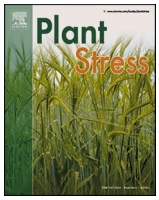
Plant Stress 16 (2025) 100863

Contents lists available at ScienceDirect

Plant Stress

journal homepage: www.sciencedirect.com/journal/plant-stress



Review

The role of arbuscular mycorrhizal fungi in abiotic stress management in viticulture under climatic shifts

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ARTICLE INFO

Keywords:
Arbuscular mycorrhizal fungi- AMF
Viticulture
Grapevine
Abiotic stress
Inoculants
Climate change adaptation

ABSTRACT

Arbuscular mycorrhizal fungi (AMF) have been shown to enhance grapevine resilience to abiotic stresses, which are becoming increasingly severe due to climate change. Grapevines, which are central to global wine production, face critical challenges such as drought, salinity, extreme temperatures, and soil degradation. These challenges have the potential to compromise yield, quality, and economic sustainability. AMF establish symbiotic relationships with grapevine roots, thereby improving nutrient and water uptake, enhancing photosynthetic efficiency, and modulating stress-related pathways. These fungi also promote soil health by increasing microbial diversity, stabilizing soil structure, and reducing the need for chemical inputs. The application of AMF inoculants in viticulture presents substantial opportunities, including improved grapevine adaptation to environmental stresses, higher fruit quality, and reduced environmental impact. However, challenges such as ensuring consistent performance across diverse environmental conditions, optimizing inoculant formulations, and addressing vineyard management practices that may reduce AMF effectiveness must be overcome to maximize their benefits. Advances in precision agriculture and research into AMF-host interactions are essential to unlocking their full potential. This review explores the mechanisms by which AMF mitigate abiotic stress, the benefits of their integration into vineyard management, and the challenges that must be overcome to implement AMF-based solutions.

1. Introduction

The science, production, and study of grapes—viticulture— is intricately linked to environmental conditions, making it highly susceptible to the impacts of climate change (Bernardo et al., 2018; Di Vita et al., 2024; Torres et al., 2018a). Grapes are cultivated globally, with an estimated 7.3 million hectares of vineyards worldwide in 2022 (Cosme et al., 2024). These vineyards support a variety of uses, including wine production, juice, table grapes, and dried grapes. However, in recent years, the incidence of abiotic stresses affecting grapevines has increased due to rising global temperatures, changing precipitation patterns, and increasing soil salinity. These factors have significantly impacted grapevine growth, yield, and the quality of the resulting products, especially wine (Di Vita et al., 2024; Torres et al., 2021a). Van Leeuwen et al. (2024) reported that approximately 90 % of traditional wine regions in coastal and lowland areas of Spain, Italy, Greece, and southern California could be at risk of becoming unsuitable for quality wine production by the end of the century. These changes pose a substantial challenge for vineyard management and wine production, particularly in those regions historically regarded as optimal for grape cultivation (Bernardo et al., 2018; Van Leeuwen et al., 2019).

One potential solution to mitigate the adverse effects of climate change in viticulture involves leveraging the symbiotic relationships between plants and soil microorganisms, particularly arbuscular mycorrhizal fungi (AMF) (Biasi et al., 2023; Moukarzel et al., 2023; Pavithra and Yapa, 2018). AMF, a group of beneficial soil fungi, form symbiotic associations with the root system of most terrestrial plants, including grapevines. These fungi extend their hyphae into the soil, increasing the contact surface area available for water and nutrient uptake, particularly under stress conditions (Basiru et al., 2020; Van Leeuwen et al., 2019). AMF inoculants have shown potential in enhancing grapevine resilience to abiotic stresses such as drought,

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https://doi.org/10.1016/j.stress.2025.100863
Received 30 January 2025; Received in revised form 5 April 2025; Accepted 18 April 2025
Available online 18 April 2025

salinity and nutrient deficiencies (Cardinale et al., 2022; Karimi and Noori, 2022). This makes them a promising sustainable agronomic tool for viticulture under the current scenario (Pavithra and Yapa, 2018; Torres et al., 2021a). Given the increasing pressures posed by climate change, it is imperative to deepen our understanding of the potential of AMF inoculants to improve grapevine resilience and to develop strategies for harnessing their benefits within the context of sustainable viticulture.

The aims of this review are to: (i) provide an overview of the main environmental stressors, relevant for viticulture, that are being exacerbated by climate change; (ii) elucidate the potential role of AMF in mitigating these stressors; and (iii) highlight the challenges and opportunities associated with the integration of AMF inoculants into sustainable vineyard management practices.

2. Overview of environmental stressors in viticulture under climate change

Climate change presents significant challenges to viticulture, a practice that depends on stable and predictable environmental conditions. Grapevine cultivation is closely tied to specific climatic parameters such as temperature, precipitation, and sunlight, all of which are being disrupted by ongoing climatic shifts (Arias et al., 2022). According to the Intergovernmental Panel on Climate Change (IPCC), global surface temperatures increased by approximately 1.1 °C from 1850 to 1900 to 2011–2020, with even greater warming observed over land areas. Notably, the global surface temperature has risen more rapidly since 1970 than during any other 50-year period in at least the past 2000 years (IPCC, 2023). Rising global temperatures are altering the timing and duration of grapevine phenological stages, while shifts in precipitation patterns are affecting water availability, leading to periods of both drought and excessive rainfall (Atak, 2024). Furthermore, the increasing frequency of extreme weather events —including heatwaves, storms, and unseasonal frosts— introduces additional risks that threaten the health and productivity of vineyards.

These climatic changes expose grapevines to a range of abiotic stresses, including drought, salinity, extreme temperatures, and nutrient imbalances. Each stressor, whether occurring individually or in combination, can disrupt critical physiological processes such as photosynthesis, nutrient uptake, and water balance. The cumulative effects of these stresses often result in reduced vine growth, lower yields, and diminished grape quality, with cascading impacts on wine production (Droulia and Charalampopoulos, 2021). Consequently, climate change not only jeopardizes the economic sustainability of viticulture but also poses significant threats to preserve the distinct characteristics and quality of wines from traditional growing regions (Bernardo et al., 2018).

Additionally, the increasing variability in climatic conditions compels winegrowers to continuously adapt their practices. These adaptations include relocating vineyards, implementing advanced irrigation systems, and selecting more resilient grapevine varieties and rootstocks (Bernardo et al., 2018). Despite these efforts, the long-term sustainability of viticulture in many regions remains uncertain, emphasizing the urgent need for innovative strategies to mitigate the impacts of climate change. In this section, we provide a brief overview of the main environmental stressors affecting viticulture under climate change, highlighting key challenges to offer insight into the pressures viticulture faces amidst ongoing climatic shifts.

