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# METABOLITOS SINTETIZADOS EN LA SIMBIOSIS MICORRÍCICA: DE LA RAÍZ A LAS PARTES AÉREAS

## METABOLITES SYNTHESIZED IN THE MYCORRHIZAL SYMBIOSIS: FROM THE ROOT TO THE AERIAL PARTS

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# Metabolitos Sintetizados en la Simbiosis Micorrícica: De la Raíz a las Partes Aéreas

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## RESUMEN

Los hongos micorrícicos arbusculares (HMA) forman la asociación simbiótica más frecuente (80%) con las raíces de las plantas terrestres. Esta relación se establece mediante un diálogo de señalización que comienza en el suelo, induciendo cambios fisiológicos en toda la planta. Tras el contacto físico entre las hifas fúngicas y la raíz, los HMA desarrollan estructuras especializadas dentro de las células corticales. Posteriormente, la colonización interna del hongo facilita el intercambio de nutrientes entre ambos organismos. Hace tres décadas, se descubrió que la inoculación con HMA aumenta los niveles de ciertos aminoácidos y proteínas solubles, lo que demuestra que esta asociación simbiótica altera significativamente el metabolismo de la planta. Durante la simbiosis, los compuestos sintetizados como respuesta defensiva a la presencia del hongo pueden inducir cambios en los metabolitos secundarios y los compuestos bioactivos en diversos tejidos vegetales. Esta revisión describe cómo se activan los metabolitos en respuesta a los HMA, así como su función ante estímulos adicionales como el estrés abiótico y biótico.

***Palabras clave:*** hongos micorrícicos arbusculares; estrés; metabolitos

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# Metabolites Synthesized in the Mycorrhizal Symbiosis: From the Root to the Aerial Parts

## ABSTRACT

Arbuscular mycorrhizal fungi (AMF) form the most prevalent symbiotic association (80%) with the roots of terrestrial plants. This relationship is established through a signaling dialogue that begins in the soil, inducing physiological changes across the plant. Upon physical contact between fungal hyphae and the root, AMF develop specialized structures within the cortical cells. Subsequently, internal fungal colonization facilitates the exchange of nutrients between both organisms. Three decades ago, it was discovered that AMF inoculation increases levels of certain amino acids and soluble proteins, demonstrating that this symbiotic association significantly alters plant metabolism. During symbiosis, compounds synthesized as a defense response to the fungal presence can induce changes in secondary metabolites and bioactive compounds throughout various plant tissues. This review describes how metabolites are activated in response to AMF, as well as their role under additional stimuli such as abiotic and biotic stress.

***Keywords***: arbuscular mycorrhizal fungi; stress; metabolites

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## INTRODUCTION

Arbuscular mycorrhizal fungi (AMF) symbiosis is the most widespread among land plants; approximately 80% of species establish this association. Indeed, it is believed that terrestrial plant life was made possible by this symbiosis (Selosse & Le Tacon, 1998; Redecker *et al*., 2000; Brundrett, 2009; Wang *et al*., 2010). Root colonization by AMF alters plant physiology and the production of phytohormones. Both partners interact through a molecular dialogue initiated by physical interaction in the soil.

Strigolactones are plant hormones identified as root-exuded signals recognized by AMF. Upon perceiving these signals, fungal hyphae begin to expand to facilitate root contact. The fungus then produces chitin oligomers (CO) and lipo-chito-oligosaccharides (LCO), which act as signals to induce changes in calcium levels and gene expression within the plant. Receptors with lysin-motifs (LysM) are required for successful mycorrhization; these receptors are also involved in the perception of LCOs derived from fungal cell walls. This mechanism helps plants discriminate endosymbionts from pathogenic microorganisms using structurally related LCOs and COs (Gough & Cullimore, 2011; Oldroyd, 2013; Rush *et al*., 2020).

Among strigolactones are the so-called "branching factors" (Buee *et al*., 2000) that trigger CO production (Genre *et al*., 2013). However, the specific structure of strigolactones depends on the plant species and its interaction with the fungal species (Kee *et al*., 2023). For example, in *Eustoma grandiflorum* (Gentianaceae), the monoterpene glycosides gentiopicroside and swertiamarin were found in response to gibberellin (GA) treatment. These compounds stimulate hyphal branching in *Rhizophagus irregularis* and *R. clarus* (Glomerales) but do not induce branching in *Gigaspora margarita* (Diversisporales) (Tominaga *et al*., 2023).

When the fungal hyphae and plant root make physical contact, AMF develop structures within the inner cortical cells. The hyphae then form tree-like structures called arbuscules, which serve as the physical site for nutrient exchange: the plant receives phosphorus (P) and nitrogen (N), while the fungus receives carbon (C) from the host.

Approximately 30 years ago, it was discovered that certain amino acids and soluble proteins increased following AMF inoculation in soybean, maize, and tobacco plants (Pacovsky, 1989; Dumas *et al*., 1990;

Charest *et al*., 1993), demonstrating that this symbiotic association alters plant metabolism. A metabolome analysis represents the physiological status of the plant and provides a comprehensive view of the adaptive capacities conferred by the plasticity of each species (Sardans *et al*., 2011).

During mycorrhizal symbiosis, compounds typically associated with defensive responses to fungal colonization are synthesized. These signaling mechanisms between the host plant and fungi may induce changes in secondary metabolite content, as well as specific bioactive compounds in fruits, leaves, shoots, and roots (Table 1). Understanding the dynamics of specialized metabolites within the mutualistic or parasitic AMF relationship offers deeper molecular insight into this symbiosis. These molecules play a significant role in all stages of the process, from spore germination and hyphal branching to the establishment of a functional association (Akiyama *et al*., 2005; Genre *et al*., 2013).

