Medicago truncatula* roots well supported this hypothesis [58–60]. Several mechanistic studies, aimed at assessing the differential expression of genes encoding for some of the enzymes leading to the production of health-promoting phytochemicals, showed that they were upregulated in mycorrhizal plants, compared with controls [60–65].

Many investigations were carried out on more than 50 medicinal and aromatic plant species, including herbs and plants used for food additives, with the aim of detecting their shoot/leaves concentrations of health-promoting compounds after AMF inoculation [66]. Mycorrhizal sweet basil (*Ocimum basilicum*) showed higher levels of antioxidant molecules, such as caffeic acid and rosmarinic acid (an ester of caffeic acid and 3,4-dihydroxyphenyllactic acid; RA) [67,68], and of essential oils and anthocyanins [48,69–71]. Interestingly, AMF inoculation of sweet basil lead to the overexpression, in the leaves, of *tyrosine aminotransferase (TAT)* gene, encoding TAT, the first enzyme of tyrosine-derived metabolic pathway involved in RA biosynthesis (Table 1) [72]. These findings strongly suggest AMF utilization for the production of basil plants with increased concentrations of bioactive compounds, such as RA, known for its antioxidant, antibacterial, antiviral, and anti-inflammatory properties [73]. As in basil, other medicinal/aromatic plants showed higher accumulation of essential oils upon mycorrhizal inoculation. For example, essential oils increased by 43, 90, and 72% in *Coriandrum sativum*, *Anethum graveolens*, and *Trachyspermum ammi* fruits, 62.5% in *Foeniculum vulgare* seeds, and 66% in *Artemisia annua* leaves [74–76]. In mycorrhizal *Origanum* sp. essential oils content was higher

and showed differential profiles, in an experimental system where plants were grown with similar phenology and phosphorus (P) nutritional status, in order to rule out P nutrition-dependent effects [77]. Phytochemicals with therapeutic value were found in higher concentrations in mycorrhizal plants: for example, *Artemisia annua* leaves showed an increase of 95% in artemisin, a well-known and essential antimalarial drug [78], while in mycorrhizal *Echinacea purpurea* the levels of pigments, caffeic acid derivatives, alkylamides, and terpenes increased up to 30 times, compared with controls [79]. Higher levels of phytoestrogens showing preventive role in osteoporosis and menopausal symptoms, such as the isoflavones biochanin A, formononetin, genistein, daidzein, were produced in mycorrhizal red clover [80,81], while active sesquiterpene lactones, able to inhibit cell proliferation and tumor growth were accumulated in mycorrhizal *Arnica montana* [82,83].

In seeds and leaves of the medicinal plant *Castanospermum australe* the content of castanospermine—an alkaloid of the indolizidine type—was positively correlated with the level of mycorrhizal colonization [84]. AMF inoculation of the medicinal plant *Bituminaria bituminosa* increased the leaves content of the furanocoumarins angelicin and psoralen, and of the pterocarpans erybraedin C and bitucarpin A, chemotherapeutic agents reported as active in the induction of apoptosis in human colon carcinoma cell lines [85,86]. In addition, steviol glycosides, utilized as sugar substitutes for diabetics, were produced in higher amounts by mycorrhizal *Stevia rebaudiana* plants [87].

A number of studies reported that the production of health-promoting phytochemicals was differentially modulated by different AMF. As the concurrence between the name of the AMF species reported in the original works and the current classification is almost impossible to get, in particular for *Glomus intraradices*, here the names of the species reported in the relevant literature are maintained. *Glomus fasciculatum* enhanced the levels of essential oils in *Coriandrum sativum* shoots and fruits, compared with *Glomus macrocarpum*, increasing also the concentrations of linalool [75]. Accordingly, Copetta and coauthors [48] reported differences in the profiles of essential oils in basil leaves: camphor and alfa-terpineol contents were enhanced, while eucalyptol, linalool, eugenol levels were decreased upon inoculation with *Gigaspora rosea* and *Gigaspora margarita*, respectively. Further investigations confirmed such differential performances, showing that *Glomus clarum* increased the content of thymol derivatives in *Inula ensifolia* roots, compared with *Glomus intraradices* [88], and that a different strain of the latter fungus promoted the production of the anthraquinone derivatives hypericin and pseudohypericin in the shoots of the medicinal plant *Hypericum perforatum* [89]. Differential AMF performances were reported also in the levels of the alkaloid forskolin, a potent cardioactive and hypotensive diterpenoid molecule, in *Coleus forskohlii* roots, when plants were inoculated with different AMF species; such works allowed the detection of *Glomus bagyarajii* as the mycorrhizal symbiont producing the largest increases, up to 147% [90].

