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REVIEW

# A comprehensive review of the transcriptomic and metabolic responses of grapevines to arbuscular mycorrhizal fungi

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## Abstract

***Main conclusion*** **This review discusses the molecular modifications of grapevines by arbuscular mycorrhizal fungi, increasing anthocyanins and other phenolic molecules, potentially improving wine quality and plant stress tolerance.**

**Abstract** Grapevines are naturally associated with arbuscular mycorrhizal fungi (AMF). These fungi, as obligate symbionts, are capable of influencing molecular, biochemical, and metabolic pathways, leading to alterations in the concentrations of various molecules within the host plant. Recent studies have addressed the transcriptomic and metabolic modifications triggered by AMF in grapevines. These AMF-induced alterations are involved in cell transport, sugar metabolism, plant defense mechanisms, and increased tolerance to both biotic and abiotic stressors. Notably, the shikimate pathway exhibits heightened activity following AMF inoculation in grapevines, resulting in the accumulation of anthocyanins, flavonols, phenolic acids, and stilbenes. Phenolic compounds are the main metabolites influencing grape and wine quality attributes, such as color, flavor, and potential health benefits. This review aims to provide an updated overview of current research on the transcriptomic and metabolic aspects of AMF–grapevine interactions, focusing on their impact on plant performance and quality traits.

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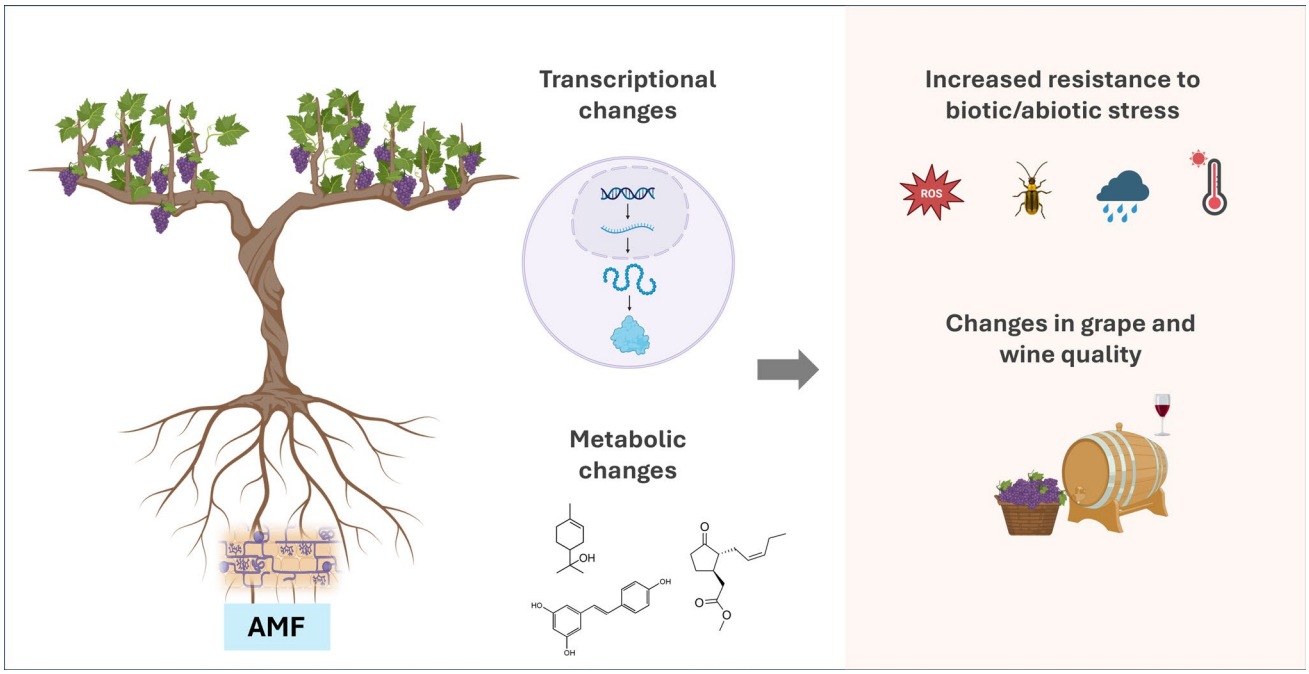
**Graphic abstract**




**Keywords** Grape quality · Anthocyanin · Mycorrhizal symbiosis · Metabolomics · Microbial *terroir*

## Introduction

Grapevine is a perennial woody plant, considered one of the most economically important crops in the world, encompassing a global cultivated area spanning 7.3 million hectares, which includes the cultivation of both wine and table grapes (OIV 2021). Various sustainable practices have been incorporated into vineyards to minimize environmental impacts (Cataldo et al. 2021). These environmentally friendly practices include the use of beneficial microorganisms, which have been extensively researched across various crops, with the aim of increasing yield and nutritional quality, and mitigating the effects of both biotic and abiotic stresses in the context of climate change (Cataldo et al. 2021; Vega-Celedon et al. 2021; Vidal et al. 2022; Larach et al. 2024). Among the beneficial microorganisms, arbuscular mycorrhizal fungi (AMF) are obligate biotrophs that belong to the phylum Glomeromycota and form one of the most widespread symbiotic associations with plant roots (Schüβler et al. 2001; Tedersoo et al. 2018). This symbiosis is estimated to be present in 70–90% of terrestrial plants (Smith and Read 2008). AMF engage with plant roots, furnishing the host plant with water and essential minerals, whereas plants reciprocate by providing fixed carbon to the fungi (Harrison 2005). Within this symbiotic relationship, AMF colonize cortical cells, establishing intricate intracellular structures, particularly highly branched hyphae known as arbuscules. These arbuscules serve as the primary sites for the symbiotic exchange of nutrients between plants and fungi (Parniske 2008).

Studies have indicated that AMF play a role in enhancing plant nutritional status, promoting growth, and bolstering resistance to various stresses (Hao et al. 2012; Trouvelot et al. 2015). However, the impact of this symbiotic relationship can vary based on factors, such as the specific grapevine cultivar, the composition of AMF communities involved, and the type of AMF inoculum utilized (Antolin et al. 2020; Moukarzel et al. 2022). These variations highlight the complexity of the interactions between grapevines and AMF, demonstrating that the outcomes of this symbiosis can be influenced by multiple factors. Despite the potential impact of AMF diversity influenced by green cover species (Bowles et al. 2016), evidence shows that AMF benefits predominantly emerge from controlled environments, often utilizing specific AMF inoculants. Under field conditions, outcomes related to plant performance tend to be less consistent. This inconsistency is attributed to the intricate nature of environmental interactions, which adds complexity to the assessment of the effects of AMF on host plants (Rosa et al. 2020). AMF enhance nutrient uptake and promote plant growth across various commercially significant grapevine cultivars and rootstocks (Trouvelot et al. 2015). Furthermore, AMF

have been observed to influence both primary and secondary metabolism in host plants, leading to increased levels of sugars, amino acids, alkaloids, terpenoids, and phenolic compounds. Even in cases where there may not be a discernible impact on grapevine growth, alterations in metabolite concentrations have been detected (Torres et al. 2019). This highlights the intricate ways in which AMF may affect grapevines, potentially influencing various aspects of their physiology and biochemistry.

Grapevines generate a wide spectrum of metabolites that are crucial for various aspects of plant physiology, defense mechanisms, and inter-plant communication. These metabolites also serve as protective agents against various abiotic stresses, such as drought, radiation, high temperatures, and oxidative damage (Ferrandino et al. 2023). Although diverse metabolites are continually produced throughout the plant's life cycle, under environmental stress, plants may trigger de novo synthesis or elevate the production of specific compounds (Holopainen and Gershenzon 2010; Yang et al. 2021). This adaptive strategy allows grapevines to adjust their metabolic pathways in response to changing environmental conditions, thereby enhancing resilience and survival under challenging circumstances. Stress signals are recognized by plant cell receptors, which activate diverse transcription factors, and therefore, downstream defense gene expression (Jan et al. 2021). The specific mechanisms through which AMF regulate metabolite production in grapevines remain largely elusive and are yet to be comprehensively understood.

This study aims to review the influence of AMF–grapevine colonization on gene regulation and metabolite production. Additionally, this study discusses the involvement of these metabolic shifts in grapevines' resilience to biotic and abiotic stresses, potentially impacting grape and wine quality.

## Effect of AMF on grapevine transcriptomics

Arbuscular mycorrhizal (AM) colonization initiates a cascade of molecular events within grapevines, resulting in notable changes in gene expression patterns. These alterations activate pathways associated with plant defense mechanisms and the cell transportome (Table 1). A recent study by Goddard et al. (2021) provided compelling evidence of the systemic impact of AM symbiosis on grapevines. Their research revealed significant transcriptomic shifts occurring not only in the roots but also in the leaves of AM plants. This systemic effect underscores the comprehensive nature of the molecular responses triggered by AM symbiosis throughout the grapevine, highlighting the intricate interplay between root and shoot tissues in mediating plant response to AM colonization. These findings deepen our understanding of the molecular mechanisms underlying the symbiotic relationship between grapevines and AMF, offering valuable insights into how these interactions influence plant physiology, defense mechanisms, and overall health. Soportes et al. (2023) analyzed 10 grapevine rootstocks and identified over 300 genes regulated by arbuscular mycorrhizal (AM) symbiosis across all rootstocks. Furthermore, by comparing this gene set to their *Medicago truncatula* homologs, the authors found that more than 97% was expressed in at least one mycorrhizal transcriptomic study in *Medicago*, highlighting a shared subset of AM-responsive genes.