**Table 1**. Metabolites that have been investigated for single AMF effects and/or upon biotic-abiotic.

| **Specie** | **Fungal specie** | **Tissue** | **Metabolite** | **Analytical method** | **Reference** |
|---|---|---|---|---|---|
| Libidibia ferrea | C. etunicatum | Leaves | Gallic acid | HPLC-PDA | (Queiroz et al., 2014) |
| Ocimum basilicum | G. intraradices<br>G. etunicatum<br>G. fasciculatum$^1$ | Aerial parts | Linalool,<br>Eugenol, Ocimene, Methyl chavicol, Farnesol and Humulene | GC<br>UFC | (Rasouli-sadaghiani et al., 2010b) |
| Artemisia annua | G. macrocarpum<br>G. fasciculatum$^1$ | Leaves | Artemisinin | HLPC | (Evelin and Kapoor, 2014) |
| Anadenanthera colubrine | G. albida<br>A. longula | Leaves | Carbohydrates, Flavonoids, Phenolics and Tannins | Spectrophotometer | (Pedone-bonfim et al., 2012) |
| Ocimum basilicum | G. caledonium$^1$<br>G. mosseae | Shoots$^3$<br>Roots | Rosmarinic acid and Caffeic acid | HLPC | (Toussaint et al., 2007) |
| Hypericum perforatum | R. intraradices<br>F. mosseae$^2$<br>AMF mix<br>(G. constrictum,<br>G. geosporum,<br>F. mosseae, and<br>R. intraradices) | Shoots | Hypericin and Pseudohypericin | HPLC-FLD,<br>HPLC-DAD | (Zubek et al., 2012) |
| Inula ensifolia | G. intraradices$^3$<br>G. clarum$^1$ | Roots<br>Shoots$^3$ | Thymol derivatives | NMR<br>MS | (Zubek et al., 2010) |
| Cynara scolymus | G. intraradices$^1$<br>G. mosseae | Leaves<br>Flowers | Phenolic content and Antioxidant activity | spectrophotometer. | (Ceccarelli et al., 2010) |
| Arnica montana | G. geosporum<br>G. constrictum<br>G. intraradices$^1$<br>Mixture thereof and<br>G. mosseae | Shoots<br>Roots$^2$ | Sesquiterpene lactones | UV spectra | (Jurkiewicz et al., 2010) |
| | | Leaves | Phenolic content | HPLC-DAD<br>MS-API-ESI | |
| Vitis vinifera | G. mosseae$^1$<br>G. fasciculatum<br>G. intraradices<br>Mixture thereof | Leaves<br>Roots$^2$ | Phenol content | UV spectrophotometry | (Eftekhari et al., 2012) |
| | | Leaves<br>Stem | Flavonoid quercetin | HPLC | |

| | | | | | |
|---|---|---|---|---|---|
| Solanum lycopersicum | R. irregularis<br>F. mosseae | Roots | Ferulic acid, Cumaryl alcohol, Coniferyl alcohol, Benzylisoquinoline Alkaloids, Spermidine,<br>Triferuloyl spermidine,<br>Products derived from the oxylipin pathway and Amino acids[3]<br>(Tryptophan, Tyrosine, Phenylalanine, Alanine, and Leucine) | HPLC<br>LC–ESI Q-TOF MS | (Rivero et al., 2015) |
| Triticum durum Desf | AMF Mix<br>(S. calospora, A. laevis, G. aggregatum, R. irregulare, F. mosseae, G. fasciculatum, G. etunicatum, G. deserticola, and G. margarita)<br>PGPR+AMF[1] | Roots | Amino acids[3]<br>(Glutamic acid, Alanine, Asparagine and Phenylalanine) and<br>Fatty acids[3] | GC-TOF-MS<br>HILIC-Q-TOF-MS | (Saia et al., 2015) |
| Lotus japonicus | G. mosseae | Source leaves<br>Sink leaves | Amino acid metabolism[3]<br>(Glutamic acid, Aspartic acid, Glycine, Asparagine, 4-aminobutanoic acid, 2-methyl-malic acid)<br>Organic acids[3]<br>(Malic acid, Citric acid and Succinic acid)<br>Kestose, Xylitol and Myo-inositol | GC–MS | (Fester et al., 2011) |
| Salix purpurea | R. irregularis | Leaves | Amino acids[3], Carbohydrates[3]<br>Coumaroylquinate,<br>Caffeoyl-shikimate,<br>OPC6-CoA, trans-2-enoyl-OPC6-CoA,<br>JA, Iso-JA,<br>Pinostrobin, Isoformononetin,<br>Rutin, Luteolin-7-O-glucoside,<br>Porphyrin, Chlorophyll,<br>Phenolic glycosides and Terpenoids | MS<br>H NMR | (Aliferis et al., 2015a) |
| Zea mays | G. intraradices | Leaves | Amino acids[3]<br>Organic acids, Lipids, Fatty acids, Carotenoids, Antioxidants, Carbohydrates, α- amyrin and β-amyrin | ICP-MS<br>LC-MS<br>HPLC | (Gerlach et al., 2015a) |