Investigations on phytochemical contents of food crops as affected by mycorrhizal symbioses were performed on few plant species, including *Solanum lycopersicum* (tomato), *Capsicum annuum* (pepper), and *Allium cepa* (onion), followed by *Cynara cardunculus* (artichoke), *Lactuca sativa* (lettuce), *Fragaria* spp. (strawberry), and *Zea mais* (maize) (Table 1).

In onion, the use of an AMF commercial inoculum increased the antioxidant activity and the concentrations of quercetin glucosides [91]. Moreover a mixture of six species belonging to the genus *Glomus*, highly enhanced not only bulb fresh biomass, but also bulb antioxidant capacity, compared with the single inoculum of *G. intraradices* [92].

Contrasting results were obtained with mycorrhizal tomato, both in greenhouse and field experiments, in relation to the production of lycopene, ascorbic acid, and phenols, whose contents in tomato fruits varied not only with the use of mixed inocula vs. single species-inoculum [93], but also depending on AMF species and plant cultivar [20]. More consistent results were shown by mycorrhizal lettuce, in relation with phenolics content and antioxidant activity, whose concentrations in the leaves were increased by diverse AMF and plant varieties [94,95]. In particular, when comparing the effects of two AMF, *Rhizoglomus irregulare* and *Funneliformis mosseae*, on secondary metabolism of two lettuce cultivars, the inoculation of *R. irregulare* resulted in higher contents of leaves total

phenolics and in a higher antioxidant activity in both cultivars, Eluarde and Panisse. In addition, in the red-leaved Eluarde lettuce plants anthocyanins levels increased by 165% and 306% upon *F. mosseae* and *R. irregulare* inoculum, respectively, compared with control plant levels [96]. Such results suggest that mycorrhizal inoculation represents a valuable biological tool to obtain lettuce plants enriched in beneficial phytochemicals, provided that an efficient AMF isolate is selected for inoculation.

Accordingly, when globe artichoke plants were inoculated with a mixture of two AMF species, *Glomus mosseae* and *G. intraradices*, the combination of the two symbionts produced large increases in total polyphenolic content (47 and 55.7%) and antioxidant activity (53 and 32 % in the first and second year in the field, respectively) in flower heads [97]. This result is very important, as flower heads, the edible part of the plant, represent a good dietary source of nutraceutical compounds [98]. Recently, the functional diversity of six different AM symbionts was demonstrated in two artichoke varieties, allowing the detection of *Claroideoglomus claroideum* 22W3 as the most efficient isolate in the promotion of leaves content of total phenols and chlorogenic acid, and of *C. claroideum* 22W3 and *F. mosseae* IMA1, as the two isolates enhancing leaves antioxidant activity, compared with control plants [99].

Mycorrhizal strawberries, fruits that innately show a high antioxidant capacity, were assessed for their content in anthocyanins: the fruits produced by plants of the cultivar Selva had increased contents in ascorbic acid and pelargonidin 3-glucoside, pelargonidin 3-rutinoside and pelargonidin malonyl glucoside, when treated with a commercial inoculum including *Rhizophagus intraradices*, *Glomus aggregatum*, *Glomus viscosum*, *Claroideoglomus etunicatum*, *Claroideoglomus claroideum* [100,101]. Other cultivars, inoculated with different AMF, showed variable effects, depending not only on plant genotype and fungal isolate, but also on inoculation time and nitrogen fertilization [102,103].

Variable biochemical changes in the leaves of micropropagated *Vitis vinifera* plants (var. Pusa Navrang) during hardening were observed, depending on AMF identity. While all the AMF utilized increased carotenoids, *Acaulospora scrobiculata* and *Scutellospora heterogama* gave the best results in tissue chlorophyll content and *Acaulospora laevis* increased proline and phenols levels by 286% and 900%, respectively, compared with the controls [104]. When in vitro-cultured grapevine plantlets cv. Sangiovese were transplanted into soil and grown in greenhouse, the concentration of volatile organic compounds (VOCs), that are important in plant communication and defense [105], was increased by 85% in the leaves of plants inoculated with *F. mosseae*. Moreover, mycorrhizal inoculation significantly increased volatiles related to plant defenses, such as (*E*)-2-hexenal, 3-hexenal, geraniol, benzaldehyde, and methyl salicylate [106]. On the basis of these results further works should be performed in order to verify whether quantitative or qualitative changes in VOCs and phytochemicals may be found not only in leaves, but also in grapes.