2.1. Drought stress

Drought is one of the most critical abiotic stress factors affecting viticulture, particularly in Mediterranean and semi-arid regions. As a consequence of climate change, shifts in precipitation patterns and increased evaporation rates lead to heightened exposure of grapevines to prolonged periods of water scarcity (Muhammad et al., 2024). The impacts of drought stress on grapevines are multifaceted, encompassing reductions in photosynthetic efficiency, alterations in water-use efficiency, and effects on berry development (Droulia and Charalampopoulos, 2021; Gambetta et al., 2020; Van Leeuwen et al., 2019).

From a physiological perspective, drought conditions lead to reduced stomatal conductance, limiting the uptake of carbon dioxide necessary for photosynthesis (Biasi et al., 2023). This restriction diminishes photosynthetic activity, impairs growth, and reduces overall vine vigor (Gambetta et al., 2020). Additionally, drought stress decreases leaf water potential and stomatal conductance, directly influencing grape quality (Hewitt et al., 2023). While moderate drought stress can enhance the concentration of sugars and phenolic compounds, severe water stress has been shown to reduce berry size, lower yields, and compromise the development of key flavor compounds (Van Leeuwen et al., 2019). Moreover, prolonged water scarcity elevates the production of reactive oxygen species (ROS), which can overwhelm antioxidant defenses, leading to oxidative damage to photosynthetic apparatus and cellular structures (Ye et al., 2023).

The extent of drought-induced stress on grapevines is strongly influenced by the rootstock employed. Drought-tolerant rootstocks, such as 110R, 140Ru, and 1103P, demonstrated the ability to improve grapevine resilience by enhancing water-use efficiency and maintaining shoot growth under limited water availability (Medrano et al., 2015; Ollat et al., 2015). However, the overall response of grapevines to drought stress is highly variable, depending on a combination of factors including the cultivated genotypes (both scion and rootstock) (Bianchi et al., 2018), the severity and duration of water scarcity, soil characteristics, and vineyard management practices (Losciale et al., 2024).

2.2. Temperature extremes

Grapevine cultivation faces significant challenges from both high and low temperature extremes. Elevated air temperatures, particularly during critical stages such as flowering and veraison, can cause physiological damage and compromise grape quality (Van Leeuwen et al., 2024; Yadav et al., 2024). Climate change-induced warming accelerates phenological events, resulting in earlier bud break (Dinu et al., 2021), flowering, and harvest (Van Leeuwen et al., 2019). In response to elevated temperatures, grapevines employ various defensive mechanisms, including the reorganization of photosynthetic membranes within chloroplasts. However, these adaptations often lead to reduced photosynthetic and respiratory efficiency, ultimately hindering growth and fruit development (Bernardo et al., 2018).

Elevated temperatures also trigger ROS accumulation, exacerbating oxidative stress and contributing to reduced photosynthetic efficiency and fruit development (Hewitt et al., 2023). During the ripening phase, high temperatures can also disrupt grape composition, leading to an imbalance between sugar accumulation and acidity. This imbalance results in wines with higher alcohol content and altered flavor profiles, often diminishing desirable sensory attributes (Drappier et al., 2019). Additionally, extreme heat shortens the growing season, which can negatively impact overall yield. Over the past 40 years, grape harvests in most wine-growing regions globally have advanced by 2–3 weeks (Van Leeuwen et al., 2024). This trend is particularly pronounced in the Mediterranean, where rising temperatures have led to reduced yields and impaired photosynthetic processes (Bernardo et al., 2018; Torres et al., 2018a; Van Leeuwen et al., 2024).

Conversely, low temperatures present distinct challenges. Prolonged exposure to cold or sudden frost events can damage critical vine structures, including buds, shoots, and roots, resulting in significant yield losses and diminished fruit quality (Arias et al., 2022). These effects are especially detrimental during critical stages of vine development (Martínez-Lüscher et al., 2016). However, the reduced accumulation of winter chilling, due to higher minimum temperatures and climate change, is highlighted as one of the main threats to the survival of local viticulture, as it can delay or disrupt budburst and negatively affect vine

development (Cameron et al., 2021).

Among the factors influencing vineyard systems, soil temperature emerges as a critical determinant of grapevine physiology, growth, and productivity. Soil temperature regulates numerous physical and biological processes at the soil surface, including crop and weed phenology, growth, and respiration (Costa et al., 2023; Howell et al., 2020). At deeper soil layers, it affects root metabolism, soil respiration, water and nutrient uptake, microbial diversity and activity, organic matter dynamics, and soil biochemistry (Akter et al., 2015; Onwuka and Mang, 2018; Mehdizadeh et al., 2020). Over the past century, soil temperatures have increased at rates comparable to or exceeding those of air temperatures (Santos et al., 2020). This trend, observed in German vineyard regions (Schultz, 2022), is expected to be more pronounced in Southern Europe. The Mediterranean region, characterized by a warm-season transitional climate, faces heightened vulnerability as evapotranspiration is constrained by low soil moisture rather than solar radiation (Feng et al., 2022). Reduced soil moisture is projected to amplify heat anomalies and extreme temperature events (Feng et al., 2022; Seneviratne et al., 2010), with significant implications for soil processes and vineyard sustainability.

Most soil processes influenced by increased soil temperatures are closely tied to the biological components of the soil, which are critical for agricultural ecosystems, including vineyards. Soil biota, comprising a diverse array of macro- and microorganisms such as insects, nematodes, bacteria, fungi, and actinomycetes, perform essential ecological functions (Costa et al., 2023). These include organic matter decomposition, nutrient cycling, soil structure enhancement (e.g., improved aeration and water retention), and pest and disease control (Giffard et al., 2022). Elevated soil temperatures accelerate organic matter mineralization, potentially altering soil carbon dynamics and nutrient availability (Blanco et al., 2024; Conant et al., 2011). This thermally induced enhancement of microbial activity expedites the decomposition of organic compounds, increasing CO_2 emissions and risking soil carbon depletion (Ray et al., 2020; Schindlbacher et al., 2011). While enhanced mineralization may temporarily boost nitrogen and phosphorus availability for grapevines (Bai et al., 2013), the concurrent increase in microbial biomass can intensify competition for soil nutrients (Kuzyakov and Xu, 2013). Over time, these dynamics may reduce soil organic matter content (Gonzalez et al., 2023), impair water retention capacity, and compromise soil structure (Wei et al., 2016). These changes threaten vineyard sustainability, necessitating adaptive soil management strategies to maintain soil health, mitigate carbon loss, and optimize grapevine performance under changing climatic conditions (Fraga, 2020).