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|---|---|---|---|---|---|
| Hordeum vulgare | AMF mix<br>(G. mosseae and G. intraradices) | Leaves | Sucrose[3],<br>Amino acids[3]<br>(Glutamic acid and Aspartate),<br>Chlorophyll[3], Lutein[3], and Glutathione[3]<br>Free hexoses (3PGA, PEP, RuBP, Glc1P),<br>Free inorganic phosphate and Carboxylates isocitrate and malate | ESI-MS<br>ion exchange chromatography<br>HPLC<br>Spectrophotometer | (Kogel et al., 2010) |
| Medicago truncatula | R. irregularis | Roots | Amino acids<br>(Glutamic acid, Aspartic acid, and Asparagine)<br>Trehalose, Palmitic acid, Oleic acids, Cyclohexanone, Mycorradicin derivatives, Daidzein, ononin, Malonylononin cyclohexanone, Mycorradicin derivatives,<br>Glucosides of blumenol C,<br>13-hydroxyblumenol C,<br>Malonyl conjugates and<br>Tyrosol | GC–MS<br>HPLC<br>LC–MS. | (Schliemann et al., 2008) |
| Medicago truncatula | R. irregularis | Roots | Propionyl carnitines,<br>Butyryl carnitines,<br>13-hydroxylblumenol C 9-O-β-malonylglucoside,<br>blumenol C 9-O-β-malonylglucoside,<br>Daidzein, Ononin and Malonylononin | UHPLC–HR–MS<br>MS-Q-TOF | (Laparre et al., 2014) |
| Lotus japonicus | R. irregularis | Roots | glucosylceramide,<br>dihexosylceramide,<br>inositolphosphorylceramide,<br>palmitic acid,<br>palmitvaccenic acid,<br>free sterols, sterol esters, sterol glucosides, acylated sterol glucosides<br>palmitvaccenic (di-16:1)[2]<br>tetracosanoic (24:1) acyl groups[2] | MS/MS Q-TOF<br>TLC<br>GC<br>HPL | (Wewer et al., 2014) |
| | | Extraradical mycelium | palmitvaccenic (di-16:1) and tetracosanoic (24:1) acyl groups | | |
| Solanum lycopersicum | G. mosseae | Fruits | Amino acids<br>(Glutamine and asparagine) and | GC-MS | (Zouari et al., 2014) |
| Veronica chamaedrys | R. irregularis | Leaves | Sugar alcohol mannitol | GC–MS<br>LC-MS<br>GC-DSQII | (Schweiger et al., 2014) |
| Medicago truncatula | | Leaves | Pinitol,<br>Ononitol, | | |

| | | | | | |
|---|---|---|---|---|---|
| | | | Organic acids$^{3}$ (Citrate, Malate, Fumarate, Succinate and Isocitrate) | uHPLC-ToF-MS | |
| Plantago lanceolata and Plantago major | | Leaves | Sorbitol,<br>Catalpol (only in P. lanceolata) | | |
| Plantago lanceolata, Plantago major and Veronica chamaedrys | | Leaves | Aucubin and Verbascoside<br>Organic acids$^{3}$ (Citrate, Malate, Fumarate, Succinate and isocitrate) | | |
| Poa annua | | Leaves | Organic acids$^{3}$ (Citrate, Malate, Fumarate, Succinate and isocitrate) | | |
| Plantago lanceolata and fungivores treatmen (Folsomia candida) | G. intraradices$^{1}$<br>G. custos$^{2}$<br>Mixture thereof | Shoots | Catalpol$^{3}$, Verbascoside and Aucubin$^{2}$ | HPLC | (Duhamel et al., 2013) |
| | | Roots | Catalpol,$^{2}$ Verbascoside$^{3}$ and Aucubin$^{2}$ | | |
| | | Hyphae | Catalpol | | |
| Plantago lanceolata | G. intraradices | Roots | Aucubin | HPLC | (Kempel et al., 2010) |
| Plantago lanceolata | G. intraradices | Roots | Aucubin | HPLC | (De Deyn et al., 2009) |
| Medicago truncatula and Medicago truncatula mutant mtha1-2$^{2}$ | G. intraradices | Leaves | Phosphate, Sulfate,<br>Nitrate, Citrate, Fumarate and Chloride | HPAE | (Hubberten et al., 2015) |
| Solanum lycopersicum | G. mosseae$^{1}$<br>G. intraradices | Roots | OPDA, JA-Ile and SA | UPLC-MS | (López-Ráez et al., 2010) |
| Olea europaea | G. intraradices | Leaves | α-linolenic acid (C18:3ω3 | GC | (Mechri et al., 2014) |
| Trigonella foenumgraecum | G. intraradices | Leaves<br>Roots | Antioxidant capacity<br>Ascorbic acid, α-tocopherol, Glutathione, and Carotenoids | spectrophotometer | (Evelin and Kapoor, 2014) |
| Solanum lycopersicum | G. mosseae | Roots | Antioxidant capacity and Malonaldehyde$^{2}$ | spectrophotometer | ( ZhongQun et al., 2007) |
| Solanum lycopersicum | G. intraradices | Shoots | Proline and<br>Reactive oxygen species | spectrophotometer | (Hajiboland et al., 2010) |
| Cajanus cajan | G. mosseae | Roots<br>Shoots | Proline and<br>Glycine betaine | spectrophotometer | (Garg and Manchanda, 2009) |
| Zea mays | Other AMF<br>G. etunicatum$^{1}$<br>G. intraradices$^{1}$ | Leaves | Proline,<br>Malondialdehyde and<br>Soluble sugar | spectrophotometer | (Chen et al., 2014) |