4. The Production of Beneficial Phytochemicals as Affected by PGPB- and AMF-Associated Bacteria

Some studies revealed that the production of phytochemicals may be promoted by bacteria, in particular by PGPB, that have been reported to interact with plant secondary metabolism, for example by producing plant hormones and altering plant gene expression (Table 1) [107,108]. In greenhouse experiments, tomato fruits produced by plants co-inoculated with AMF, *Pseudomonas* sp. 19Fv1T and *Pseudomonas fluorescens* C7 showed increased levels of sugars, vitamins, and β -carotene [109,110], whereas strawberries inoculated with mycorrhizal fungi and different PGPB strains belonging to the genus *Pseudomonas* showed increased content of anthocyanins, sugars, ascorbic, and folic acids [100,101,111]. When canola plants were inoculated with *Azospirillum brasilense*, seed protein and oil contents were enhanced and glucosinolate and erucic acid in oil decreased [112]. Accordingly, sunflower seeds showed higher content of oil and protein upon plant inoculation with strains of the rhizobacteria *Azospirillum* and *Azotobacter* [113]. In different vegetables, such as *Trigonella foenum-graecum*, *L. sativa*, *Spinacia oleracea*, and *Daucus carota*, a PGPB strain of *Bacillus lentimorbus* mediated the induction of dietary antioxidants [114]. Co-inoculation of spinach plants with *G. fasciculatum*, *G. mosseae* and PGP *Azotobacter chroococcum*, *Bacillus mucilaginosus* and *Bacillus megaterium* strains considerably enhanced the

concentration of total phenolic compounds, flavonoids, and phenolic acid contents [115]. In the field, the strain *Bacillus* OSU-142 enhanced fruit quality of sweet cherry, by significantly promoting weight, length, diameter, seed weight, and soluble solids content [116], while the PGPB strain *P. fluorescens* Pf4 affected maize grain nutritional level, increasing grain starch content [117]. Interestingly, a synergistic effect between AMF and bacteria was detected in *Artemisia annua* plants, which showed a higher artemisin content when inoculated with the AM fungus *G. mosseae* and a strain of *Bacillus subtilis* isolated from its rhizosphere [118].

So far, the studies investigating the significance of bacteria isolated from the mycorrhizosphere (i.e., living in close association with AMF) revealed diverse functions related to plant nutrition and health, as discussed earlier. Only recently a few experimental works provided information on the role of AMF-associated bacteria in the production of beneficial phytochemicals. Two PGP bacterial strains isolated from spores of *R. intraradices* -*Sinorhizobium meliloti* TSA41 and *Streptomyces* sp. W43N- inoculated in *O. basilicum* var. Tigullio rhizosphere, triggered the overexpression of genes encoding for key enzymes involved in RA biosynthesis, i.e., tyrosine amino-transferase (*TAT*), hydroxyphenylpyruvate reductase (*HPPR*), and p-coumaroyl shikimate 3'-hydroxylase isoform 1 (*CS3'H iso1*) genes, in basil leaves. In particular, *TAT* expression levels showed 5.7-fold increase, *HPPR* 2-fold, and *CS3'H iso1* 1.5-fold [72]. Accordingly, successive experiments carried out under commercial production conditions in order to produce basil plants with similar phenology and P nutritional status and to rule out any P-nutrition-dependent effect on secondary metabolism, confirmed that the dual inoculation of *R. intraradices* and of its associated PGPB *S. meliloti* TSA41 and *Streptomyces* sp. W43N enhanced RA content in the leaves of the red-leaved basil cultivar Dark Opal. Moreover, the dual inoculation increased also the content of other health-promoting compounds, such as anthocyanins and leaves antioxidant activity [119]. Such a synergism represents an important starting point for the forthcoming studies aimed at utilizing AMF and their associated bacteria in order to promote plant production of beneficial phytochemicals.

Table 1. Secondary metabolites as affected by inoculation of arbuscular mycorrhizal fungi (AMF), plant growth-promoting bacteria, and AMF-associated bacteria (*) in selected food plants.