Balestrini et al. (2017) reported that diverse nutrient transporter genes are upregulated in roots after AMF inoculation. Nodulin genes, previously recognized as being regulated by AMF, exhibit heightened expression levels in grapevine, as demonstrated by Balestrini et al. (2017). Moreover, it has been documented that AMF enhance phosphate uptake by upregulating the expression of phosphate transporter 1 (PHT1) family genes (Rausch et al. 2001; Harrison et al. 2002). Notably, putative phosphate transporter genes VvPHT1-1 and VvPHT1-2 were found to be significantly induced in the roots of AM grape rootstock 41 B MGt, whereas transcripts were either low or absent in non-AM plants (Valat et al. 2017). In addition, VvPT4 and VvPT8 were consistently regulated in ten grapevine rootstocks (Soportes et al. 2023). Nerva et al. (2023) reported two nitrate transporters, VvNRT1.3 and VvNRT2.4, exhibiting distinct patterns of expression in response to AMF and D-glucose, used as a colonization inducer. VvNRT1.3 showed an increased expression in AMF-inoculated plants compared to all other treatments, while VvNRT2.4 was primarily influenced by the application of the D-glucose inducer.

AMF also influence sugar metabolism in host plants. In grapevines, 12 genes belonging to the Sugars Will Eventually be Exported Transporters (SWEET) family have been identified (Denancé et al. 2014). The SWEET protein family serves as both intra- and intercellular transporters of sugars and plays diverse roles in physiological functions, such as facilitating sucrose transport for phloem loading, regulating seed development, contributing to abiotic stress tolerance, and aiding in reproductive organ development (Sosso et al. 2015; Li et al. 2020; Huang et al. 2022; Zhu et al. 2022).

In a study conducted by Goddard et al. (2021), no notable changes were observed in the expression levels of the *Vv*SWEET4 and *Vv*SWEET12 genes within the roots of AM grapevines when compared to non-AM plants. However, in leaves, the expression of *Vv*SWEET17c transcripts decreased in AM-colonized plants. These results are in contrast with those observed in potato roots, where major changes were found in SWEET gene expression after inoculation with *Rhizophagus irregularis* (Manck-Götzenberger and Requena 2016). Although SWEET genes have been implicated in AM

**Table 1** Regulation of gene expression in grapevine by AMF in different grapevine tissues

| Plant tissue | Mycorrhizal inoculation† | Growing conditions | Grapevine cultivar | Gene description | Effect of AMF inoculation on gene regulation | References |
|---|---|---|---|---|---|---|
| Leaves | Agronutrition (Carbonne, France): containing *Rhizophagus irregularis* | Potted-grapevines grown in greenhouse under 27 °C with a 16 h photoperiod (150 $\mu Em^{-2} \cdot s^{-1}$ light irradiance) | Gewurztraminer CL-643 | Allene oxide synthase | ↑ | Goddard et al. (2021) |
| | | | | DNA binding protein WRKY2 | ↓ | |
| | | | | SWEET 17C | ↓ | |
| | INOQ GmbH (Schnega, Germany): containing *Rhizophagus irregularis* and *Funneliformis mosseae* | Potted-grapevines grown in greenhouse with or without inducer application (D-glucose) | Glera grafted onto 1103P rootstock | 9-*cis*-Epoxycarotenoid dioxygenase 3 | AMF: ↑; AMF + D-glucose: no effect | Nerva et al. (2022) |
| | | | | Glucosyltransferase | AMF: ↑; AMF + D-glucose: ↑ | |
| | | | | *β*-Glucosidase 1 | AMF: ↑; AMF + D-glucose: ↑ | |
| | | | | Stilbene synthase 1 | AMF: ↑; AMF + D-glucose: ↓ | |
| | | | | Stilbene synthase 48 | AMF: ↑; AMF + D-glucose: no effect | |
| | | | Glera grafted onto SO4 rootstock | 9-*cis*-Epoxycarotenoid dioxygenase 3 | AMF: ↑; AMF + D-glucose: no effect | |
| | | | | ABA 8'-hydroxilase 1 | AMF: ↑; AMF + D-glucose: no effect | |
| | | | | Glucosyltransferase | AMF: ↑; AMF + D-glucose: no effect | |
| | | | | *β*-Glucosidase 1 | AMF: ↑; AMF + D-glucose: ↑ | |
| | | | | Stilbene synthase 1 | AMF: ↑; AMF + D-glucose: ↑ | |
| | Agrifood Research and Technology-IRTA (Catalonia, Spain): containing *Rhizoglomus irregulare* | Potted-grapevines grown in growth chamber under 26 ± 5° C and 58 ± 12% relative humidity | Touriga Nacional grafted onto 1103 Paulsen rootstock | miR164a | ↑ | Campos et al. (2023) |
| | | | | miR156g-5p.1 | ↑ | |
| | | | | miR393a-5p.3 | ↑ | |
| | | | | miR393b-5p | ↑ | |

**Table 1** (continued)

| Plant tissue | Mycorrhizal inoculation[†] | Growing conditions | Grapevine cultivar | Gene description | Effect of AMF inoculation on gene regulation | References |
|---|---|---|---|---|---|---|
| | | | | miR167a.1 | ↑ | |
| | | | | miR166p | ↑ | |
| | | | | miR156g-3p | ↑ | |
| | | | | miR156d | ↑ | |
| | | | | miR157a-5p | ↑ | |
| | | | | miR535 | ↑ | |
| | | | | miR166f-3p | ↑ | |
| | | | | miR3640-5p | ↓ | |
| | | | | miR3632-5p | ↓ | |
| | | | | miR397a-5p | ↓ | |
| | | | | miR3627-3P | ↓ | |
| | | | | miR398c-3p.1 | ↓ | |
| | | | | miR3627-5p | ↓ | |
| | | | | miR3634-5p | ↓ | |
| | Symbiom (Czech Republic): containing *Funneliformis mosseae* | Potted-grapevines grown in growth chamber under 26 ± 5° C and 58 ± 12% relative humidity | Touriga Nacional grafted onto 1103 Paulsen root-stock | miR167a.1 | ↑ | |
| | | | | miR156g-5p.1 | ↑ | |
| | | | | miR396a-5p.1 | ↑ | |
| | | | | miR393b-5p | ↑ | |
| | | | | miR393a-5p.3 | ↑ | |
| | | | | miR162-3p.1 | ↑ | |
| | | | | miR403f | ↑ | |
| | | | | miR166b | ↑ | |
| | | | | miR396c | ↑ | |
| | | | | miR166f-3p | ↑ | |
| | | | | miR3640-5p | ↓ | |

**Table 1** (continued)

| Plant tissue | Mycorrhizal inoculation† | Growing conditions | Grapevine cultivar | Gene description | Effect of AMF inoculation on gene regulation | References |
|---|---|---|---|---|---|---|
| Roots | Agronutrition (Carbonne, France): containing *Funneliformis mosseae* | Potted-grapevines grown in greenhouse under 24/20 °C day/night temperature and 16-h photoperiod (150 $\mu Em^{-2}\ s^{-1}$ light irradiance) and 60% humidity | Rootstock 41B MGt | Phosphate transporter 1–1 (PHT1) | ↑ | Valat et al. (2018) |
| | | | | Phosphate transporter 1–2 (PHT1) | ↑ | |
| | Agronutrition (Carbonne, France): containing *Rhizophagus irregularis* | Potted-grapevines grown in growth chamber under 27◦C with a 16 h photoperiod (150 $\mu Em^{-2}{\cdot}s^{-1}$ light irradiance) | Gewurztraminer CL-643 | Pathogenesis-related protein 6 bis | ↑ | Goddard et al. (2021) |
| | | | | Pathogenesis-related protein 7 | ↑ | |
| | | | | Pathogenesis-related protein 7 bis | ↑ | |
| | | | | Lipoxygenase 3 | ↓ | |
| | | | | Lipoxygenase 9 | ↓ | |
| | | | | Allene oxide synthase | ↓ | |
| | | | | Amine oxidase copper containing 1 | ↓ | |
| | | | | Sucrose transporter 11 | ↓ | |
| | | | | Sucrose transporter 12 | ↓ | |
| | | | | Sucrose transporter 27 | ↓ | |
| | MycoApply (USA): containing *Funneliformis* mosseae, *Glomus aggregatum* and *Claroideoglomus etunicatum* | Potted-grapevines grown in greenhouse under 20/25 °C temperature and 12/14 h of light condition | Ecolly | 9-*cis*-Epoxycarotenoid dioxygenase | ↑ | Ye et al. (2023) |
| | | | | Pyrroline-5-carboxylate synthase | ↑ | |
| | | | | Small and basic intrinsic protein | ↑ | |
| | | | | Plasma membrane intrinsic protein 1;2 | ↑ | |
| | | | | Tonoplast intrinsic protein 2;1 | ↑ | |