| | | | | | |
|---|---|---|---|---|---|
| Zea mays | G. etunicatum | Shoots<br>Roots | Photosynthetic capacity | - | (Zhu et al., 2010) |
| Zea mays | G. mosseae | Leaves | Amino acids,[3]<br>Proline,[3]<br>Formic acid[3] and<br>Succinic acid[3] | HPLC | (Sheng et al., 2011) |
| Fragaria ananassa | G. mosseae | Leaves | Antioxidant capacity<br>proline | - | (Yin et al., 2010) |
| Zea mays | G. etunicatum | Leaves<br>Roots[3] | Proline | - | (Zhu et al., 2011) |
| Solanum lycopersicum | AFM Mix (G. mosseae, G. intraradices and Glomus sp.) | Leaves<br>Roots[3] | Essential Isoprenoids (α-thujene, α-pinene, D4-carene, β-phellandrene, Limonene and linalool) and Nonessential Isoprenoids[3] | T-system to two-stage traps<br>GC-MS<br>HPLC | (Asensio et al., 2012) |
| | | Roots | Apocarotenoids, and Strigolactones | | |
| Calopogonium mucunoides | G. etunicatum | Leaves | Aspartate, Glutamine, Glycine, Threonine, Alanine, Isoleucine and Gamma-aminobutiric acid<br>Asparagine[3],<br>Histidine[3]<br>and Arginine[3] | RP-HPLC | (Souza et al., 2014) |
| Cichorium intybus | R. irregularis | Shoots | Caftaric acid and Cichoric acid | RF-HPLC | (Rozpadek et al., 2014) |
| | | Roots | Sesquiterpene lactones,<br>8-DeoxyLC, Jacq and LPikr | | |
| Sorghum spp. | AFM mix (G. intraradices, G. mosseae, G. aggregatum, and G. etunicatum) | Roots<br>Shoots | Glycerol-3-galactoside,<br>Erythrose, adenine,<br>5-methoxytryptamine,<br>4-hydroxybenzoate,<br>Arginine, Proline,<br>Starch and Sucrose metabolism and<br>lipid metabolism (only with PGPB) | ALEX-CIS<br>GC-TOF MS | (Dhawi et al., 2016) |
| Asclepias spp. | R. intraradices, F. mosseae, G. aggregatum, and C. etunicatum | Root | Non-Polar<br>Cardenolides and Polar cardenolides | UPLC | (Vannette et al., 2013) |
| | | Leaves | Non-Polar cardenolides | | |
| Plantago lanceolata | G. intraradices | Shoots | (Z)-3-hexenyl acetate | GC-MS<br>HPLC<br>LC-MS | (Fontana et al., 2009) |
| Zea mays | G. mosseae | Roots<br>Leaves | 2,4-dihydroxy-7-methoxy-2H-1,4-benzoxazin-3(4 H)-one | HPLC | (Song et al., 2013) |

1. More efficient symbiont

2. No differences being noted

3. Lowest concentration/or negative impact/down-regulate

Since modulating the plant metabolome can prevent antagonistic defense responses, it may also prepare plants for enhanced tolerance to environmental stress. These metabolites influence the outcome of the association through the composition and exchange of both primary and specialized compounds. Thus, the specificity of the plant-AMF interaction is regulated by changes in the plant's primary and specialized metabolome (Kaur & Suseela, 2020).

Although the leaf metabolome in AMF associations has been previously reported (Schweiger & Müller, 2015), the roots of mycorrhizal plants have often been overlooked. This review describes current findings on metabolites triggered in response to AMF, while also considering additional stimuli such as abiotic or biotic stress across all plant tissues.

## METHODOLOGY

The methodology includes the revision of research documents from the last 37 years. Similarly, for this literature review, authors were added based on their relevance and pertinence, according to the topics presented.

### Metabolic changes upon AMF colonization in medicinal plants

Currently, while the synthesis of specific compounds is possible, low yields often make it economically unviable for drug production. However, AMF can enhance the concentrations of certain compounds. A notable example is gallic acid in *Libidibia ferrea*; when inoculated with *Claroideoglomus etunicatum*, the plant shows an increase in production compared to non-inoculated controls. A proposed mechanism for this influence is the activation of the shikimic acid metabolic pathway, which is a precursor to phenolic compounds (Silva *et al*., 2014).

Furthermore, essential oil content was evaluated in the aerial parts of basil (*Ocimum basilicum*) inoculated with *Glomus intraradices*, *Glomus etunicatum*, and *Glomus fasciculatum*. The results revealed that plants inoculated specifically with *G. fasciculatum* showed a significant increase in linalool, followed by eugenol, ocimene, methyl chavicol, farnesol, and humulene, among other compounds (Rasouli-Sadaghiani *et al*., 2010).

In some cases, the availability of phosphorus (P), nitrogen (N), or both in the soil enhances the efficiency of mycorrhizal inoculation and improves metabolite production. Examples include increased levels of artemisinin (Kapoor *et al*., 2007), proteins and carbohydrates (Pedone-Bonfim *et al*., 2012), antioxidant phytochemicals (Toussaint *et al*., 2007; Zubek *et al*., 2010, 2012), and colchicine (Pandey *et al*., 2014).

Specifically, inoculation with *Glomus macrocarpum* and *G. fasciculatum* increased the artemisinin concentration in *Artemisia annua*, with *G. fasciculatum* proving to be the more efficient symbiont. However, phosphate fertilization can alter the extent of these AMF-induced effects on artemisinin production (Kapoor et al., 2007).

In cebil plants inoculated with a mixed consortium of *Gigaspora albida* and *Acaulospora longula*, the content of proteins, carbohydrates, flavonoids, phenolics, and tannins in the leaves increased. Nevertheless, this benefit to primary metabolism was mitigated at higher P levels (Pedone-Bonfim *et al*., 2012). Similarly, in pepper seedlings (*Capsicum chinense*) inoculated with *Entrophospora etunicata*, significant metabolic increases were recorded compared to the control: 77% higher soluble carbohydrates, 147% more total proanthocyanidins, 140% more total phenols, and 136% more total saponins. These increases were also reflected in the concentrations of total proteins and foliar flavonoids (Ribeiro da Luz *et al*., 2023).

Higher accumulation of antioxidant compounds, such as rosmarinic and caffeic acids, has been reported in sweet basil shoots (*Ocimum basilicum*) inoculated with different *Glomus* species, specifically *G. caledonium* and *G. mosseae*. However, these effects might be attributed to improved phosphorus (P) nutrition via AMF. Plants colonized by *G. caledonium* yield higher concentrations of these acids compared to non-mycorrhizal plants.