Phytochemicals	Plant Species	Microorganisms		Effect on Phytochemical Concentration	Source			
		AMF	Bacteria					
Phenolics	Total phenolics		<i>Glomus fasciculatum</i>	increased concentration or no effect depending on cultivar	[94]			
			<i>Glomus intraradices</i> + <i>Glomus mosseae</i> (Atens, Spain)	increased concentration or no effect depending on cultivar	[94]			
		<i>Lactuca sativa</i> L.	<i>Glomus intraradices</i> + <i>Glomus mosseae</i> (Atens, Spain)	no effect	[95]			
			<i>Rhizoglomus irregulare</i>	increased concentration	[96]			
			<i>Funneliformis mosseae</i>	no effect	[96]			
				<i>Bacillus lentimorbus</i> B-30488	increased concentration	[114]		
				<i>G. intraradices</i> NPI, USA	no effect	[70]		
				<i>G. mosseae</i> BEG 12	no effect	[68]		
				AMF	Bacteria			
			<i>Ocimum basilicum</i> L.			no effect	With AMF With bacterial mix	[119]
				<i>Rhizophagus intraradices</i>	<i>Sinorhizobium meliloti</i> TSA41 * + <i>Streptomyces</i> sp. W43N *	decreased concentration or no effect depending on the cultivar	With co-inoculation of AMF+bacterial mix	
				<i>G. intraradices</i> (Premier Tech Biotechnologies, Canada)		no effect		[102]
	<i>Fragaria x ananassa</i> Duch.	<i>Glomus iranicum</i> var. <i>tenuihypharum</i> (Mycogrowth®, Spain)		increased concentration	At early inoculation	[103]		

Table 1. Cont.

Phytochemicals	Plant Species	Microorganisms	Effect on Phytochemical Concentration		Source	
Caffeic acid	<i>Cynara cardunculus</i> L. var. <i>scolymus</i>	<i>G. mosseae</i> <i>G. intraradices</i>	increased concentration	With <i>G. intraradices</i> With AMF mix	[97]	
		<i>F. mosseae</i> 2W3 <i>F. mosseae</i> IMA1 <i>F. mosseae</i> IN101C <i>Claroideoglonus claroideum</i> 22W3	increased concentration	With 2W3	[99]	
		<i>R. irregulare</i> IMA6 <i>Glomus</i> sp. 14W1	no effect	With all the other AMF (single inoculation)		
	<i>Allium cepa</i> L.	Mix ¹ Plantworks, UK	no effect		[91]	
	Hydroxycinnamic acids	<i>Ocimum basilicum</i> L.	<i>G. intraradices</i> BEG 159 <i>Glomus caledonium</i> BEG 162 <i>G. mosseae</i> NBR 1–2	increased concentration	With <i>G. caledonium</i>	[67]
			<i>G. mosseae</i> BEG 12	no effect		[68]
			<i>G. intraradices</i> BEG 159 <i>G. caledonium</i> BEG 162 <i>G. mosseae</i> NBR 1–2	increased concentration	With <i>G. caledonium</i> With <i>G. mosseae</i> (single inoculation)	[67]
			<i>G. mosseae</i> BEG 12	no effect		[68]
			<i>G. intraradices</i> (NPI, USA)	no effect		[70]
	Rosmarinic acid	<i>Ocimum basilicum</i> L.	<i>R. intraradices</i>	increased or decreased concentration depending on the cultivar	With co-inoculation of AMF + bacterial mix	[119]
	<i>S. meliloti</i> TSA41 * + <i>Streptomyces</i> sp. W43N *		decreased concentration or no effect depending on the cultivar	With bacterial mix		
			decreased concentration	With AMF		
Chicoric acid		<i>G. intraradices</i> (NPI, USA)	no effect		[70]	

Table 1. Cont.