Climate change and rising soil temperatures are also expected to influence soil microbial diversity and community dynamics, potentially disrupting the soil food web and its associated ecosystem services (Fu et al., 2023). Vineyard soils serve as a primary reservoir of microorganisms for grapevine phyllosphere and endosphere communities. Each growing season, grapevine leaves and berries acquire much of their microbial community from the soil (Costa et al., 2023; Griggs et al., 2021). Balanced grapevine-associated microbial communities are essential for plant growth, stress tolerance, and biotic resilience (Pinto et al., 2014). Moreover, these microbial communities influence berry composition, fermentation dynamics, and ultimately, wine quality (Belda et al., 2017). Consequently, changes in soil microbial composition and structure driven by rising soil temperatures could directly and indirectly affect grapevine growth, health, and berry development, with cascading effects on wine quality.

2.3. Soil salinity

Soil salinity constitutes another significant abiotic stress factor, with climate change expected to exacerbate soil salinization through multiple mechanisms, including soluble salts accumulation due to a change in hydrological balance, sea salt intrusion, and windborne salt deposition (Hassani et al., 2021). Rising temperatures are expected to accelerate evapotranspiration rates, intensifying the accumulation of salts in the upper soil layers. Additionally, shifts in precipitation patterns, especially in arid and semi-arid regions, are projected to diminish the effectiveness of soil leaching processes, further aggravating soil salinization challenges (Karmakar et al., 2016). Moreover, rising sea levels are projected to amplify saltwater intrusion in coastal zones (Ullah et al., 2021).

The effects of salt stress on grapevines include the imposition of osmotic stress, which reduces water availability (Han and Li, 2024). This results in osmotic imbalances that create water deficit conditions similar to those observed during drought. The accumulation of toxic ions, such as sodium and chloride, intensifies the stress by disrupting cellular processes and inhibiting nutrient uptake (Lu and Fricke, 2023). Furthermore, salt stress induces the overproduction of ROS, which disrupts cellular homeostasis and aggravates the inhibition of nutrient uptake and photosynthetic processes (Ullah et al., 2021). Grapevines are considered moderately sensitive to salinity, with the severity of its impact influenced by factors such as rootstock-scion combinations, soil type and irrigation practices (Ollat et al., 2015). Certain rootstock varieties exhibited enhanced tolerance to salinity by limiting chloride ion uptake (Silva et al., 2024). However, excessive salt in the soil can lead to stunted grapevine development, decreased harvests, and inferior fruit quality (Al-Taey and Al-Ameer, 2023). Salinity stress notably impairs the accumulation of anthocyanins and other phenolic compounds, which are essential for maintaining optimal wine quality (Zhao et al., 2024).

2.4. CO_2 increases

Climate change is intrinsically tied to the rise in atmospheric CO_2 concentrations, a key driver of global warming and associated environmental changes. An increase in CO_2 concentration has been observed to stimulate photosynthesis in grapevines, potentially enhancing growth rates and biomass production (Van Leeuwen et al., 2024). This phenomenon, known as the "CO_2 fertilization effect", can result in larger vine canopies and greater grape yields under favorable conditions (Glenn et al., 2013; Wohlfahrt et al., 2019). Nevertheless, the influence of elevated CO_2 levels on grape composition remains less predictable. While enhanced growth may lead to higher yields, it may also alter berry composition (Arrizabalaga-Arriazu et al., 2020). Furthermore, elevated CO_2 levels interact with other environmental stress factors, including drought and nutrient deficiencies. Although enhanced CO_2 availability can improve photosynthetic carbon gain and water use efficiency, it simultaneously intensifies the plant's demand for essential resources. When combined with additional stress factor such as drought or extreme heat, elevated CO_2 may indirectly contribute to the accumulation of ROS, potentially counteracting some of the benefits associated with increased photosynthetic gains (Leakey et al., 2009).

Recent advancements in experimental techniques, such as the VineyardFACE (Free Air Carbon Dioxide Enrichment) experiment at Hochschule Geisenheim University, Germany (Wohlfahrt et al., 2022), provided valuable insights into the long-term effects of elevated CO_2 in real-world vineyard conditions. This open-air system simulates increased atmospheric CO_2 concentrations without altering the natural environment, bridging the gap between controlled laboratory studies and field applications. The VineyardFACE experiment demonstrated that elevated CO_2 levels enhanced photosynthesis and thus plant biomass production (Wohlfahrt et al., 2022). However, a moderate increase in CO_2 level has been reported to reduce the total anthocyanin concentration in berry skin (Kahn et al., 2022). These findings underscore the complexity of predicting how rising CO_2 levels will influence viticulture and wine quality in the future, emphasizing the necessity of integrated management strategies to address the compounded effects of climate change.

2.5. Radiation

Excessive radiation can cause sunburn symptoms in grapevines, affecting the wine quality (Rustioni et al., 2023). For example, ultraviolet (UV) radiation is an emerging abiotic stress factor with the potential to significantly impact grapevine physiology and berry development. As a result of climate change, grapevines are increasingly exposed to elevated levels of UV radiation. This exposure can decrease photosynthetic activity, promote the overproduction of ROS, and increase the production of polyphenols in fruit (Van Leeuwen et al., 2024). Specifically, UV-B radiation has been shown to positively affect the concentration of skin phenolics and may also influence the aromatic profile of grapes, thereby impacting wine quality (Bernardo et al., 2018). Also, an excess in photosynthetically active radiation (in the visible part of the spectrum) could cause sunburn symptoms, modifying the grape composition (Rustioni et al., 2015).

Despite these challenges, moderate levels of excessive radiation, below the threshold of cellular damage, can yield beneficial effects by stimulating the production of secondary metabolites such as flavonoids and phenolics, which are critical for grape quality (Matus, 2016). These compounds, as well as the ones formed by their oxidation, function as natural sunscreens for the plant, absorbing UV radiation and protecting cellular structures from damage (Del-Castillo-Alonso et al., 2021; Rustioni, 2017). Consequently, while radiation poses a stressor to viticulture, it also offers opportunities to modify the phenolic content and antioxidant capacity of grapes, and, thus, the quality of the resulting wines.