**Table 1** (continued)

| Plant tissue | Mycorrhizal inoculation† | Growing conditions | Grapevine cultivar | Gene description | Effect of AMF inoculation on gene regulation | References |
|---|---|---|---|---|---|---|
| | *Glomus versiforme* | Potted-grapevines grown in greenhouse under 25/15 °C day/night temperature with a 16 h photoperiod at a photon flux density of 300 µmol $m^{-2}$ $s^{-1}$, and 60% relative humidity | Shuangyou | Class III Chitinase | ↑ | Li et al. (2006) |
| | INOQ GmbH (Schnega, Germany): containing *Rhizophagus irregularis* and *Funneliformis mosseae* | Potted-grapevines grown in greenhouse with or without inducer application (D-glucose) | Rootstock 1103P | ABA 8'-hydroxilase 1 | AMF: ↑; AMF + D-glucose: ↓ | Nerva et al. (2022) |
| | | | | Phosphate transporter 1–3 | AMF: ↑; AMF + D-glucose: ↑ | |
| | | | | *β*-Glucosidase 1 | AMF: ↓; AMF + D-glucose: ↓ | |
| | | | | Glucosyltransferase | AMF: ↓; AMF + D-glucose: ↓ | |
| | | | | 9-cis-Epoxycarotenoid dioxygenase 3 | AMF: ↓; AMF + D-glucose: ↓ | |
| | | | Rootstock SO4 | ABA 8'-hydroxilase 1 | AMF: ↑; AMF + D-glucose: ↑ | |
| | | | | Phosphate transporter 1–3 | AMF: ↑; AMF + D-glucose: no effect | |
| | | | | *β*-Glucosidase 1 | AMF: ↓; AMF + D-glucose: ↓ | |
| | | | | 9-*cis*-Epoxycarotenoid dioxygenase 3 | AMF inoculum: ↓; AMF + D-glucose: ↓ | |
| | MycAgro (Bretenière, France): containing *Funneliformis mosseae* | Potted-grapevines grown in greenhouse under natural day/night conditions | Pinot noir grafted onto Richter 110 rootstock | Nodulin MtN21 family | ↑ | Balestrini et al. (2017) * |
| | | | | Nitrite reductase | ↑ | |
| | | | | Basic helix–loop–helix family (VIT_13s0064g01290) | ↑ | |
| | | | | Uroporphyrin III methylase | ↑ | |
| | | | | Nodulin MtN3 family | ↑ | |
| | | | | Pectinesterase family | ↑ | |
| | | | | Nitric oxide reductase, cytochrome b-containing subunit I | ↑ | |

**Table 1** (continued)

| Plant tissue | Mycorrhizal inoculation† | Growing conditions | Grapevine cultivar | Gene description | Effect of AMF inoculation on gene regulation | References |
|---|---|---|---|---|---|---|
| | | | | Nitrate reductase 2 | ↑ | |
| | | | | Basic helix–loop–helix family (VIT_14s0068g01580) | ↑ | |
| | | | | Laccase | ↑ | |
| | | | | Cellulase CEL2 | ↓ | |
| | | | | Sugar transporter ERD6-like 16 | ↓ | |
| | | | | Lipid transfer protein | ↓ | |
| | | | | Isoflavone methyltransferase/orcinol *O*-methyltransferase 1 | ↓ | |
| | | | | Acidic endochitinase (CHIB1) | ↓ | |
| | | | | Galactinol synthase | ↓ | |
| | | | | Cyclin B2;4 | ↓ | |
| | | | | Alpha-expansin 1 precursor | ↓ | |
| | | | | Blight-associated protein p12 precursor | ↓ | |
| | | | | Expansin-like B1 | ↓ | |
| | *Rhizophagus irregularis* DAOM197198 | Potted-grapevines grown in greenhouse | Rootstocks 110 Richter, 140 Ruggeri, 1103 Paulsen, Selection Oppenheim4, 420A Millardet et de Grasset, 41B Millardet et de Grasset, 101.14 Millardet et de Grasset, *V. riparia*, *V. rupestris* and *V. berlandieri* | Germin-like protein 8 | ↑ | Soportes et al. (2023)** |
| | | | | MEE39 (Maternal effect embryo arrest 39) | ↑ | |
| | | | | F-box family protein | ↑ | |
| | | | | Leucine-rich repeat family protein (Vitvi17g01689) | ↑ | |
| | | | | Leucine-rich repeat family protein (Vitvi13g02370) | ↑ | |
| | | | | Phosphate transporter 1–1 (PHT1) | ↑ | |

**Table 1** (continued)

| Plant tissue | Mycorrhizal inoculation[†] | Growing conditions | Grapevine cultivar | Gene description | Effect of AMF inoculation on gene regulation | References |
|---|---|---|---|---|---|---|
| | | | | Germin-like protein (Vitvi10g01014) | ↑ | |
| | | | | Vitvi14g02850 | ↑ | |
| | | | | Zinc finger family protein (Vitvi09g00432) | ↑ | |
| | | | | Zinc finger family protein (Vitvi06g01710) | ↑ | |
| | INOQ GmbH (Schnega, Germany): containing *Rhizophagus irregularis* and *Funneliformis mosseae* | Potted-grapevines grown in greenhouse with or without inducer application (D-glucose) | Glera grafted onto 1103P rootstock | Nitrate transporter (VvNRT1.3) | AMF: ↑; AMF + D-glucose: ↓ | Nerva et al. (2023) |
| | | | | Nitrate transporter (VvNRT 2.4) | AMF: ↓; AMF + D-glucose: no effect | |
| | | | | High-affinity nitrate transporter (VvHNT1) | AMF: ↓; AMF + D-glucose: ↓ | |
| | | | Glera grafted onto SO4 rootstock | Nitrate transporter (VvNRT1.3) | AMF: no effect; AMF + D-glucose: ↓ | |
| | | | | Nitrate transporter (VvNRT 2.4) | AMF: ↓; AMF + D-glucose: ↑ | |
| | | | | High-affinity nitrate transporter (VvHNT1) | AMF: ↓; AMF + D-glucose: ↓ | |

[†] Names of mycorrhizal fungi species has been maintained as reported in the studies

↑ = Up-regulated; ↓ = Down-regulated

[*] The 10 most up- and down-regulated genes were mentioned in this review

[**] The 10 most consistently expressed grapevine genes in response to AM symbiosis were mentioned in this review

symbiosis, their precise role in this context remains unclear (Manck-Götzenberger and Requena 2016). The gene expression pattern of the sucrose transporter (SUT), which is involved in long-distance sugar transport in plants, has also been shown to be affected by AMF. This may be explained by the fact that AMF enhance the redirection of sucrose from the leaves to the roots (Roth and Paszkowski 2017). During the initial stages of colonization, AM *M. truncatula* and tomato plants exhibited an upregulation of SUT genes in both leaves and roots (Boldt et al. 2011; Doidy et al. 2012). Nevertheless, there were no differences in SUT expression in the leaves of AM *Vitis vinifera* cv. Gewurztraminer was observed, while in roots, downregulation was reported compared to control plants (Goddard et al. 2021). Similarly, studies have noted a heightened concentration of sucrose in roots during the early phases of AM colonization. However, in grapevines, a decrease in sucrose concentration has been observed at the onset of AMF inoculation (Schubert et al. 2004; Kaur and Suseela 2020; Goddard et al. 2021). These contradictory results may be explained by a large number of woody species that passively load solutes by maintaining high concentrations of sucrose in the mesophyll cells (Turgeon 2010).

Regarding plant defense, AM colonization upregulates defense-related genes, thereby increasing resistance to biotic stress. Hao et al. (2012) reported that colonization of the rootstock SO4 by *Glomus intraradices* was associated to an improved protection against the nematode *Xiphinema index*. The AM fungus strongly induced the expression of chitinase 1b, glutathione S-transferase, stilbene synthase 1, pathogenesis-related (PR) protein 10, 5-enolpyruvyl shikimate-3-phosphate synthase, a heat shock protein 70-interacting protein, and miscellaneous RNA, thereby enhancing the protection of grapevines. Li et al. (2006) observed increases of VCH3 (class III chitinase gene) expression in *V. amurensis* colonized with *G. versiforme,* which conferred resistance against the root-knot nematode *Meloidogyne incognita*. Previous studies have demonstrated that chitinases play an important role in plant defense and that their expression is modulated by AMF (Salzer et al. 2000, 2004; Liu et al. 2003; Schäfer et al. 2012). PR proteins are another group of plant defense proteins that are induced after pathogen infection (Sels et al. 2008). In grapevines, PR6 bis, PR7, and PR7 bis genes were highly expressed in the roots of AM plants (Goddard et al. 2021). PR6 bis belongs to a subclass of serine proteinase inhibitors, whereas PR7 and PR7 bis belong to the subtilisin-like serine protease (subtilase) family (Sels et al. 2008; Figueiredo et al. 2016). Research indicates that the expression of subtilase genes is boosted by AMF across various plant species, aiding the development of AM symbiosis (Taylor and Qiu 2017). Additionally, inhibition of certain subtilases has been found to decrease AM fungal structures in *Lotus japonicus* roots (Takeda et al. 2009).

It has been widely reported that AMF induce plant priming for enhanced defense, increasing the transcription of defense-related genes in aerial parts (Pozo and Azcón-Aguilar 2007; Pozo et al. 2009; Song et al. 2019). Several studies have shown that AMF can induce the expression of genes involved in the biosynthesis of terpenoids, polyphenols, and diverse fatty acid-derived alcohols and aldehydes. Bruisson et al. (2016) showed that stilbenoids, such as resveratrol, were slightly modified in grapevine leaves of AM-colonized plants; however, enhancement in the expression of phenylalanine ammonia lyase (PAL), stilbene synthase (STS), and resveratrol *O*-methyltransferase (ROMT) was also observed. Conversely, AM-colonized grapevines, when inoculated with the pathogens *Plasmopara viticola* and *Botrytis cinerea*, exhibited a significant increase in the concentration of various stilbenoids compared to non-AM plants. This suggests that AMF may sensitize grapevines to mount a stronger defense response. Enzymes, such as PAL, STS, and ROMT, which are involved in the shikimate pathway (SK), have been associated with plant defense mechanisms. Their expression has been shown to increase under a pathogen attack in diverse grapevine cultivars, including Cabernet Sauvignon, Chardonnay, Chasselas, Pinot Noir, and Riesling (Bézier et al. 2002; Kortekamp 2006; Mohamed et al. 2007; Perazzolli et al. 2012; Dufour et al. 2013; Bruisson et al. 2016).