A possible mechanism by which *G. caledonium* and *G. mosseae* increase these phytochemical concentrations is through enhanced nitrogen (N) assimilation. This could contribute to the production of amino acids like tyrosine and phenylalanine, which are essential precursors for phenylalanine ammonia-lyase (PAL), the primary enzyme involved in the biosynthesis of rosmarinic and caffeic acids (Toussaint *et al*., 2007). In *Hypericum perforatum*, inoculation with *Rhizophagus intraradices* and an AMF consortium (*Glomus constrictum*, *G. geosporum*, *Funneliformis mosseae*, and *R. intraradices*) improved the concentration of the anthraquinone derivatives hypericin and pseudohypericin in shoots, even with relatively high soil P content; notably, no significant differences were observed in the *F. mosseae* treatment (Zubek *et al*., 2012).

Experiments with various fungal strains have induced distinct metabolic changes. For instance, *Inula ensifolia* was inoculated with two strains of *G. intraradices* and *Glomus clarum*. These AMF species influenced the production of thymol derivatives differently: the highest concentration of all analyzed compounds in the roots was found after *G. clarum* inoculation, while the lowest concentrations were detected in the *G. intraradices* treatments. Conversely, mycorrhizal plants were characterized by lower concentrations in the shoots (Zubek *et al*., 2010).

A significant increase in total phenolic content and antioxidant activity was recorded in the leaves and flowers of artichoke plants inoculated with *G. intraradices* and *G. mosseae* in both greenhouse and field experiments, with *G. intraradices* being more effective in stimulating these secondary metabolites (Ceccarelli *et al*., 2010).

Mycorrhization was performed in *Arnica montana* at low N and P levels using different AMF species, namely *G. geosporum*, *G. constrictum*, *G. intraradices*, and a consortium composed of the aforementioned species plus *G. mosseae*. The analysis showed that the concentration of sesquiterpene lactones was significantly higher in shoots than in roots. In leaves, the total phenolic acid concentration was higher in plants inoculated with *G. intraradices* (Jurkiewicz *et al*., 2010).

On the other hand, the treatments significantly increased the levels of sesquiterpenic acids in the rhizomes and roots of *Valeriana officinalis* (Nell et al., 2010). Similarly, a study on *Melissa officinalis* reported an increased content of two phenolic compounds (rosmarinic and lithospermic acids) in the presence of three AMF mixtures; however, these compounds decreased in *Majorana hortensis* (Engel *et al*., 2016).

Finally, the vegetative parts (leaf and stem) of various grape varieties were inoculated with *G. mosseae*, *G. fasciculatum*, *G. intraradices*, and a consortium of these three species. The results showed a significantly higher total phenol content in leaf tissues compared to control plants, whereas no significant differences were found in root tissues. Furthermore, the vegetative parts of grape plants inoculated with AMF were found to be rich sources of the flavonoid quercetin (Eftekhari *et al*., 2012).

**Metabolites in Targeted and Untargeted Approaches**

Metabolomics approaches allow for the separation and detection of a wide range of metabolites through gas chromatography-mass spectrometry (GC-MS), liquid chromatography-mass spectrometry (LC-

MS), and nuclear magnetic resonance (NMR). These procedures offer the highest capacity for determining extensive metabolite sets, estimated between 100,000 and 200,000 (Sardans *et al*., 2011).

Observations on metabolic alterations by Rivero and coworkers identified significant shifts in tomato roots inoculated with two common AMF: *Rhizophagus irregularis* and *F. mosseae*. Products derived from amino acids, such as phenolic alcohol derivatives, benzylisoquinolines, and conjugated polyamines, were significantly affected in AMF colonized plants.

Specifically, high quantities of ferulic acid, coumaryl alcohol, coniferyl alcohol, benzylisoquinoline alkaloids, polyamines (and their conjugates), a putative spermidine, triferuloyl spermidine, and oxylipin pathway derivatives were found in colonized roots. Conversely, a negative impact was observed on free amino acids such as tryptophan, tyrosine, phenylalanine, alanine, and leucine. The lower concentration of these free amino acids suggests their role as precursors for secondary metabolites, particularly tyrosine and phenylalanine, which are essential for phenylpropanoid biosynthesis (Rivero *et al*., 2015).

Similarly, wheat roots inoculated with a consortium of AMF species (*Scutellospora calospora*, *Acaulospora laevis*, *Glomus agg*regatum, *G. etunicatum*, *G. deserticola*, *Gigaspora margarita*, *R. irregularis*, *F. mosseae*, and *G. fasciculatum*) showed decreased concentrations of glutamic acid, alanine, asparagine, phenylalanine, and saturated fatty acids. In contrast, dual inoculation with PGPR and AMF increased their accumulation, suggesting that PGPR enhances nitrogen (N) availability, particularly ammonium and nitrate, for the host plant (Saia *et al*., 2015).

A decrease in amino acid metabolism has been previously reported in the association between *Lotus japonicus* and *G. mosseae*. This symbiosis results in a reduction of amino acid metabolism — specifically affecting glutamic acid, aspartic acid, glycine, asparagine, 4-aminobutanoic acid (GABA), and 2-methylmalic acid— in both source and sink leaves. Furthermore, organic acids involved in central catabolic pathways, such as malic, citric, and succinic acids, are also reduced. Conversely, an increase in kestose, xylitol, and myo-inositol has been observed; these compounds serve as indicators of stress response in *L. japonicus* (Fester *et al*., 2011).

In another association involving willow and R. irregularis, leaf metabolic content was significantly altered. Results revealed that mycorrhization has a negative impact on primary metabolism, primarily affecting amino acids and carbohydrates. In contrast, an up-regulation was observed in several biosynthetic pathways, including those for phenylpropanoids, flavonoids, isoflavonoids, coumaroylquinate, and caffeoyl-shikimate. Additionally, increases were noted in jasmonic acid (JA), iso-JA, pinostrobin, isoformononetin, rutin, luteolin-7-O-glucoside, porphyrins, chlorophyll, phenolic glycosides, and terpenoids. Many of these compounds are directly linked to resistance against environmental stress (Aliferis *et al*., 2015).