2.6. Heavy metal stress

The accumulation of heavy metals in vineyard soils represents a significant and persistent agro-environmental issue, with implications for ecosystem health, grape quality, and human safety. Viticulture, as a long-established agricultural practice, has historically relied on various agrochemicals, including copper-based fungicides, which have contributed substantially to soil contamination over time (Komárek et al., 2010). Recent studies have elucidated the extent and complexity of heavy metal pollution in viticultural regions globally. Copper (Cu) and zinc (Zn) frequently emerge as the predominant contaminants, at times exceeding regulatory thresholds (Mahlungulu et al., 2023; Pham et al. 2022). The persistence of these elements in soil matrices is particularly concerning, as they can persist for decades, potentially centuries, post-application (Besnard et al., 2001).

The sources of heavy metal contamination in vineyards are multifaceted. While copper-based fungicides remain a primary contributor, other anthropogenic activities such as industrial emissions, vehicular exhaust, the use of contaminated irrigation water and the application of certain fertilizers also play significant roles (Brunetto et al., 2014). Moreover, the topography and soil characteristics of many viticultural regions can exacerbate the problem, with sloping terrains facilitate the accumulation of contaminants in lower-lying areas through erosion and runoff processes (Fernández-Calviño et al., 2008). Additionally, alterations in precipitation patterns and the increased frequency of extreme meteorological events may exacerbate this issue by promoting soil erosion and runoff, which can mobilize heavy metals previously sequestered in the soil (Paltseva and Neaman, 2020). The ramifications of heavy metal contamination extend beyond soil health. Plants exposed to heavy metal contamination experience disrupted nutrient and water uptake, leading to reduced growth, chlorosis, and diminished photosynthesis (Siyar et al., 2020). Elevated levels can negatively impact soil microbial communities, potentially disrupting crucial ecosystem services such as nutrient cycling and organic matter decomposition (Nunes et al., 2016). Furthermore, the potential for heavy metal uptake by grapevines raises concerns about wine quality and food safety (Tariba, 2011; Betancur-Agudelo et al., 2020).

2.7. High rainfall

High-intensity rainfall events, anticipated to become more frequent and severe due to climate change, pose significant challenges to viticulture by disrupting vine physiology, soil health, and fruit quality (Atak, 2024; Martel et al., 2021). Excessive precipitation often results in waterlogged vineyard soils, reducing oxygen availability to roots and impairing the uptake of essential nutrients such as nitrogen and phosphorus. Under hypoxic conditions, grapevine roots adapt by shifting from aerobic to anaerobic respiration, maintaining energy production, which triggers metabolic reprogramming, the accumulation of toxic metabolites, and hormonal imbalances (Atak, 2024; Ruperti et al., 2019).

Rainfall during spring months (April to June) may stimulate vine growth; however, it also increases vulnerability to fungal diseases. Similarly, heavy precipitation during the harvest period (August to October) is linked to a decline in grape quality, heightened risks of fungal outbreaks, reduced yields, and operational disruptions during harvesting (Sanderson et al., 2023).

Waterlogged conditions further exacerbate these challenges by adversely affecting plant physiology. Limited oxygen availability impairs root function, leading to stomatal closure, which restricts carbon dioxide uptake and reduces both photosynthesis and transpiration rates (Pais et al., 2023). Additionally, hypoxic conditions promote the accumulation of ROS, which can damage cellular structures and further reduce photosynthetic efficiency. These physiological stresses culminate in decreased biomass production and compromised fruit development (Topali et al., 2024).

Oxygen depletion in waterlogged soils also disrupts key soil processes, including mineralization, organic matter decomposition, and nutrient uptake. These disturbances result from significant changes in the composition and functionality of the soil microbiome (Francioli et al., 2021, 2022), which is essential for the regulation of these processes (Sprunger et al., 2023).

3. Strategies for coping with abiotic stress in viticulture

In response to escalating impacts of climate change, viticulture has introduced adaptive strategies to mitigate the multifaceted challenges associated with abiotic stresses. Although grapevines possess inherent coping mechanisms, these intrinsic responses often require additional interventions to ensure optimal growth and productivity under fluctuating environmental pressures. Key physiological adaptations include morphological changes, such as the regulation of stomatal opening to reduce water loss, accumulation of protective compounds and alterations in leaf structure, such as decreasing the leaf area/volume ratio and increasing leaf rolling (Tzortzakis et al., 2020). Furthermore, grapevines exhibit modifications in gene expression to regulate stress-related pathways and utilize metabolic adjustments to bolster their capacity for stress tolerance and recovery (Wei et al., 2022). Additionally, grapevines respond to environmental stress by accumulating osmolytes—such as proline, glycine betaine, and soluble sugars—and antioxidant molecules (SOD, CAT, POD, polyphenols), which help maintain cellular homeostasis and protect against oxidative damage (Ye et al., 2023; Yadav et al., 2024). To complement these natural responses, agronomic interventions, including strategic irrigation (Losciale et al., 2024; Pappaccogli et al., 2024), protected cropping systems (Domanda et al., 2024; Li et al., 2022; Pallotti et al., 2023), and the application of biostimulants (Cataldo et al., 2022; Jindo et al., 2022), have been implemented.

Additional measures, such as the selection of stress-tolerant rootstocks (Bianchi et al., 2018; Rustioni et al., 2016), the breeding of resilient grapevine varieties (Yadav et al., 2024), irrigation strategies and refined nutrient (Dinu et al., 2022) and canopy management (Rustioni et al., 2023), play crucial roles in maintaining physiological efficiency and enhancing environmental adaptability (Naulleau et al.,

2021). Emerging technologies, such as precision viticulture, biocontrol, and artificial intelligence (AI)-driven tools, provide innovative solutions to monitor and mitigate abiotic stresses (Godavari et al., 2024). By integrating these approaches throughout the grapevine growth cycle, vineyard managers can establish robust, tailored strategies for stress management, thereby ensuring the production of high-quality grapes despite increasingly challenging climatic conditions. In this context, viticultural practices must also evolve to align with the changing climate. Adaptations such as adjustments in trunk height, leaf area-to-fruit weight ratios, and pruning schedules are essential to preserve harvest dates in optimal environmental conditions depending on the growing regions (Van Leeuwen et al., 2019).

The overarching objective of vineyard management strategies aimed at mitigating abiotic stresses is to address critical areas of concern. In drought-prone regions, optimized irrigation techniques, such as regulated deficit irrigation, are employed to reduce water usage while preserving grape quality (Bernardo et al., 2018; Losciale et al., 2024). In areas affected by soil salinity, effective soil management practices, including mulching and improved drainage systems, are pivotal for preventing salt accumulation and promoting vine health (Cataldo et al., 2021; Phogat et al., 2023). Organic mulching is also effective in reducing the amplitude of soil thermal waves in high-temperature regions (Blanco et al., 2024).