Regarding abiotic stress, studies on grapevines have indicated that AMF enhance tolerance to drought stress by regulating the expression of specific genes. For instance, Ye et al. (2023) observed that a mixed inoculum of several AMF species increased the expression of 9-*cis*-epoxycarotenoid dioxygenase (NCED), abscisic acid 8'-hydroxylase 4 (CYP), and beta-glucosidase (BG) genes in grapevine cv. Ecolly under drought conditions. *Vv*NCED, *Vv*CYP, and *Vv*BG are involved in abscisic acid (ABA) metabolism, which helps reduce water loss and increase drought tolerance. They also noted that AMF upregulated the expression of δ1-pyrrolin-5-carboxylate synthetase (P5CS) and tonoplast intrinsic proteins (TIP). P5CS serves as a pivotal enzyme in proline and ornithine synthesis, whereas TIPs are aquaporins typically localized to the vacuolar membrane, facilitating water transport across this subcellular compartment (Gattolin et al. 2010; Pérez-Arellano et al. 2010). Upregulation of these genes has also been observed in other AM-colonized plant species, conferring a higher tolerance to drought and salt stress (Porcel et al. 2004). In addition, it was recently reported that AMF protect grapevines from high temperatures. Inoculation with *Funneliformis mosseae* or *R. irregularis* affected the expression of diverse stress-inducible miRNAs, suggesting that mycorrhizal colonization may result in enhanced gene regulation in response to heat stress. In particular, plants inoculated with *R. irregularis* showed a higher number

of differentially expressed miRNAs in grapevines treated at 40 °C (Ye et al. 2023). Some of these miRNAs belong to the miR156/miR529/miR535 superfamily and may be involved in the modulation of plant growth and development (Wang et al. 2015; Ye et al. 2023).

Despite progress made in understanding the molecular and metabolic changes triggered by AMF in grapevines, several key questions remain. For instance, although genes related to nutrient transport and defense have been identified, the mechanism by which these genes interact within complex regulatory networks still needs to be clarified. The contrasting patterns observed in sugar transporters and metabolites between grapevines and herbaceous species also suggest that the influence of AMF may vary considerably depending on the life form or tissue type of the plant. Additionally, the precise conditions under which AMF-driven metabolic shifts enhance stress tolerance, improve grape quality, and yield consistent outcomes in different environmental and phenological contexts are yet to be determined. Addressing these open questions will deepen our understanding of AMF–grapevine symbiosis, ultimately guiding more effective and sustainable management strategies in viticulture and other perennial cropping systems.

## Metabolic changes in grapevine by mycorrhizal fungi

The effect of AMF on primary and secondary metabolism in host plants has been thoroughly investigated. Numerous studies have indicated that AMF increase the levels of various metabolites, with a particular emphasis on those of special interest for human health (Kapoor et al. 2017; Kumar et al. 2021). An increase in metabolite content might be linked to improved nutrient acquisition by AM fungal hyphae, particularly phosphorus (P), because many secondary metabolites are synthesized by phosphate-dependent enzymes. However, AMF may not only induce metabolic pathways through heightened P absorption but also by boosting enzyme activity and stimulating the production of plant growth regulators or elicitors. These compounds can trigger intracellular signaling cascades, ultimately enhancing the production of various molecules (Kapoor et al. 2017; Welling et al. 2016). For instance, Goddard et al. (2021) observed an increased concentration of jasmonic acid (JA) and salicylic acid (SA) in the leaves of mycorrhizal grapevines inoculated with *R. intraradices*, showing activation of the lipoxygenase (LOX) and shikimate (SK) pathways. Additionally, *F. mosseae* has been shown to enhance the production of elicitors, such as (*E*)-2-hexenal, a green leaf volatile, and methyl salicylate, a volatile compound synthesized from salicylic acid in the leaves of *V. vinifera* cv. Sangiovese, which may be associated with a higher resistance of grapevines to unfavorable conditions (Velásquez et al. 2020a). In contrast, Goddard et al. (2021) reported that inoculation with the AM fungus *R. irregularis* did not affect the concentrations of JA and JA-isoleucine (JA-Ile) in AM-colonized grapevine roots, while a significant reduction in SA was observed.

AMF have been suggested to have an impact on the mevalonate/2-C-methyl-D-erythritol 4-phosphate pathway, increasing the expression of deoxyxylulose 5-phosphate synthase, geranyl diphosphate synthase, and diverse terpene synthase genes, which leads to a higher biosynthesis of terpenic compounds (Welling et al. 2016; Kapoor 2017). Although it has been reported that AMF enhances the synthesis of terpenoids in host plants, most studies performed in grapevines have shown a significant increase in the content of phenolic compounds, which are synthesized through the SK pathway (Table 2). Velásquez et al. (2020b) reported that *F. mosseae* induced only terpenes in *V. vinifera* cv. Cabernet Sauvignon root tissue showed a significant increase in terpene alcohols in the *p*-menthane series.

Phenolic compounds are metabolites of special interest in grapevines because of their importance in environmental stress alleviation as well as in the quality of grapes and wine (Merkyté et al. 2020). Phenols have been shown to be highly induced by AMF in grapevine leaves and fruit (Krishna et al. 2005; Karoglan et al. 2021; Bruisson et al. 2016). Among phenolic compounds, flavonoids are commonly reported to be affected by AM colonization. Karoglan et al. (2021) observed that diverse anthocyanins and flavanols significantly increased in the berry skin of AMF-inoculated plants in a two-year experiment. Similarly, Torres et al. (2016) found that AMF increased total anthocyanin content; however, contradictory results were observed. Ganugi et al. (2023) used seven different mycorrhizal inocula and reported no significant changes in the levels of anthocyanins in any treatment of non-mycorrhizal plants. Antolin et al. (2020) analyzed metabolic responses in diverse ancient grapevine varieties to AMF colonization, finding dissimilar responses regarding the phenol content. The authors observed that changes in phenolic compounds are not only dependent on AM colonization but also on the interaction of AMF × grapevine variety/cultivar. For instance, Nerva et al. (2023) reported that mycorrhizal treatments increased the stilbene viniferin content in the leaf tissue of cv. Galera grafted onto 1103P rootstock, whereas no changes were observed when cv. Galera was grafted onto the SO4 rootstock. Additionally, analysis of Malvasia di Candia Aromatica berry revealed significant differences in phenolic acids and stilbenes depending on the mycorrhizal inoculum used (Ganugi

**Table 2** Primary and secondary metabolites affected by AMF in different grapevine tissues, grape juice, or wine

| Tissue/product | Mycorrhizal inoculation[†] | Growing conditions | Grapevine cultivar | Metabolite[††] | Effect of AMF inoculation on metabolite concentration | References |
|---|---|---|---|---|---|---|
| Fruit | Bioradis Gel (Bioera SLU, Tarragona, Spain): containing *Septoglomus deserticola, Funneliformis mosseae, Rhizoglomus intraradices, Rhizoglomus clarum* and *Glomus aggregatum* | Potted-grapevines grown in greenhouse under 25/15 °C and 50/90% relative humidity (day/night) | Tempranillo | Total anthocyanins | ↑ | Torres et al. (2018b) |
| | | | | Abscisic acid glucosyl ester | ↑ | |
| | | | | 7-hydroxy-ABA | ↑ | |
| | | | | Dihydrophaseic acid | ↓ | |
| | | | | Phaseic acid | ↓ | |
| | Bioradis Gel (Bioera SLU, Tarragona, Spain): containing *Septglomus deserticola, Funneliformis mosseae, Rhizoglomus intraradices, Rhizoglomus clarum* and *Glomus aggregatum* | Potted-grapevines grown in greenhouse under 25/15 °C and 50/90% relative humidity (day/night) | Tempranillo CL-260 | Total phenolic compounds | ↑ | Torres et al. (2019) |
| | | | | Glucose | ↑ | |
| | | | | Delphinidin | ↓ | |
| | | | | Quercetin-3-O-galactoside | ↑ | |
| | | | | Quercetin-3-O-glucoside | ↓ | |
| | | | | Serine | ↑ | |
| | | | | Tyrosine | ↑ | |
| | | | | Phenylalanine | ↑ | |
| | | | | Asparagine | ↑ | |
| | | | | Threonine | ↑ | |
| | | | | Isoleucine | ↑ | |
| | | | | Glutamic acid | ↑ | |
| | | | | Arginine | ↑ | |

**Table 2** (continued)

| Tissue/product | Mycorrhizal inoculation† | Growing conditions | Grapevine cultivar | Metabolite†† | Effect of AMF inoculation on metabolite concentration | References |
|---|---|---|---|---|---|---|
| | | | | γ-aminobutyric acid | ↑ | |
| | | | | Alanine | ↑ | |
| | | | | Valine | ↑ | |
| | Bioradis Gel (Bioera SLU, Tarragona, Spain): containing *Septoglomus deserticola, Funneliformis mosseae, Rhizoglomus intraradices, Rhizoglomus clarum*, and *Glomus aggregatum* | Potted-grapevines grown in greenhouse under 25/15 °C and 50/90% relative humidity (day/night | Tempranillo CL-T23 | Total anthocyanins | ↑ | Antolin et al. (2020) |
| | | | Vidadillo CL-T75 | Total anthocyanins | ↓ | |
| | | | | Extractable anthocyanins | ↓ | |
| | | | Grand Noir CL-T48 | Total anthocyanins | ↑ | |
| | | | Tinto Velasco CL-73 | Total anthocyanins | ↑ | |
| | | | | Extractable anthocyanins | ↑ | |
| | | | | Total polyphenol index | ↓ | |
| | | | Graciano CL-72 | Total anthocyanins | ↑ | |
| | | | | Extractable anthocyanins | ↓ | |
| | | | | Total polyphenol index | ↓ | |
| | | | Morate CL-71 | Total polyphenol index | ↓ | |
| | | | Pasera CL-85 | Malic acid | ↓ | |
| | | | | Total anthocyanins | ↑ | |
| | | | Ambrosina CL-46 | Total soluble sugars | ↑ | |
| | | | | Total anthocyanins | ↑ | |
| | GLOMYGEL (Mycovitro S.L., Pinos Puente, Spain): containing of *Rhizophagus irregularis* | Potted-grapevines grown in greenhouse under 24/14 °C or 28/18 °C (day–night) | Tempranillo CL-1048 | Tartaric acid | ↑ | Torres et al. (2016) |
| | | | | Total anthocyanins | ↑ | |
| | | | Tempranillo CL-1089 | Total anthocyanins | ↑ | |