Phytochemicals		Plant Species	Microorganisms		Effect on Phytochemical Concentration	Source	
Flavonols	Quercetin	<i>Fragaria x ananassa</i> Duch.	<i>G. intraradices</i> (Premier Tech Biotechnologies Company, Canada)		increased concentration	[102]	
	Kaempferol				increased concentration		
	Catechin				no effect		
Anthocyanidins	Pelargonidin 3-glucoside, pelargonidin 3-rutinoside		Mix ² (Mybasol, Italy)	<i>Pseudomonas fluorescens</i> Pf4 <i>Pseudomonas</i> sp. 5Vm1K	increased concentration	With Mix With P5Vm1K With co-inoculation Mix + Pf4 [100]	
					no effect	With Mix With Pf4 With co-inoculation Mix + P5Vm1K	
	Pelargonidin 3-glucoside	<i>Fragaria x ananassa</i> Duch.	<i>Septogloium viscosum</i>	<i>P. fluorescens</i> 19Fv1t <i>P. fluorescens</i> Pf4 <i>Pseudomonas</i> sp. 5Vm1K	no effect	With co-inoculation of AMF + any bacterial isolate [111]	
					increased concentration	With co-inoculation of AMF + P5Vm1K	
	Pelargonidin malonyl glucoside		<i>Rhizophagus irregularis</i> DAOM197-200	<i>P. fluorescens</i> 19Fv1t <i>P. fluorescens</i> Pf4 <i>Pseudomonas</i> sp. 5Vm1K	no effect	With co-inoculation of AMF + any bacterial isolate	
	Pelargonidin malonyl glucoside		Mix ² (Mybasol, Italy)	<i>G. intraradices</i> (Premier Tech Biotechnologies Company, Canada)	<i>P. fluorescens</i> Pf4 <i>Pseudomonas</i> sp. 5Vm1K	no effect	[102]
						increased concentration	With AMF Mix With co-inoculation Mix + Pf4 [100]
					no effect	With Pf4 With P5Vm1K With co-inoculation Mix + P5Vm1K	

Table 1. Cont.

Phytochemicals	Plant Species	Microorganisms	Effect on Phytochemical Concentration	Source		
Pelargonidin acetyl glucoside		Mix ² (Mybasol, Italy)	<i>P. fluorescens</i> Pf4 <i>Pseudomonas</i> sp. 5Vm1K	no effect	With all combination [100]	
		Cyanidin 3-glucoside	Mix ² (Mybasol, Italy)	<i>P. fluorescens</i> Pf4 <i>Pseudomonas</i> sp. 5Vm1K	increased concentration	With P5Vm1K With co-inoculation Mix + PV5m1K [100]
					no effect	With Pf4 With co-inoculation Mix + P5Vm1K
			<i>G. intraradices</i> (Premier Tech Biotechnologies Company, Canada)	increased concentration	[102]	
Total anthocyanins	<i>Ocimum basilicum</i> L.	<i>R. intraradices</i>	<i>S. meliloti</i> TSA41 * + <i>Streptomyces</i> sp. W43N *	increased concentration	With co-inoculation AMF + bacterial mix	
				no effect	With bacterial mix	
				decreased concentration	With AMF	
		<i>G. intraradices</i> (NPI, USA)	increased concentration	[70]		
Terpenoids	Total carotenoids	<i>Ocimum basilicum</i> L.	<i>R. intraradices</i>	<i>S. meliloti</i> TSA41 * + <i>Streptomyces</i> sp. W43N *	decreased concentration	With AMF With bacterial mix [119]
					decreased concentration or no effect depending on cultivar	With co-inoculation of AMF + bacterial mix
		<i>Solanum lycopersicum</i> L.	<i>F. mosseae</i> BEG12 <i>R. irregularis</i> BB-E (Agrauxine, F)	increased concentration	With co-inoculation [93]	
				no effect	With BEG12 With BB-E (single inoculation)	
	<i>R. irregularis</i> (Premier Tech Inc., Canada)	increased concentration	[93]			

Table 1. Cont.

Phytochemicals	Plant Species	Microorganisms	Effect on Phytochemical Concentration	Source			
Carotenes	Lycopene	<i>Solanum lycopersicum</i> L.	Mix ² (Mybasol, Italy)	<i>P. fluorescens</i> C7 <i>Pseudomonas</i> sp. 19Fv1T	no effect	With all combinations	[109]
			Mix ² (Mybasol, Italy)	<i>P. fluorescens</i> C7 <i>Pseudomonas</i> sp. 19Fv1T	decreased concentration	With co-inoculation Mix + single bacterial isolate With triple inoculation	[110]
			<i>F. mosseae</i> BEG12 <i>R. irregularis</i> BB-E (Agrauxine, F)	increased concentration	With BEG12 With BB-E (single inoculation)	[93]	
				no effect	With co-inoculation		
			Mix ² (Mybasol, Italy)	<i>P. fluorescens</i> C7 <i>Pseudomonas</i> sp. 19Fv1T	decreased concentration	With AMF Mix With C7 (single inoculation)	[109]
				no effect	With 19Fv1T With co-inoculation Mix + single bacterial isolate With triple inoculation		
	β-carotene	<i>Solanum lycopersicum</i> L.	Mix ² (Mybasol, Italy)	<i>P. fluorescens</i> C7 <i>Pseudomonas</i> sp. 19Fv1T	decreased concentration	With co-inoculation Mix + single bacterial isolate	[110]
				no effect	With triple inoculation		
			<i>F. mosseae</i> BEG12 <i>R. irregularis</i> BB-E (Agrauxine, F)	increased concentration	With co-inoculation	[93]	
				no effect	With BEG12 With BB-E (single inoculation)		
			Mix ² (Mybasol, Italy)	<i>P. fluorescens</i> C7 <i>Pseudomonas</i> sp. 19Fv1T	increased concentration	With co-inoculation Mix + single bacterial isolate	[110]
				no effect	With triple inoculation		
Xanthophylls	Luteine	<i>Solanum lycopersicum</i> L.	Mix ² (Mybasol, Italy)	<i>P. fluorescens</i> C7 <i>Pseudomonas</i> sp. 19Fv1T	increased concentration	With co-inoculation Mix + single bacterial isolate	[110]