Canopy management is another vital practice, facilitating the regulation of vine growth, ameliorating assimilate allocation to productive shoots, and improving ventilation and reducing relative humidity around the berry (Faralli et al., 2022). Additionally, in environmental contexts that provide sufficient basic resources (e.g. water) to support both the main crop and the cover crop, the establishment of cover crops between vine rows has been shown to strengthen soil structure, reduce erosion, and improve water retention, thus providing abiotic stress resilience to grapevines (Ribera-Fonseca et al., 2023). In some cases, relocating vineyards to higher altitudes or cooler regions may be necessary to counteract the adverse effects of rising temperatures (Meladze et al., 2023; Naulleau et al., 2021). However, establishing new vineyards in mountainous regions often requires substantial investment due to the logistical challenges associated with steep slopes, which can hinder mechanization and necessitate labor-intensive manual practices. A long-term approach involves selecting rootstocks and grapevine varieties with enhanced tolerance to drought, salinity, and other abiotic stressors, thereby improving adaptability to changing climates (Ollat et al., 2015). For instance, local grapevine germplasm from regions of warm and dry climates may serve as an alternative for developing heat-stress-tolerant varieties or clones (Venios et al., 2020). Recent studies have also identified specific cultivars such as “775 (p)” “Ziyun Niagara” “Shenyue” and “Cuihong” as highly resistant to heat stress (Zhang et al., 2024). Their introduction into warmer climates could help maintain grape quality and yield potentially reducing the need for vineyard relocation. However, the substitution of traditional cool-climate cultivars with heat-tolerant alternatives depends on both viticultural feasibility and consumer acceptance.

In addition to physical and genetic strategies, biological approaches are gaining prominence as complementary tools to address abiotic challenges in viticulture. The use of biostimulants has emerged as a key sustainable strategy for enhancing grapevine resilience against stress (Monteiro et al., 2022). Among these, the application of arbuscular mycorrhizal fungi (AMF) inoculants has shown significant promise. These inoculants enhance nutrient uptake, increase water-use efficiency, and improve the overall resilience of grapevines to environmental stressors (Torres et al., 2021a; Uwamungu et al., 2022). By forming symbiotic associations with grapevine roots, AMF inoculants enable more efficient access to water and nutrients, thereby supporting the sustainability of viticulture in the context of increasingly severe climatic conditions.

4. Arbuscular mycorrhizal fungi: key players in sustainable viticulture

Arbuscular Mycorrhizal Fungi (AMF) have gained considerable attention for their potential role in promoting sustainable viticulture, particularly in the context of the intensifying challenges posed by climate change. These symbiotic fungi establish mutualistic relationships with plant roots, enhancing nutrient and water uptake. By leveraging these natural associations, vineyard managers can improve grapevine health, reduce environmental impacts, and potentially improve wine quality while simultaneously fostering long-term soil health and ecosystem stability.

The concentration and diversity of AMF can be increased primarily through two principal strategies: (i) the adoption of agricultural practices that promote and safeguard AMF diversity, such as reduced tillage, organic amendments, cover cropping, and crop rotation, and (ii) the application of commercial AMF inoculants designed to enhance colonization and restore natural levels of AMF richness (Berruti et al., 2016; Soti et al., 2023). In viticulture, AMF inoculants have emerged as promising tools for improving grapevine resilience to drought, salinity, temperature extremes, and nutrient deficiencies, which are increasingly prevalent under changing climatic conditions. A detailed illustration of the structural components, symbiotic functions, and interrelated factors that define the role of arbuscular mycorrhizal fungi in improving soil health and increasing vine resilience is presented in Fig. 1.

4.1. AMF biology and function

Arbuscular mycorrhizal fungi, ancient symbionts belonging to the subphylum Glomeromycotina of the phylum Mucoromycota, associate with the root system of nearly 71 % of all vascular plant species (Dowarah et al., 2022). These fungi possess three primary structures —hyphae, arbuscules, and vesicles— that play vital roles in nutrient exchange and soil health (Fig. 1). Upon initial contact with the root epidermis, tip-growing hyphae differentiate to form a structure known as a hyphopodium. Hyphae are filamentous extensions that increase nutrient and water absorption by exploring soil regions beyond the rhizosphere. Arbuscules, tree-like structures formed within plant root cells, act as nutrient exchange sites, while vesicles serve as storage organs in certain AMF species (Khaliq et al., 2022). The AMF life cycle involves distinct stages, including spore germination, root colonization, and the formation of extensive hyphal networks in the soil (Uwamungu et al., 2022). Establishing AM symbiosis is a dynamic process characterized by pre-symbiotic communication, root tissue penetration, cortex invasion, arbuscule development, and the eventual formation of vesicles and spores (Choi et al., 2018).

AMF provide numerous ecological and agronomic benefits. They enhance nutrient acquisition—particularly phosphorus and nitrogen—by extending the effective root system into nutrient-rich zones of the soil inaccessible to non-mycorrhized plants (Khaliq et al., 2022). Additionally, AMF improve plant water relations, contributing to increased drought resilience, and release glomalin, a glycoprotein that enhances soil structure by binding soil particles (Pathan et al., 2023; Singh et al., 2022). These fungi also confer resistance to both biotic and abiotic environmental stresses, such as pathogens and heavy metal contamination (Begum et al., 2019). Furthermore, AMF play a pivotal ecological role in shaping plant community dynamics, facilitating nutrient cycling, and supporting carbon sequestration, all of which are critical to maintaining ecosystem functionality (Diagne et al., 2020; Uwamungu et al., 2022).