**Table 2** (continued)

| Tissue/product | Mycorrhizal inoculation† | Growing conditions | Grapevine cultivar | Metabolite†† | Effect of AMF inoculation on metabolite concentration | References |
|---|---|---|---|---|---|---|
| | GLOMYGEL (Mycovitro S.L., Pinos Puente, Spain): containing *Rhizophagus intraradices* | Potted-grapevines grown in greenhouse under 25/15 °C and 50/90% relative humidity (day/night) | Tempranillo CL-260 | Total polyphenol index | ↓ | Torres et al. (2018a) |
| | | | Tempranillo CL-1089 | Total soluble solids | ↑ | |
| | | | | Malic acid | ↓ | |
| | | | | Total polyphenol index | ↓ | |
| | | | | Anthocyanins | ↓ | |
| | | | Tempranillo CL-843 | Malic acid | ↓ | |
| | Myco Apply EndoMaxx (Mycorrhizal Applications LLC, OR, United States): containing *Rhizophagus intraradices, Funneliformis mosseae, Glomus aggregatum,* and *Glomus etunicatum* | Field conditions. Vines were treated with full irrigation or half irrigation | Merlot CL-181 grafted onto 3,309 C rootstock | Quercetin-3-*O*-galactoside | Veraison: no effect; Harvest: ↑ | Torres et al. (2021) |
| | | | | Quercetin-3-*O*-glucoside | Veraison: ↓; Harvest: no effect | |
| | | | | Laricitrin-3-*O*-glucoside | Veraison: ↑; Harvest: no effect | |
| | | | | Syringetin-3-*O*-glucoside | Veraison: no effect; Harvest: ↑ | |
| | | | | Total flavonols | Veraison: ↑; Harvest: no effect | |
| | Mykoflor (Mykoflor, Polland): containing *Rhizophagus irregularis, Funneliformis mosseae,* and *Claroideoglomus etunicatum* | Field conditions. Average temperature 18/18.2 °C, average precipitation 518.9/596.0 mm | Cabernet Sauvignon grafted onto SO4 rootstock | Quercetin-glucuronide | ↑ | Karoglan et al. (2021) |
| | | | | Quercetin-glucoside | ↑ | |
| | | | | Total flavonols | ↑ | |
| | | | | Procyanidin b1 | ↑ | |
| | | | | Epigallocatechin | ↑ | |

**Table 2** (continued)

| Tissue/product | Mycorrhizal inoculation† | Growing conditions | Grapevine cultivar | Metabolite†† | Effect of AMF inoculation on metabolite concentration | References |
|---|---|---|---|---|---|---|
| | | | | Catechin | ↑ | |
| | | | | Procyanidin b2 | ↑ | |
| | | | | Epicatechin | ↑ | |
| | | | | Total flavan-3-ols | ↑ | |
| | | | | Delphinidin-3-glucoside | ↑ | |
| | | | | Cyaniding-3-glucoside | ↑ | |
| | | | | Petunidin-3-glucoside; | ↑ | |
| | | | | Peonidin-3-glucoside | ↑ | |
| | | | | Malvidin-3-glucoside | ↑ | |
| | Bioradis Plant (Bioera SLU, Tarragona, Spain): containing *Septoglomus deserticola, Funneliformis mosseae, Rhizoglomus intraradices, Rhizoglomus clarum and Glomus aggregatum* | Potted-grapevines grown in greenhouse under 24/14 °C or 28/18 °C | Tempranillo CL-843 | Fructose | AMF 24/14 °C: no effect; AMF 28/18 °C: ↓ | Goicoechea et al. (2023) |
| | | | | Glycine | AMF 24/14 °C: no effect; AMF 28/18 °C:↑ | |
| | | | | Isoleucine | AMF 24/14 °C: ↑; AMF 28/18 °C: no effect | |
| | | | | Glutamic acid | AMF 24/14 °C: no effect; AMF 28/18 °C: ↓ | |
| | | | | Malvidin | AMF 24/14 °C: no effect; AMF 28/18 °C:↑ | |
| | | | | Quercetin-3-*O*-galactoside | AMF 24/14 °C: not determined; AMF 28/18 °C: ↓ | |
| | | | | Laricitrin-3-*O*-glucoside | AMF 24/14 °C: no effect; AMF 28/18 °C: ↓ | |
| | | | | Kaempferol-3-*O*-glucoside | AMF 24/14 °C: ↑; AMF 28/18 °C: no effect | |

**Table 2** (continued)

| Tissue/product | Mycorrhizal inoculation† | Growing conditions | Grapevine cultivar | Metabolite†† | Effect of AMF inoculation on metabolite concentration | References |
|---|---|---|---|---|---|---|
| Grape juice | Mykoflor (Mykoflor, Polland): containing *Rhizophagus irregularis*, *Funneliformis mosseae*, and *Claroideoglomus etunicatum* | Field conditions. Average temperature18/18.2 °C, average precipitation 518.9/596.0 mm | Cabernet Sauvignon | Citric acid | ↑ | Karoglan et al. (2021) |
| | | | | Tartaric acid | ↑ | |
| | | | | Titratable acidity | ↓ | |
| Leaves | Mixed inoculation with *Glomus intraradices, Glomus aggregatum, Glomus mosseae, Glomus clarum, Glomus monosporus, Glomus deserticola, Glomus brasilianum, Glomus etunicatum*, and *Gigaspora margarita* | Potted-grapevine grown in incubation room under 24 ± 1 °C and 16/8 h day/night conditions | Rootstock Kober 5 BB | Chlorophyll a | ↑ | Cetin et al. (2014) |
| | | | | Chlorophyll b | ↑ | |
| | | | | Total chlorophyll | ↑ | |
| | | | | Soluble sugars content | ↑ | |
| | | | | Total phenolic compounds | ↑ | |
| | | | Rootstock 41 B | Chlorophyll a | ↑ | |
| | | | | Chlorophyll b | ↑ | |
| | | | | Total chlorophyll | ↑ | |
| | | | | Soluble sugars content | ↑ | |
| | | | | Total phenolic compounds | ↑ | |
| | | | Rootstock 110 R | Chlorophyll a | ↑ | |
| | | | | Chlorophyll b | ↑ | |
| | | | | Total chlorophyll | ↑ | |
| | | | | Soluble sugars content | ↑ | |
| | | | | Total phenolic compounds | ↑ | |
| | *Funneliformis mosseae* | Potted-grapevines grown in greenhouse under natural day/night conditions | Sangiovese | 1-Octanol | ↑ | Velásquez et al. (2020a) |
| | | | | 1-Octen-3-ol | ↑ | |
| | | | | (*E*)-2-Hexenal | ↑ | |
| | | | | (*E*)-2-Hexenol | ↑ | |

**Table 2** (continued)

| Tissue/product | Mycorrhizal inoculation† | Growing conditions | Grapevine cultivar | Metabolite†† | Effect of AMF inoculation on metabolite concentration | References |
|---|---|---|---|---|---|---|
| | | | | 3-Hexenal | ↑ | |
| | | | | (*E*)-2-Decenal | ↑ | |
| | | | | 4-Hexen-3-one, 5-methyl- | ↑ | |
| | | | | Geraniol | ↑ | |
| | | | | Benzaldehyde | ↑ | |
| | | | | Ethylbenzene | ↑ | |
| | | | | Methyl salicylate | ↑ | |
| | | | | Styrene | ↑ | |
| | | | | *α*-Ionone | ↓ | |
| | | | | *β*-Ionone | ↓ | |
| | | | | *β*-Ionon-5,6-epoxide | ↓ | |
| | Single inoculations of *Acaulospora laevis, Acaulospora. scrobiculata, Entrophospora colombiana, Gigaspora gigantea, Glomus manihotis*, and *Scutellospora heterogama*. Mixed inoculation of AMF | Potted-grapevines grown in glass-house under 27 ± 1 °C, 80/85% relative humidity and 630 µmol $m^{-2}$ $s^{-1}$ PPFD | Pusa Navrang | Total chlorophyll | Single species inoculation: ↑; mixed inoculation: ↑ | Krishna et al. (2005) |
| | | | | Total carotenoids | Single species inoculation: ↑; mixed inoculation: ↑ | |
| | | | | Proline | Single species inoculation: ↑; mixed inoculation: ↑ | |
| | | | | Total phenols | Single species inoculation: ↑; mixed inoculation: ↑ | |
| | Turan Biotech Co. (Shahroud, Iran): Single inoculations *of Glomus mosseae, Glomus fasciculatum,* and *Glomus intraradices*. Mixed inoculation of AMF | Potted-grapevines grown in glass-house under 25 °C. Plants were irrigated about 80% of field capacity | Asgari | Chlorophyll b | Single species inoculation: ↑ (*G. mosseae*); mixed inoculation: no effect | Eftekhari et al. (2010) |
| | | | | Total chlorophylls | Single species inoculation↑ (*G. mosseae*); mixed inoculation: no effect | |