Similarly, in maize plants, symbiosis with *G. intraradices* led to a down-regulation of amino acid content in the leaves, while secondary metabolism was up-regulated, specifically for organic acids, lipids, fatty acids, carotenoids, antioxidants, and carbohydrates. Interestingly, the terpenoids alpha-amyrin and beta-amyrin showed strong accumulation (Gerlach *et al*., 2015).

In other experiments, four genotypes of barley were analyzed using a mixture of the mycorrhizal fungi *G. mosseae* and *G. intraradices*. Leaf contents of sucrose, the two major amino acids (glutamic acid and aspartate), chlorophyll, lutein, and glutathione decreased in response to AMF. Conversely, levels of free hexoses, central phosphorylated intermediates (3PGA, PEP, RuBP, Glc1P), free inorganic phosphate, and the carboxylates isocitrate and malate increased. In general, phosphorylated intermediates of central metabolism were more abundant in the leaves of AMF-colonized plants (Kogel *et al*., 2010).

Regarding amino acid content in symbiotic associations, rhizobia exhibit the opposite phenomenon: an increase in metabolites connected to amino acid metabolism and a decrease in those related to plant stress (Fester *et al*., 2011).

Amino acid dynamics have been discussed by Rivero *et al*. (2015), particularly their role as precursor compounds for amino acid-derived secondary metabolites. Certain amino acids, such as glutamate and aspartate, are crucial for nitrogen (N) uptake by the AMF extra-radical mycelium. Other studies have shown that AMF have a high N demand and retain most of the N acquired as organic compounds for their own growth (Hodge & Fitter, 2010). Conversely, increases in amino acid levels have been interpreted as an indicator of enhanced plastid activity in colonized root cells rather than having direct nutritional significance (Lohse *et al*., 2005; Schliemann *et al*., 2008; Fester *et al*., 2011).

Changes in mycorrhizal roots have been well studied, particularly in the model plant *Medicago truncatula* and the AMF strain *R. irregularis*. Compared to other experiments, mycorrhization raised the levels of certain amino acids, such as glutamic acid, aspartic acid, and asparagine. It also increased the concentrations of specific metabolites like trehalose, palmitic and oleic acids, cyclohexanone, mycorradicin derivatives, daidzein, ononin, and malonylononin (Schliemann *et al*., 2008). Interestingly, oleic acid has been found to increase spore germination at concentrations of $10^{-8}$ M (Rush *et al*., 2020). Years later, Laparre et al. (2014), using the same symbiotic association, performed metabolomics and biological screens based on gene expression responses, identifying two significant compounds: propionyl and butyryl carnitines. These new symbiotic signals may serve as markers of fungal root colonization, although further studies are required with other AMF species to confirm their universality (Laparre *et al*., 2014).

Root colonization of *L. japonicus* by *R. irregularis* revealed specific lipid responses upon mycorrhization. Glycosylated sphingolipids (glucosylceramide, dihexosylceramide), inositolphosphorylceramide, free sterols, sterol esters, sterol glucosides, and acylated sterol glucosides were detected in *R. irregularis*, primarily containing two predominant fatty acids: palmitic acid and palmitvaccenic acid.

Notable differences between extraradical mycelium (ERM) and mycorrhizal roots were detected; specifically, some of the major phosphatidylcholine (PC) molecular species present in the ERM —such as those containing palmitvaccenic and tetracosenoic acyl groups—are absent from mycorrhizal roots (Wewer *et al*., 2014).

The amino acid composition of tomato fruits is modified upon colonization with *G. mosseae*, which also accelerates flowering and fruit development while increasing yield. Symbiosis enhances amino acid abundance, with glutamine and asparagine being the most responsive. In general, mycorrhizal plants exhibit a higher total free amino acid content compared to control fruits. Although this metabolic shift was supported by transcriptomic data, no significant differences were noted in gene expression within the fruits themselves.

The authors propose two possibilities to explain this:

1. Transport Mechanism: The two amides were not synthesized de novo in the fruit but were translocated from the host roots. These amino acids are recognized as primary nitrogen transport compounds from source to sink organs, serving as nitrogen reserves.

2. Fungal Synthesis: These amino acids could be synthesized directly by the AMF (Salvioli *et al*., 2012).

Analysis of leaves from *R. irregularis* colonized plants showed a common core of 850 metabolic features shared between dicotyledonous and monocotyledonous plants. However, metabolic responses to AMF were highly species-specific. For example:

- The sugar alcohol mannitol was only detectable in *Veronica chamaedrys*.
- The cyclic polyols pinitol and ononitol were characteristic of *Medicago truncatula*.
- Sorbitol was common to the genus *Plantago*.
- Aucubin and verbascoside were found exclusively in the Plantaginaceae.

Several organic acids from the citric acid cycle (citrate, malate, fumarate, and partially succinate and isocitrate) decreased under AMF conditions in *P. lanceolata*, *P. major*, *V. chamaedrys*, and *M. truncatula*, but increased in the grass *Poa annua*. Interestingly, the grass was the least responsive to AMF symbiosis, although catalpol —a secondary metabolite involved in direct plant defense— was significantly increased by AMF in *P. lanceolata* (Schweiger *et al*., 2014).

Previously, catalpol has been detected in *G. intraradices* hyphae during symbiosis with *P. lanceolata*. AMF inoculation led to a decrease in verbascoside content in roots but increased its concentration in shoots only when fungivores were present. In contrast, AMF inoculation consistently reduced catalpol concentrations in shoots and had no effect in roots. While aucubin was detectable in all samples, no treatment significantly affected its concentration in shoots. Notably, catalpol was consistently found in AMF hyphae when host plants were exposed to fungivores (Duhamel *et al*., 2013).