4.2. Symbiosis between AMF and grapevine plants

The symbiosis between AMF and grapevines is pivotal in enhancing vineyard productivity and resilience. The genomes of grapevine rootstocks contain specific gene sets associated with arbuscular mycorrhizal

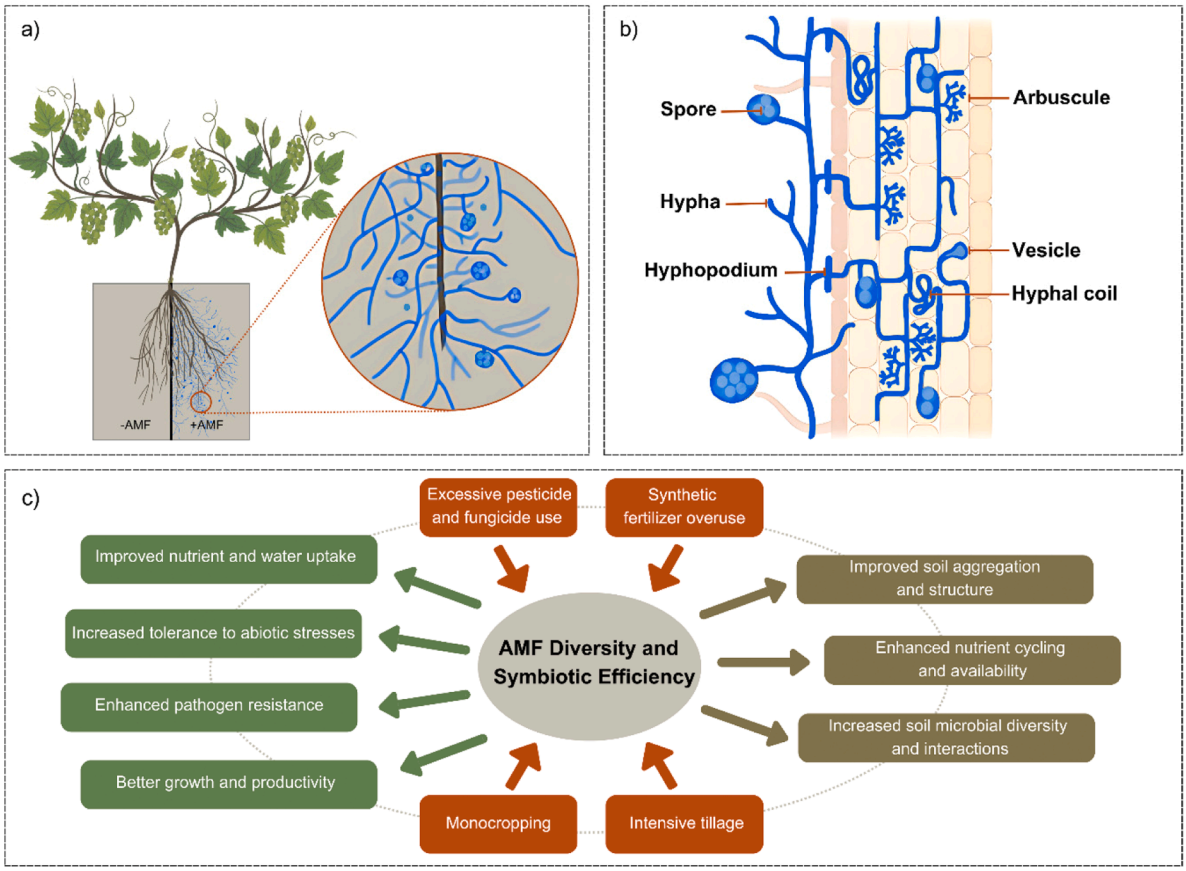

Fig. 1. Representation of Arbuscular Mycorrhizal Fungi in Viticulture: Structure, function, and interactions. a) Comparative diagram illustrating the presence (+AMF) and absence (-AMF) of AMF in grapevine roots, highlighting the extension of fungal hyphae into the soil. b) Key symbiotic structures of AMF within roots, including hyphopodium, arbuscules, vesicles, hyphae, hyphal coils and spores, which facilitate nutrient exchange between the fungus and the plant. c) Interactions among AMF diversity, symbiotic efficiency, and influencing factors. The brown elements represent soil-regulated parameters, while the green elements illustrate plant benefits. The dashed oval indicates the interconnected nature of these factors, highlighting how AMF-mediated benefits depend on balanced interactions between soil conditions and plant responses. Intensive agricultural practices, illustrated in orange, such as excessive pesticide and fertilizer use, monocropping, and tillage negatively impact AMF diversity and functionality.

symbiosis, which are integral to nutrient transport, defense mechanisms, and growth promotion, highlighting their favorable response to AMF colonization (Balestrini et al., 2017). A recent study investigating the responses of ten grapevine rootstocks to AMF symbiosis with *Rhizophagus irregularis* DAOM197198, using RNA sequencing-based transcriptome profiling, revealed both shared regulatory mechanisms and rootstock-specific responses (Sportes et al., 2023). The authors identified a core set of 353 genes regulated by AMF symbiosis across all rootstocks, generating over 2000 transcriptome profiles from diverse grapevine varieties and tissues related to mycorrhizal associations. These findings suggest that within the genetic diversity of grapevine rootstocks, some hidden mechanisms, such as specific mycorrhizal-mediated effects, may influence both aboveground and belowground vine growth and development across various rootstock and scion combinations.

The establishment of AMF-grapevine symbiosis begins when AMF hyphae penetrate the grapevine root, forming specialized structures known as arbuscules. These arbuscules facilitate bidirectional nutrient exchange: the grapevine provides carbohydrates produced by photosynthesis to the fungi, while the fungi supply essential nutrients such as phosphorus, nitrogen, and micronutrients. The formation of this symbiotic interface is regulated by plant signaling pathways, including strigolactones, which stimulate fungal spore germination and hyphal branching, and mycorrhiza-specific transcription factors, which coordinate host gene expression essential for colonization (Choi et al., 2018; Trouvelot et al., 2015). It has been reported that AMF-grapevine associations significantly enhance root biomass, nutrient acquisition, and overall plant growth, particularly under environmental stress (Moukarzel et al., 2023; Santos and Figueiredo, 2023; Torres et al., 2021a).

Among AMF genera, *Glomus* is the most prevalent and diverse in the grapevine root system and rhizosphere, with species such as *Glomus intraradices, G. mosseae* and *G. irregulare* (Cangahuala-Inocente et al., 2011; Cesaro et al., 2021; Schreiner and Mihara, 2009). Other AMF genera, including *Rhizophagus* (e.g., *R. irregularis*) and *Funneliformis* (e.g., *F. mosseae*), are also present in grapevine roots, though less frequently than *Glomus* spp. (Fors et al., 2023). Additional genera such as *Acaulospora, Claroideoglomus*, and *Paraglomus*, have also been identified, further highlighting the diversity of AMF species associating with grapevine (Lailheugue et al., 2024; Zhang et al., 2024). The AMF diversity is shaped by soil type, climate, and vineyard management practices, which collectively contribute to enhance grapevine health and productivity (Catalani et al., 2024; Fors et al., 2023; Torres et al., 2018a).