**Table 2** (continued)

| Tissue/product | Mycorrhizal inoculation† | Growing conditions | Grapevine cultivar | Metabolite†† | Effect of AMF inoculation on metabolite concentration | References |
|---|---|---|---|---|---|---|
| | | | Khalili | Chlorophyll b | Single species inoculation: no effect; mixed inoculation: ↑ | |
| | | | | Total chlorophylls | Single species inoculation: no effect; mixed inoculation: ↑ | |
| | | | | Leaf total phenols | Single species inoculation: no effect; mixed inoculation: ↑ | |
| | | | Keshmeshi | Chlorophyll b | Single species inoculation: ↑; mixed inoculation: no effect | |
| | | | | Total chlorophylls | Single species inoculation: ↑ (*G. mosseae and G. fasciculatum*); mixed inoculation: no effect | |
| | Turan Biotech Co. (Shahroud, Iran): Single inoculations of *Glomus mosseae, Glomus fasciculatum,* and *Glomus intraradices*. Mixed inoculation of AMF | Potted-grapevines grown in glass-house under 35/25 °C day/night temperatures and 70% relative humidity | Asgari | Quercetin | Single species inoculation: ↓ (*G. mosseae and G. fasciculatum*); mixed inoculation: ↓ | Eftekhari et al. (2012a) |
| | | | Khalili | Quercetin | Single species inoculation: ↑ (*G. mosseae*); mixed inoculation: ↑ | |
| | | | Keshmeshi | Quercetin | Single species inoculation: ↑; mixed inoculation: ↑ | |
| | Turan Biotech Co. (Shahroud, Iran): Single inoculations of *Glomus mosseae, Glomus fasciculatum*, and *Glomus intraradices*. Mixed inoculation of AMF | Potted-grapevines grown in glass-house under 35/25 °C day/night temperatures and 80–85% relative humidity | Asgari | Total chlorophyll | Single species inoculation: ↑ (*G. mosseae* and *G. fasciculatum*); mixed inoculation: no effect | Eftekhari et al. (2012b) |
| | | | | Total sugars | Single species inoculation: ↑ (*G. mosseae*); mixed inoculation: ↑ | |

**Table 2** (continued)

| Tissue/product | Mycorrhizal inoculation† | Growing conditions | Grapevine cultivar | Metabolite†† | Effect of AMF inoculation on metabolite concentration | References |
|---|---|---|---|---|---|---|
| | | | Khalili | Total chlorophyll | Single species inoculation: no effect; mixed inoculation: ↑ | |
| | | | | Total sugars | Single species inoculation: ↑ (*G. mosseae*); mixed inoculation: no effect | |
| | | | Keshmeshi | Total chlorophyll | Single species inoculation: ↑; mixed inoculation: no effect | |
| | Unibiotis (Biotisa, France): containing *Rhizophagus irregularis* | Potted-grapevines grown in greenhouse under 26/15 °C day/night temperature and 70% relative humidity | Pinot Noir CL- 459 grafted onto 41 B MGt rootstock | Resveratrol | ↓ | Bruisson et al. (2016) |
| | | | Chasselas CL-14/33–4 grafted onto 41 B MGt rootstock | Piceid | ↑ | |
| | | | Divico grafted onto 41 B MGt rootstock | Piceid | ↑ | |
| | | | | Ɛ-Viniferin | ↑ | |
| | Bioradis Plant (Bioera SLU, Tarragona, Spain): containing *Rhizophagus irregularis*, *Funneliformis mosseae*, *Septoglomus deserticola*, *Claroideoglomus claroideum* and *Claroideoglomus etunicatum* | Potted-grapevines grown in greenhouse under 400 ppm $CO_2$ at ambient temperature, with or without drought stress | Tempranillo grafted onto R110 rootstock | Proline | AMF: ↑; AMF + drought: no effect | Karsikova et al. (2024) |
| | | | | Total soluble sugars | AMF: no effect; AMF + drought: ↑ | |
| | | | Cabernet Sauvignon grafted onto R110 rootstock | Proline | AMF: no effect; AMF + drought: ↑ | |
| | | Potted-grapevines grown in greenhouse under 700 ppm $CO_2$ at ambient temperature + 4 °C, with or without drought stress | Cabernet Sauvignon grafted onto R110 rootstock | Proline | AMF: ↑; AMF + drought: ↑ | |

**Table 2** (continued)

| Tissue/product | Mycorrhizal inoculation† | Growing conditions | Grapevine cultivar | Metabolite†† | Effect of AMF inoculation on metabolite concentration | References |
|---|---|---|---|---|---|---|
| | Bioradis Plant (Bioera SLU, Tarragona, Spain): containing *Septoglomus deserticola, Funneliformis mosseae, Rhizoglomus intraradices, Rhizoglomus clarum and Glomus aggregatum* | Potted-grapevines grown in greenhouse under 24/14 °C or 28/18 °C | Tempranillo CL-843 | Total soluble sugars | AMF 24/14 °C: no effect; AMF 28/18 °C:↑ | Goicoechea et al. (2023) |
| | | | | Proteins2 | AMF 24/14 °C: ↓; AMF 28/18 °C:↑ | |
| Roots | *Funneliformis mosseae* | Potted-grapevines grown in greenhouse under natural day/night conditions | Cabernet Sauvignon | (−)-Myrtenol | ↑ | Velásquez et al. (2020b) |
| | | | | Geranic acid | ↑ | |
| | | | | p-Cymen-7-ol | ↑ | |
| | | | | p-Menth-2-en-7-ol.cis- | ↑ | |
| | | | | p-Mentha-1(7).8(10)-dien-9-ol | ↑ | |
| | | | | p-Mentha-1.4-dien-7-ol | ↑ | |
| | | | | p-Mentha-1.5-dien-7-ol | ↑ | |
| | | | | p-Mentha-1.8-dien-7-ol | ↑ | |
| | | | | γ-Gurjunenepoxide-(2) | ↑ | |
| Stem | Turan Biotech Co. (Shahroud, Iran): Single inoculations of *Glomus mosseae, Glomus fasciculatum,* and *Glomus intraradices*. Mixed inoculation of AMF | Potted-grapevines grown in glass-house under 35/25 °C day/night temperatures and 70% relative humidity | Asgari | Quercetin | Single species inoculation: ↓ (*G. fasciculatum* and *G. intraradices*); mixed inoculation: ↑ | Eftekhari et al. (2012a) |
| | | | Khalili | Quercetin | Single species inoculation: ↑ (*G. mosseae* and *G. intraradices*), ↓ (G. fasciculatum); mixed inoculation: ↓ | |
| | | | Keshmeshi | Quercetin | Single species inoculation: ↑; mixed inoculation: ↑ | |
| | | | Shahroodi | Quercetin | Single species inoculation: ↓; mixed inoculation: ↓ | |

**Table 2** (continued)

| Tissue/product | Mycorrhizal inoculation[†] | Growing conditions | Grapevine cultivar | Metabolite[††] | Effect of AMF inoculation on metabolite concentration | References |
|---|---|---|---|---|---|---|
| Wine | MICOSAT F (Quart (AO), Italy): containing *Glomus* spp. and *Rhizophagus* spp. | Field conditions | Sangiovese | Polyphenols | ↑ | Gabriele et al. (2016) |
| | | | | Flavonoids | ↑ | |
| | | | | Flavonols | ↑ | |
| | | | | Anthocyanins | ↓ | |
| | | | | Gallic acid | ↑ | |
| | | | | 3,4-Dihydroxybenzoic acid | ↑ | |
| | | | | Tyrosol | ↑ | |
| | | | | Resveratrol | ↑ | |
| | | | | Caffeic acid | ↑ | |
| | | | | Quercetin | ↑ | |
| | | | | Isorhamnetin | ↑ | |
| | | | | Malvidin chloride | ↑ | |

[†] Names of mycorrhizal fungi species has been maintained as reported in the studies

[††] Only metabolites determined quantitatively were considered for this review

↑ = Increased concentration; ↓ = Decreased concentration

et al. 2023). Quercetin is another subclass of flavonoids that has been shown to be modified in response to AMF. Single and mixed inoculations with *G. mosseae*, *G. fasciculatum*, and *G. intraradices* showed to increase the content of quercetin in *V. vinifera* cv. Khalili and Keshmeshi leaf tissues, whereas in cv. A decreased concentration of Agari was observed (Eftekhari et al. 2012a).

Regarding primary metabolites, it has been reported that both chlorophyll a and b, as well as the total chlorophyll content, are highly affected by AMF (Krishna et al. 2005; Cetin et al. 2014). However, Eftekhari et al. (2012b) did not observe an increase in all treatments, showing a different effect depending on the cultivar or on the type of mycorrhizal inoculum (single or mixed inoculum); nevertheless, the authors suggest that in grapevines, AMF increase or at least maintain chlorophyll content. In addition, research has revealed elevations in the concentrations of mono- and disaccharides, amino acids, and various organic acids across a diverse range of AM-colonized host plants, with respect to non-colonized plants. Specifically, AMF have been observed to induce higher levels of total soluble sugars in grapevine leaf tissue and berries (Eftekhari et al. 2012b; Cetin et al. 2014; Torres et al. 2019; Antolin et al. 2020, Ganugi et al. 2023). Nevertheless, inoculation with *R. intraradices* reduced certain sugars such as sucrose in the leaves of *V. vinifera* cv. Gewurztraminer. These results may be associated with increases in hexose transport from leaves to fruit in AM-colonized plants, as suggested by Zouari et al. (2014), in which one hexose transporter gene with high sequence similarity to a glucose/$H^+$ symporter was upregulated by *F. mosseae* in tomato plants, strongly inducing fruit maturity. Similarly, the concentration of glucose in grape berries was significantly higher in AM grapevines than in non-colonized grapevines (Antolin et al. 2020).