Finally, when different genotypes of *P. lanceolata* (containing high and low levels of iridoid glycosides, IG) were inoculated with *G. intraradices*, results suggested that high root concentrations of aucubin may have deleterious effects on arbuscular development. Interestingly, AMF increased root aucubin concentrations specifically in the high-IG genotype (De Deyn *et al*., 2009).

The mutant mtha1-2 is defective in the symbiotic transfer of nutrients across the periarbuscular space, which precludes phosphate uptake. In this mutant, no changes were observed in leaf metabolite levels, such as phosphate, sulfate, nitrate, citrate, fumarate, and chloride, when compared with wild-type plants inoculated with AMF (Hubberten *et al*., 2015).

Using the tomato plant as a model, an integrative analysis of the host response to different mycorrhizal fungi was performed. Levels of 12-oxo-phytodienoic acid (OPDA) were significantly higher in roots colonized by *G. mosseae* and *G. intraradices*. While JA levels remained unaltered, its bioactive derivative, JA-isoleucine (JA-Ile), and salicylic acid (SA) were higher only in the *G.* mosseae association. Abscisic acid (ABA) content did not change in either fungal association. Combined transcriptional analyses suggest that the oxylipin pathway could regulate AMF symbiosis, specifically through jasmonate-mediated regulation (López-Ráez *et al*., 2010).

Additionally, the amount of glycolipids in the leaves of mycorrhizal olive trees (*Olea europaea*) was found to be altered. Glycolipid content was higher in plants inoculated with *G. intraradices*, which also increased the levels of alpha-linolenic acid within the glycolipid fraction (Mechri *et al*., 2014).

**Metabolites and Biotic/Abiotic Stress**

Abiotic and biotic stresses adversely affect plant physiology; however, AMF symbiosis can enhance plant tolerance to varying degrees. The association with AMF influences interactions between plants and their natural enemies through several mechanisms, including genetic variability among plants and fungal species, as well as the susceptibility of these enemies to secondary metabolites triggered by the AMF-host interaction.

Enhanced antioxidant capacity in both leaves and roots has been observed in *Trigonella foenum-graecum* (fenugreek) inoculated with Glomus intraradices under salinity stress. Despite a reduction in root colonization as salt stress increased, there was a significant rise in the activity of antioxidant enzymes, such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), peroxidase (PX), and glutathione reductase (GR) and in the concentration of antioxidant molecules, including ascorbic acid, alpha-tocopherol, glutathione, and carotenoids (Evelin & Kapoor, 2014). Similar findings were previously reported in tomato plants inoculated with *G.* mosseae (ZhongQun *et al*., 2007) and *G. intraradices* (Hajiboland *et al*., 2010), as well as in *Cajanus cajan* inoculated with *G. mosseae*, which showed increased osmolyte synthesis and accumulation (Garg & Manchanda, 2009).

Regarding thermal stress, maize plants inoculated with four different AMF species exhibited higher proline content at low temperatures. Specifically, only *G. etunicatum* and *G. intraradices* showed elevated levels of malondialdehyde and soluble sugars under these stress conditions (Chen et al., 2014).

Furthermore, maize plants inoculated with G. etunicatum demonstrated higher stomatal conductance, alongside improved water status and photosynthetic capacity (Zhu et al., 2010). Conversely, a decrease in the relative abundance of total free amino acids, proline, formic acid, and succinic acid was detected in maize plants inoculated with *G. mosseae* under salt stress (Sheng et al., 2011).

*Glomus mosseae* has been shown to increase the activity of protective enzymes, osmoregulation, and antioxidant capacity in strawberry leaves. This symbiosis also promotes the accumulation of free proline and soluble proteins, while improving the transport speed of soluble sugars under drought stress (Yin et al., 2010). These findings align with reports on maize inoculated with *G. etunicatum*, where the symbiosis increased leaf proline content but decreased it in the roots during drought. In these maize plants, peroxidase activity was higher in both leaves and roots, whereas superoxide dismutase activity increased exclusively in the roots (Zhu et al., 2011).

In other studies, tomato plants inoculated with a commercial consortium (*G. mosseae*, *G. intraradices*, and *Glomus* sp.) prioritized the leaf production of essential isoprenoids over non-essential ones, particularly under drought conditions. The primary volatile compounds emitted were monoterpenes, including alpha-thujene, alpha-pinene, delta-4-carene, beta-phellandrene, limonene, and linalool.

Conversely, AMF symbiosis has been found to decrease the root content of volatile isoprenoids while stimulating the production of other isoprenoid-derived compounds. These include apocarotenoids and strigolactones, which originate from the oxidative cleavage of carotenoids. Both groups are vital for various growth processes, with strigolactones being particularly crucial for the functional establishment of the AMF symbiosis. Authors suggest that this shifts carbon allocation toward specific secondary compounds, as all isoprenoids share common precursors (Asensio et al., 2012).

In relation to amino acid profiles, mycorrhization in *Calopogonium mucunoides* inoculated with *G. etunicatum* during heavy metal exposure led to an increase in foliar levels of aspartate, glutamine, glycine, threonine, alanine, isoleucine, and gamma-aminobutyric acid (GABA). In contrast, a depletion of asparagine, histidine, and arginine was observed. Notably, only amino acids derived from 3-phosphoglycerate and pyruvate were significantly higher in mycorrhizal plants (Souza et al., 2014).