The AMF-grapevine symbiosis also supports the accumulation of secondary metabolites, such as phenolics, which can improve grape quality by enhancing antioxidant properties (Torres et al., 2019). These metabolites play a dual role: bolstering plant resilience to stress and contributing to the sensory profile of wine (Torres et al., 2018b). Understanding the impact of mycorrhization on grapevine metabolism is critical, as metabolic adaptations significantly influence grapevine resilience to both abiotic and biotic stresses. For instance, studies on the

Tempranillo variety, widely cultivated in Mediterranean regions, have demonstrated that AMF inoculation modifies primary metabolite profiles, increasing glucose and amino acid levels in berries (Torres et al., 2019). AMF colonization in Tempranillo grapevines has also been associated with elevated anthocyanin levels and alterations in abscisic acid (ABA) metabolism (Torres et al., 2018b). Furthermore, AMF symbiosis promotes the accumulation of phenolics, hydroxycinnamic acids, and carotenoids in grapevine leaves, with specific variations depending on the clone analyzed (Goddard et al., 2021). Recent studies have also reported significant increases in volatile organic compounds (VOCs), including terpenes and monoterpene alcohols associated with plant communication and defense, in the leaves of *V. vinifera* cv. Sangiovese following colonization by *Funneliformis mosseae* (Velásquez et al., 2020). These findings underscore the ecological and viticultural significance of AMF in enhancing grapevine resilience and wine quality through metabolic and biochemical modulation.

4.3. AMF sustain soil health and beneficial microbial communities

AMF are integral to vineyard soil ecosystems, influencing biological and chemical processes that sustain agricultural systems (Khaliq et al., 2022). They enhance soil structure and stability through glomalin production, a glycoprotein that improves water retention, while their hyphal networks bind soil particles, mitigating erosion (Singh et al., 2022). Recent research highlights that AMF enhance plant nutrient uptake not only by expanding root surface area but also by interacting with the hyphosphere microbiome—a soil zone shaped by hyphal exudates (Zhang et al., 2022). These exudates, rich in sugars, amino acids, and secondary metabolites, stimulate microbial growth and influence community composition. Certain hyphosphere-associated bacteria facilitate phosphorus and nitrogen mineralization, complementing AMF functions and improving nutrient availability under suboptimal conditions (Kuyper and Jansa, 2023).

AMF also establish symbioses with beneficial bacteria, including plant growth-promoting rhizobacteria, nitrogen-fixing bacteria, and saprophytic fungi, enhancing microbial diversity and resilience (Ramasamy et al., 2011; Ujvári et al., 2021; Ferreira et al., 2021). By modifying rhizosphere dynamics, AMF contribute to a stable soil microbiome, improving fertility, reducing dependence on chemical inputs, and supporting vineyard sustainability (Aguilera et al., 2022). However, certain bacterial phyla can suppress AMF functionality, underscoring the complexity of soil microbial networks and the necessity for careful management to optimize AMF ecological benefits in viticulture (Svenningsen et al., 2018).

4.4. The role of agricultural practices in shaping AMF communities

Agricultural practices significantly shape AMF communities, influencing soil health, crop productivity, and vineyard resilience. These practices alter soil properties such as pH, organic matter content, and nutrient availability, directly affecting AMF functionality and hyphosphere microbiome recruitment (Kuyper and Jansa, 2023). The impact of farming methods on AMF diversity, abundance, and function highlights the need for sustainable management to maximize their ecological and agronomic benefits (Aguilar-Paredes et al., 2024; Bender et al., 2016).

Tillage practices strongly influence AMF communities. Conservation tillage, including reduced and no-till systems, better preserves fungal networks than conventional tillage, enhancing nutrient cycling and plant stress tolerance (Schalamuk and Cabello, 2010; Trouvelot et al., 2015). Similarly, organic farming supports AMF diversity and activity by reducing reliance on synthetic inputs. Organic vineyard soils exhibit higher AMF colonization rates (20–35 %) compared to conventional systems (6–31 %), alongside greater AMF diversity, with dominant species such as *Funneliformis verruculosum, Septoglomus* sp., and *Septoglomus constrictum* (Aguilar-Paredes et al., 2024). Organic amendments, including manure, plant residues, and compost, further enhance microbial functionality and AMF biomass (Liu et al., 2023).

The use of cover crops and intercropping systems represents another effective strategy to enhance AMF diversity and functionality. Cover crops improve soil structure and organic matter content, while continuously providing root exudates that stimulate AMF activity. Given the strong relationship between plant diversity and AM fungal diversity, employing diverse cover crop mixtures can expand the range of AM fungal partners available to crops. This increases the likelihood of forming symbioses with multiple AM fungi that effectively mitigate both abiotic and biotic stresses (Vukicevich et al., 2016).

Integrating conservation tillage, organic farming, and sustainable land use practices into vineyard management enhances AMF diversity, productivity, and long-term resilience. These strategies are particularly crucial in mitigating climate change impacts, promoting a more sustainable and efficient agricultural system.

4.5. AMF as an inoculant

The use of AMF as biofertilizers or microbial inoculants in viticulture is gaining increasing attention due to their capacity to enhance both plant growth and resilience to environmental stressors (Aguilera et al., 2022; Lueck et al., 2024). Commercial AMF inoculants typically contain propagules, including spores, hyphae, and/or colonized root fragments, which are capable of establishing symbiotic relationships with grapevines (Köhl et al., 2016; Rosa et al., 2020). These inoculants are applied to vineyards with the aim of augmenting soil AMF populations or introducing more efficient fungal strains, particularly in soils where native AMF communities are diminished or less effective (Köhl et al., 2016).

The effectiveness of AMF inoculants depends on several factors, including the selection of suitable fungal strains, the physicochemical properties of the soil, and the compatibility of the inoculant with the existing microbial community and grapevine genotype (Lueck et al., 2024; Rosa et al., 2020). Thus, the strategic selection and application of AMF inoculants are critical for enhancing soil fertility and promoting sustainable vineyard management. However, additional research is required to optimize inoculant formulations and application techniques across diverse viticultural contexts.

5. Mechanisms of AMF in abiotic stress mitigation in grapevine

As climate change continues to intensify environmental stressors such as drought, salinity, and temperature extremes, the role of AMF in enhancing grapevine resilience is becoming increasingly significant. Various biological mechanisms underpin the ability of AMF to enhance plant tolerance to these stressors. These mechanisms include the development of extensive hyphal networks that facilitate improved water and nutrient uptake, the modulation of stress-related signaling pathways, and the accumulation of osmolytes. Furthermore, AMF symbiosis enhances photosynthetic efficiency and biomass production while alleviating oxidative stress through the regulation of reactive oxygen species (ROS) (Begum et al., 2019). Fig. 2 provides a comparative overview of grapevines with and without AMF inoculation under abiotic stress conditions. It underscores the pivotal role of AMF in sustaining physiological stability and functional resilience in grapevines.