AM colonization plays an important role in nutrient acquisition, including nitrogen, which has been proven to favor the synthesis and transport of amino acids to the aerial parts. For example, in tomato fruits, Zouari et al. (2014) observed that AMF upregulated genes associated with amino acid production, whereas Salvioli et al. (2012) reported an increased content of glutamine and asparagine in AM-colonized plants, potentially linked to elevated amide production. Torres et al. (2019) found that AMF increased the levels of various amino acids in *V. vinifera* cv. Tempranillo, specifically phenylalanine, a precursor of phenolic compounds, was significantly enhanced, which could contribute to the higher total phenol content.

Despite these advancements, key questions remain regarding the precise mechanisms and broad consistency of AMF-driven metabolic changes in grapevines. For instance, although AMF are known to enhance the synthesis of various metabolites, including phenolics, terpenoids, amino acids, and sugars, the variability in responses across cultivars, rootstocks, and inoculum types underscores the complexity of these interactions. It remains unclear why certain phenolic compounds or primary metabolites respond positively to AM colonization in some grapevine varieties, while remaining unchanged or even decreasing in others. Likewise, the relative contribution of enhanced nutrient uptake, altered enzyme activity, and induction of signaling molecules to these metabolic shifts requires further elucidation. Disentangling the roles of different AM fungal species and understanding the environmental conditions under which their benefits are maximized will be crucial. More research is needed to determine how these metabolic adjustments translate into long-term improvements in grape and wine quality under field conditions. Ultimately, addressing these open questions will help refine management strategies and optimize the use of AMF in viticulture.

## Role of AMF-induced metabolites in the tolerance to abiotic stress

Abiotic stress leads to economic losses in viticulture. Grapevines are highly affected by drought, salinity, and heavy metals, causing serious problems in growth and productivity (Cataldo et al. 2022). Most wine-growing regions are located in Mediterranean and semi-arid climates, characterized by warm and dry summers, where grapevines are regularly exposed to saline soils, prolonged periods of drought, high radiation, and increase in temperature (Lionello et al. 2006; del Pozo et al. 2019). Climate change, driven by rising greenhouse gasses, is causing temperature increase (2.2–3.7 °C by 2100) and elevated $CO_2$ levels (669–935 ppm), interacting with water deficits (IPCC 2013). These abiotic stresses, including reduced water availability, extreme drought, and rising temperatures, along with biotic stress from pathogens, threaten the viability of *Vitis vinifera* (OIV, 2019; Aguilera et al. 2023). For instance, the Mediterranean areas of Europe face severe impacts, with rainfall expected to decrease by 4–22% and heatwaves becoming more frequent. Such changes affect phenology, development, physiological responses, grape yield, and quality, thereby compromising viticulture in major wine-producing countries (IPCC 2013; OIV, 2019, Aguilera et al. 2021). The application of AMF enhances vine tolerance to abiotic stresses, such as drought and high temperatures, and improves water potential, stomatal conductance, and $CO_2$ assimilation. Nevertheless, the effect of increased temperature on AMF is not yet clear as some studies have reported an increase in mycorrhizal abundance, while others have observed a decrease in colonization levels (Torres et al. 2018b, Aguilera et al. 2021). Kozikova et al. (2024) analyzed the role of AMF in improving the resilience of two grapevine varieties, Tempranillo and Cabernet Sauvignon, to climate change conditions,

which included different concentrations of $CO_2$ and irrigation levels, and temperature. The authors observed that drought reduced leaf conductance and transpiration in both varieties, especially in mycorrhizal plants, but photosynthesis remained stable, thereby improving water use efficiency WUE. AMF alter stomatal density and size, enhancing adaptation to water deficit, particularly under elevated $CO_2$ and temperature conditions.

Abiotic stressors prompt plants to accumulate reactive oxygen species (ROS), leading to oxidative damage. ROS consist of a group of molecules, such as OH-, $H_2O_2$, $\bullet O_2^-$, and $O^{2-}$, which cause the transfer of high-energy electrons to molecular oxygen, resulting in higher membrane permeability and loss of ions from the cells (Gill and Tuteja 2010). Excessive ROS generation disturbs cell functions by attacking several biomolecules, such as nucleic acids, proteins, and membrane lipids (Foyer and Noctor 2005). It has been reported that AMF may enhance plant performance under unfavorable conditions, decreasing the rates of the negative impacts of abiotic stress (Begum et al. 2019). AMF have been shown to protect plants under adverse conditions by improving nutrient acquisition, increasing water uptake, maintaining osmotic equilibrium, enhancing photosynthetic efficiency, and preventing damage by ROS (Begum et al. 2019; Evelin et al. 2019; Santander et al. 2020).

Plants protect themselves from ROS through enzymatic and non-enzymatic mechanisms. The enzymatic system consists of higher activities of superoxide dismutase, peroxidase, catalase, ascorbate peroxidase, and glutathione reductase. Non-enzymatic antioxidant molecules include acetylsalicylic acid, glutathione, carotenoids, and α-tocopherol, which participate in ROS quenching (Gill and Tuteja 2010). Several studies have shown that AMF enhance the activity of antioxidant enzymes and molecules that alleviate oxidative stress (Evelin and Kapoor 2014). Particularly in grapevines, Torres et al. (2016) observed an increased total antioxidant capacity in grapevines inoculated with AMF, which may prevent the oxidation of lipids, proteins, and nucleic acids, while Krishna et al. (2005) showed that AMF increased the content of total carotenoids and total phenolic compounds by up to 800% in leaves. Specific groups of phenolic compounds, such as flavanols and anthocyanins, were usually increased in grapevines inoculated with AMF (Table 2).

Flavonols are metabolites that are typically associated with UV-B irradiance protection in plants (Ferreyra et al. 2012). Accumulation of flavonols under UV-B irradiation has been reported in diverse plant species, including *Arabidopsis thaliana*, *Capsicum annuum*, *Ligustrum vulgare*, *Fragaria* × *ananasa*, and *V. vinifera* (Mahdavian et al. 2008; Tattini et al. 2004; Berli et al. 2011; Xu et al. 2017). Low levels of irradiation tend to increase flavonols such as kaempferol, whereas high levels of UV-B increase quercetin content, especially quercetin-3-*O*-galactoside and quercetin-3-*O*-glucoside (Takemura et al. 2009). This may be explained by the fact that quercetin, which has been increased in some grapevine cultivars inoculated with AMF, is dihydroxylated and kaempferol is monohydroxylated. It has been reported that as the level of hydroxylation increases, the absorption of UV-B decreases (Lavola et al. 1997). Furthermore, Agati et al. (2013) reported that light-responsive dihydroxy flavonoids have a greater ability to quench ROS or inhibit their formation.

Phenolic compounds can also protect plants against potentially toxic elements (PTE). For instance, cadmium increased the concentrations of rutin and myricetin in *Erica andevalensis* and *Prosopis farcta* (Márquez-García et al. 2012; Zafari et al. 2016), whereas copper mainly increases the concentration of 5-caffeoylquinic acid, orientin, and cyanidin-3-malonylglucoside (Vidal et al. 2020). Zafari et al. (2016) reported higher quercetin root exudates in maize plants exposed to aluminum. Similar results have also been observed in grapevine, where quercetin and kaempferol derivatives increased after treatment with titanium nanoparticles (Kőrösi et al. 2019). Flavonols may be involved in tolerance to PTE because of their ability to chelate metals and reduce toxicity in plant cells (Šamec et al. 2021).

It has been extensively documented that AMF enhance osmotic adjustment in plant cells (Santander et al. 2017; Vidal et al. 2022). Accumulation of proline and soluble sugars is frequently induced by mycorrhizal fungi, as well as by abiotic stresses, such as salt and drought stress (Garg and Baher 2013; Santander et al. 2019; 2020). Proline plays a crucial role in scavenging ROS and stabilizing membranes, proteins, and DNA against oxidation induced by abiotic stress (Kaur and Asthir 2015). AMF may induce proline accumulation through various mechanisms, including the upregulation of genes encoding enzymes, such as P5CS and glutamate dehydrogenase, as well as enhancing the activity of these enzymes. Additionally, it has been observed that AMF induce inactivation of proline dehydrogenase, an enzyme that participates in the degradation of proline (Abo-Doma et al. 2016). Regarding soluble sugars, it has been shown that glucose, sucrose, dextrin, and maltose play a key role in osmoprotection and as a source of carbon storage (Parvaiz and Satyawati 2008). Under abiotic stress, plants exhibit an accumulation of soluble sugars, a response that is amplified in AM-colonized plants because of the enhanced photosynthetic efficiency and increased activity of enzymes, such as $\alpha$- and $\beta$-amylases, acid invertase, and sucrose synthase induced by AMF (Garg and Baher 2013; Yu et al. 2015; Zhu et al. 2018). Notably, not all soluble sugars play identical roles in plant cell metabolism. For instance, glucose and sucrose serve as substrates for cellular respiration or act as osmolytes to maintain cell homeostasis (Gupta and Kaur 2005), whereas fructose may be linked to the synthesis of

erythrose-4-phosphate, a precursor for lignin and phenolic compound production (Hilal et al. 2004).

Despite the progress made in characterizing AMF-induced metabolic shifts that enhance grapevine tolerance to abiotic stress, numerous questions remain unanswered. Although it is clear that proline, soluble sugars, phenolics, and flavonols contribute to osmoprotection and ROS mitigation, the precise regulatory networks linking these metabolites to improved stress resilience require clarification. It is not fully understood how differing environmental variables or soil conditions influence AMF-mediated metabolic changes, nor is it clear why certain grapevine cultivars or rootstocks respond more robustly than others do. Moreover, the interplay between specific metabolites, such as quercetin, fructose, and proline, and particular stress conditions remains to be fully delineated. Another unresolved area is how these metabolic adjustments translate into long-term improvements in vine health, yield, and fruit quality under actual vineyard conditions. Addressing these gaps will provide the knowledge required to harness AMF more effectively as a sustainable tool for viticulture under the increasing pressure of climate change.