Table 1. Cont.

Phytochemicals	Plant Species	Microorganisms	Effect on Phytochemical Concentration		Source	
			no effect	With triple inoculation		
	<i>Fragaria x ananassa</i> Duch.	Mix ² (Mybasol, Italy)	<i>P. fluorescens</i> Pf4 <i>Pseudomonas</i> sp. 5Vm1K	increased concentration	With Mix With single bacterial isolates With co-inoculation Mix + single bacterial isolate	[101]
Other	Ascorbic acid	Mix ² (Mybasol, Italy)	<i>P. fluorescens</i> C7 <i>Pseudomonas</i> sp. 19Fv1T	increased concentration	With 19Fv1T	[109]
				no effect	With co-inoculation AMF + 19Fv1T	
				decreased concentration	With Mix With C7 With co-inoculation Mix+C7	
		Mix ² (Mybasol, Italy)	<i>P. fluorescens</i> C7 <i>Pseudomonas</i> sp. 19Fv1T	increased concentration	With triple inoculation	[110]
				no effect	With co-inoculation of AMF + 19Fv1T	
				decreased concentration	With co-inoculation of AMF + C7	
Mix ³ (Symbivit, Czech Rep.) <i>G. intraradices</i> BEG140		no effect	With AMF (single inoculation)	[92]		

¹ *Glomus mosseae*, *Glomus intraradices*, *Glomus claroideum*, *Glomus microaggregatum*. ² *Rhizophagus intraradices*, *Rhizophagus aggregatus*, *Septoglomus viscosum*, *Claroideoglomus etunicatum* and *Claroideoglomus claroideum* ³ *Glomus etunicatum*, *Glomus microaggregatum*, *Glomus intraradices*, *Glomus claroideum*, *Glomus mosseae*, *Glomus geosporum*.

5. Conclusions and Perspectives for Future Studies

The studies performed so far suggest a positive role played by mycorrhizal symbioses in the production of beneficial phytochemicals by medicinal, aromatic, and food plants, although not allowing clear-cut conclusions. Indeed, not only few plant species have been investigated, but also a very low number of cultivars, which are long known to show a large natural variability with regard to their nutraceutical properties, as previously discussed [15]. For example, the data available on antioxidant activity and secondary metabolites levels of mycorrhizal tomato fruits come from experiments carried out on as few as ten varieties, while the tomato varieties described so far are more than 900 (<https://njaes.rutgers.edu/tomato-varieties/>, 13 November 2020). As a consequence, further studies should be focused on the responses of the highest possible number of plant cultivars belonging to the same species. This will avoid general statements, allowing a deeper knowledge of the intraspecific plant secondary metabolic diversity, as affected by mycorrhizal symbionts.

On the other hand, only a few AMF species and isolates have been investigated so far, mainly fungi occurring in commercial inocula and generalist symbionts such as *F. mosseae*, *R. intraradices*, and *R. irregularis*. Future studies should exploit the large diversity of these beneficial symbionts, which are available in research laboratories and international germplasm collections all over the world.

As far as bacteria are concerned, more attention should be devoted to those closely associated with AMF, that have been reported to possess several plant growth-promoting properties, i.e., IAA, antibiotics, and siderophores production, N fixation and P solubilizing activity. Indeed, such beneficial bacteria could show a higher compatibility with AMF, when co-inoculated, leading to possible synergistic effects on the production of health-promoting phytochemicals. The data obtained would allow a better understanding of the emerging properties of the previously unimagined network of interactions involving plants, mycorrhizal fungi, and their associated bacteria. Bridging the gap between basic science and the formulation of innovative and effective microbial products for the sustainable intensification of food production systems represents the real next challenge in the years to come.

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