Furthermore, in chicory plants inoculated with *Rhizophagus irregularis*, an accumulation of caffeic acid derivatives, such as caftaric and chicoric acid, was observed in the shoots. In the roots, the concentration of sesquiterpene lactones increased. However, no significant differences were found when plants were cultivated on substrates enriched with heavy metals such as Zn, Pb, and Cd (Rozpądek et al., 2014).

Sorghum plants were inoculated with a mixture of Plant Growth-Promoting Bacteria (PGPB) and an AMF consortium containing *G. intraradices*, *G. mosseae*, *G. aggregatum*, and *G. etunicatum*. The mycorrhizal treatment resulted in the up-regulation of several metabolites; notably, five were exclusively up-regulated in the mycorrhizal group: glycerol-3-galactoside, erythrose, adenine, 5-methoxytryptamine, and 4-hydroxybenzoate. Furthermore, five metabolic pathways were up-regulated, including arginine and proline metabolism and starch and sucrose metabolism. These changes were associated with enhanced uptake of macronutrients, microelements, and heavy metals such as copper and zinc.

The combined treatment of AMF and *Pseudomonas* increased lipid metabolism during the mycorrhizal symbiosis, accompanied by heightened transcriptional regulation. Additionally, three pathways involved in amino acid metabolism and energy generation were common to both the mycorrhizal and *Pseudomonas* treatments. These results suggest that mycorrhizae play a role in inducing essential amino acid precursors and the biosynthesis of plant carbohydrates from fatty acids via glyoxylate and dicarboxylate metabolism (Dhawi et al., 2016).

In respect of biotic interactions, *G. intraradices* has shown a positive effect on herbivores; for instance, a significant increase in the growth of *Spodoptera littoralis* was observed, suggesting that AMF may improve food quality for certain herbivores (Kempel et al., 2010). Furthermore, AMF can influence traits mediating plant-herbivore interactions by altering the relative distribution of secondary compounds across leaves, stems, and roots. In asclepias plants inoculated with *R. intraradices*, *F. mosseae*, *G. aggregatum*, and *C. etunicatum*, the inoculation shifted the distribution of cardenolides between root and shoot tissues. While cardenolides in fine roots occurred at equal concentrations regardless of treatment, AMF inoculation increased cardenolide non-polarity in shoots and leaves, which are generally considered more toxic than their polar counterparts (Vannette et al., 2013).

Plant responses are also highly dependent on species-specific fungal colonization. In a study where strawberry plants were colonized by *G. mosseae* and *G. fasciculatum*, dual colonization had no effect on *Otiorhynchus sulcatus* larvae. However, single-species inoculation reduced larval survival and weight. Although the exact mechanism remains unknown, the authors proposed three potential explanations: physical, nutritional, and/or chemical effects (Gange, 2001). Subsequently, Fontana et al. (2009) found that *P. lanceolata* plants inoculated with *G. intraradices* emitted lower amounts of sesquiterpenes during *Spodoptera littoralis* herbivory but showed an increased emission of the green leaf volatile (Z)-3-hexenyl acetate, which is considered an indirect defense signal.

*Medicago truncatula* plants colonized by *G. intraradices* exhibited increased resistance to the virulent bacterial pathogen *Xanthomonas campestris*. This resistance was associated with transcriptional changes in both roots and shoots; notably, many of the genes induced in the shoots are predicted to be involved in stress and defense responses (Liu et al., 2007). Similarly, tomato plants colonized with *G. fasciculatum* showed systemic induced resistance (SIR) to the foliar pathogen *Alternaria alternata*. Mycorrhizal plants displayed a three-fold increase in lipoxygenase (LOX) activity compared to control plants, a finding supported by the up-regulation of genes involved in jasmonic acid (JA) biosynthesis and salicylic acid (SA) signaling (Nair et al., 2015).

Consistent with these findings, tomato plants inoculated with *F. mosseae* demonstrated enhanced resistance to early blight caused by *Alternaria solani* Sorauer. Root colonization induced the expression of defense-related enzymes (PR1, PR2, and PR3) and genes (LOX, AOC, and PAL) in the leaves upon pathogen challenge. These results further suggest that the JA pathway is essential for mediating such systemic responses (Song et al., 2015).

In maize (*Zea mays*), inoculation with *G. mosseae* significantly reduced the incidence and severity of sheath blight caused by *Rhizoctonia solani*. This effect was observed in two varieties: Gaoyou-115 (susceptible) and Yuenong-9 (resistant). The symbiosis led to a significant increase in 2,4-dihydroxy-7-methoxy-2H-1,4-benzoxazin-3(4H)-one (DIMBOA), a critical phytoalexin in maize involved in systemic defense. DIMBOA accumulation occurred in the roots of both varieties and specifically in the leaves of the resistant plants. These chemical changes were supported by the strong activation of defense-related genes, including BX9-a key gene in the DIMBOA biosynthetic pathway-in the leaves of both varieties (Song et al., 2011).

## CONCLUSIONS

Mycorrhizal colonization induces systemic metabolic shifts that extend from the roots to the aerial components of the host plant. By integrating advanced analytical techniques, it is possible to characterize a vast array of secondary metabolites regulated by the AMF symbiosis. Plant roots not only synthesize specific compounds triggered by AMF but also enhance the biosynthesis of various metabolites in aerial tissues, such as leaves, stems, and fruits.

These symbiotic interactions typically lead to an increased concentration of antioxidants, phenolics, phytoalexins, organic acids, amino acids, lipids, fatty acids, carotenoids, terpenoids, flavonoids, isoflavonoids, and polyamines. Conversely, the symbiosis may also result in the depletion of precursor molecules as they are channeled into secondary metabolic pathways.

While the precise mechanisms by which AMF modulate metabolite concentrations remain to be fully elucidated, the current literature indicates a frequent reduction in free amino acid pools. This trend supports the hypothesis that these amino acids serve as primary substrates for the synthesis of more complex secondary compounds in both roots and shoots.

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