## Role of AM-induced metabolites in biotic stress tolerance

AMF colonization enhances protection against pathogens in host plants, leading to a systemic effect known as mycorrhizal-induced resistance (MIR) (Pozo and Azcón-Aguilar 2007; Jung et al. 2012). MIR may act on nematodes, herbivorous insects, and a wide range of pathogens, including fungi, bacteria, and viruses (Gehring and Bennett 2009; Schouteden et al. 2015; Miozzi et al. 2019). It has been proposed that MIR suppresses the SA-dependent defense pathway while inducing systemic priming of JA-dependent defenses (Pozo and Azcón-Aguilar 2007). Cameron et al. (2013) proposed that at early stages of colonization, the host plant recognizes microbe-associated molecular patterns from the AM fungus, triggering a series of signaling cascades, resulting in enhanced production of the plant defense hormone SA. However, it has been observed that AMF promote the production of ABA and JA in the colonized cells of the cortical root tissue (House et al. 2002). As ABA and JA can suppress SA-dependent defense pathways against biotrophic pathogens, AMF may induce the production of these phytohormones to establish a symbiotic association (Cameron et al. 2013). Particularly in grapevines, Hao et al. (2012) observed that in SO4 rootstock inoculated with *R. intraradices* BEG141, MIR offered protection against the ectoparasitic nematode *X. index*, reducing gall formation in roots and the number of nematodes in the surrounding soil. The authors also suggested that priming defense responses are translocated to non-AM tissues. In addition, MIR enhances the resistance to oomycetes and fungal pathogens. For instance, pre-inoculation with AMF protects grapevines against *P. viticola*, while symptoms of root rot disease, caused by *Armillaria mellea*, slowed down compared to non-AM-inoculated plants. This effect could be attributed to polyamine accumulation, which is implicated in the early signaling processes of the tolerance increase of AM-colonized grapevines against the pathogen (Nogales et al. 2009). AMF have been demonstrated to affect the expression of pathogen effectors during grapevine infection. Cruz-Silva et al. (2021) showed that pre-mycorrhizal inoculation with AMF fungus *R. irregularis* alters the expression of several *P. viticola* effectors, namely PvRxLR28, which presented decreased expression. These findings indicate that pre-inoculating grapevines with AMF might hinder pathogen infections by potentially altering the expression of pathogenicity-related genes, supporting the idea that AMF can enhance plant resistance to grapevine diseases.

In contrast, Holland et al. (2019) reported that *V. riparia* cv. Riparia gloire rootstocks inoculated with *R. irregularis* increased the abundance of the pathogen *Ilyonectria liriodendra,* and no effect on plant growth was detected. These results indicate that the protective effect may vary depending on the AM fungus-plant-pathogen interaction. Indeed, most studies have addressed the effect of AM symbiosis using single-species inoculation. Recently, Moukarzel et al. (2022) used whole AMF communities from New Zealand vineyards in young grapevine rootstocks, showing that AMF increases vine growth parameters while protecting plants from black foot disease, decreasing severity by up to 50% compared to control plants.

Bruisson et al. (2016) reported that *R. intraradices* enhanced the content of stilbenoids in grapevine, especially after infection with *P. viticola*. Stilbenoids are a class of phenolic compounds that are known to be induced by phytopathogens or herbivore attack and protect plants because of their toxic properties for plant enemies. Antipathogenic effects include antibacterial, antifungal, insecticidal, and nematicidal properties (Valletta et al. 2021). Vannozzi et al. (2018) documented increases in transcript levels of stilbene synthases in grapevine following wounding. Moreover, they observed upregulation of WRKY and R2R3-MYB transcription factors. Specifically concerning WRKY transcription factors, *Vvi*WRKY03, VviWRKY24, *Vvi*WRKY43, and *Vvi*-WRKY53 were identified as being involved in the regulation of the stilbene biosynthetic pathway. Nerva et al. (2023) conducted a two-year greenhouse experiment to investigate how AMF mitigate virus-induced oxidative stress in grapevine. The results revealed that AMF inoculation reduced the levels of ascorbate and superoxide dismutase, indicating diminished activation of the ascorbate–glutathione cycle. In

the mature phase of AM symbiosis, guaiacol peroxidase has emerged as a key enzyme for scavenging hydrogen peroxide. Additionally, decreased expression of stilbene synthase (STS1) and increased expression of enhanced disease susceptibility (EDS1) genes suggest improved ROS scavenging in AMF-inoculated plants. These findings highlight the potential of AM symbiosis to alleviate virus-induced stress in grapevines.

Despite these findings, several critical gaps remain in our understanding of how AMF-driven metabolic changes translate into consistent and durable resistance to a diverse array of pathogens. For instance, it remains unclear why certain AMF strains or communities confer more robust protection than others, or how the balance between SA-, ABA-, and JA-mediated pathways is fine-tuned to deter pathogens without compromising the symbiotic relationship. Additionally, the extent to which AMF-induced priming can be reliably transferred to non-colonized tissues and how environmental factors influence these defense responses remain poorly understood. Similarly, although increase in stilbenoids, polyamines, and other defensive metabolites have been documented, the precise molecular regulation and signaling networks underlying these responses have not been fully resolved. Addressing these open questions will be essential for leveraging AMF-mediated biotic stress tolerance in practical vineyard management to ensure more sustainable and resilient grape production under ever-changing biotic pressures.

## Role of AMF on quality of grapes and wine

A vast array of primary and secondary metabolites contributes to the organoleptic properties of fruits, influencing factors, such as color, taste, and aroma. For instance, phenolic compounds play a significant role in grape production. Fruit pigmentation in grapevines results from the accumulation of anthocyanins in the skin of the berries (He et al. 2010). While increases in total phenolic content and anthocyanin levels due to AMF have been documented in various studies (Table 2), Torres et al. (2019) observed that these changes were not correlated with color density or tonality index in *Vitis vinifera* cv. Tempranillo grapes. Polyphenols accumulate in the skin during grape ripening, and are the main compounds related to wine quality. Wine properties, such as color, flavor, and health benefits, are determined by diverse phenolic compounds, including anthocyanins, proanthocyanidins, and flavonols. Gabriele et al. (2016) demonstrated that AMF increase the content of phenolic compounds in Sangiovese wines. However, while monomeric anthocyanins were significantly reduced compared to the control plants, increases in other phenolic compounds were observed, including 3,4-dihydroxybenzoic acid, gallic acid, tyrosol, resveratrol, caffeic acid, quercetin, isorhamnetin, and malvidin. In another study, Antolin et al. (2020) analyzed the effect of AMF on eight ancient grapevine cultivars (Tempranillo, Vidadillo, Grand Noir, Tinto Velasco, Graciano, Morate, Pasera, Ambrosina). They observed that the total phenol index was reduced in the inoculated cultivars Tinto Velasco, Graciano, and Morate compared to non-AM plants; however, anthocyanins were increased in the majority of the cultivars analyzed.

Another quality factor of wine depends on the sugar and organic acid concentration in grapes, which determines the alcohol/acidity ratio and is also responsible for wine flavor balance (Ribéreau-Gayon et al. 2006). It has been observed that AMF increases their content in grapes, which is related to more alcoholic wines. Concerning organic acid, it has been shown that AMF inoculation reduces malic acid concentration and leans toward lower titratable acidity (Karoglan et al. 2021). This trend has also been observed for other plant species. For example, titratable acidity tends to decrease in strawberries inoculated with *Septoglomus viscosum* (Todeschini et al. 2018). However, Antolin et al. (2020) and Torres et al. (2021) did not find significant differences in the titratable acidity of musts in mycorrhizal grapevines compared with non-AM plants. Additionally, the authors did not observe any differences in the pH of musts associated with AMF inoculation in any of the grapevine cultivars assayed.

Torres et al. (2019) demonstrated changes in primary metabolism rather than secondary metabolism. Moreover, the authors reported that AMF increased the concentration of several amino acids in grape skin, which could induce changes in wine aroma, since amino acid-derived volatiles may play an important role in the organoleptic properties of wine (Hernández-Orte et al. 2002). Aromatic precursor amino acids, such as aspartic acid, isoleucine, phenylalanine, threonine, tyrosine, and valine, were significantly increased in the grapes of mycorrhizal plants (Torres et al. 2019). However, increases in amino acids may enhance the concentrations of biogenic amines, including tyramine, phenylethylamine, and putrescine, which are present in musts (Wang et al. 2014).

## Conclusions

In recent years, there has been growing interest in unraveling the intricate interactions between mycorrhizae and grapevines. Arbuscular mycorrhizal fungi (AMF) have been shown to modulate metabolic pathways, resulting in alterations in gene expression, primary and secondary metabolites, and the induction of enzymes that scavenge reactive oxygen species (ROS). The most frequently reported transcriptomic

modifications are associated with sugar transporters, abscisic acid (ABA) metabolism, and various defense genes. Metabolites, such as soluble sugars, proline, chlorophyll, and anthocyanins, are frequently reported to increase in AMF-inoculated plants. Some of these modifications contribute to an enhanced quality of grapes and wine, which deserves more attention in further research because AMF may influence the organoleptic properties of wine, such as residual sugars, volatile acidity, astringent sensation (tannins), and aroma. However, it is important to note that responses may vary depending on the grapevine genotype and the fungus used as the inoculum. As most studies have been conducted under greenhouse conditions, other factors, such as the inoculation period and the phenological state of the grapevine, may also influence transcriptomic and metabolic responses. Further research under field conditions is warranted to establish the optimal application of AMF and management of vineyards.

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## Declarations

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