Table 1 provides a detailed summary of reported key AMF-host interactions across various grapevine cultivars and stress conditions. It highlights the AMF species utilized in the studies, the types of abiotic stress addressed, and the corresponding physiological and biochemical responses. Collectively, these findings underscore the versatility and efficacy of AMF as a sustainable tool for mitigating environmental stresses and improving viticultural resilience.

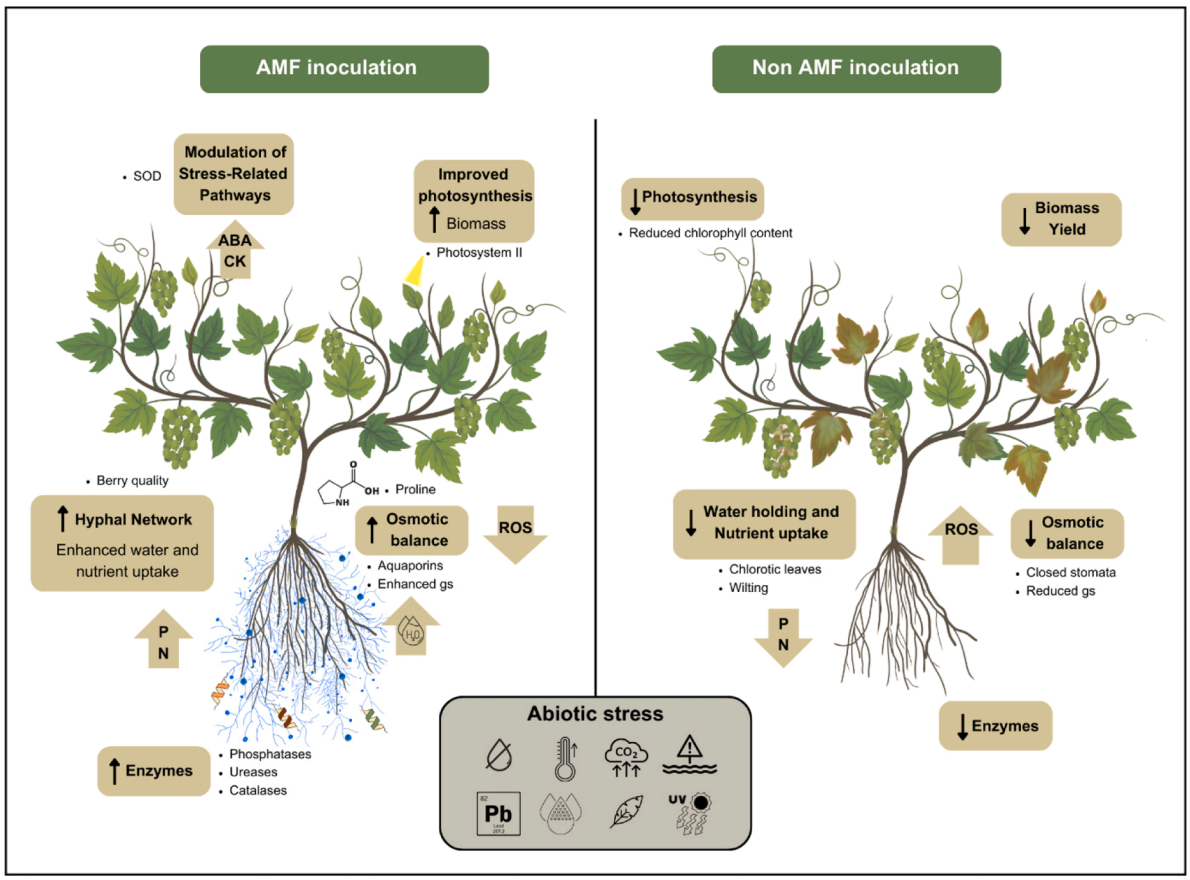

Fig. 2. Mechanisms employed by arbuscular mycorrhizal fungi (AMF) to enhance grapevine resilience against abiotic stresses. Comparative analysis of grapevines with and without AMF inoculation under abiotic stress conditions. AMF-inoculated grapevines exhibit several physiological and biochemical enhancements, including improved photosynthesis through Photosystem II, increased biomass yield, and enhanced stress modulation pathways involving abscisic acid (ABA), cytokinin (CK), and antioxidant enzymes such as superoxide dismutase (SOD). The presence of a hyphal network facilitates increased uptake of phosphorus (P) and nitrogen (N). Enzymatic activities such as phosphatases, ureases, catalases, and SOD contribute to better stress tolerance. Improved osmotic balance is achieved through aquaporins, elevated levels of proline, and enhanced stomatal conductance (gs), helping to counteract reactive oxygen species (ROS) and maintain water status.

5.1. Enhanced water and nutrient uptake

AMF play a crucial role in enhancing plant water and nutrient acquisition, particularly under challenging environmental conditions such as drought or nutrient-poor soils. By forming symbiotic relationships with plant roots, AMF significantly increase the effective root surface area. This expanded network allows plants to access water and nutrients from a broader soil volume, including otherwise inaccessible moisture pockets during dry periods (Uwamungu et al., 2022). Additionally, AMF may improve the bioavailability of essential nutrients, such as phosphorus, nitrogen, and trace elements, by enzymatically modifying soil particles and organic matter, thereby facilitating their uptake by plants (Berruti et al., 2016; Kaiser et al., 2015). Furthermore, AMF can enhance plant water uptake and maintain plant water status during drought by improving soil hydraulic conductivity (Abdalla et al., 2023). A recent meta-analysis examining the efficacy of AMF in alleviating drought stress revealed that AMF inoculation can increase root absorptive surface area by approximately 31 % and root volume by 65 %, providing crucial support during periods of water scarcity. Among the AMF species evaluated, *Rhizophagus irregularis* and *Funneliformis mosseae* were the most frequently studied (Chandrasekaran, 2022b).

In vineyard ecosystems, AMF inoculation and successful root colonization have been shown to provide substantial benefits under semi-arid and arid conditions. A field experiment conducted in southern Italy under severe summer drought conditions revealed that rooted cuttings of 1103 Paulsen (*Vitis berlandieri* × *Vitis rupestris*) —a genotype widely utilized in the region for its relatively high drought tolerance— experienced significant advantages when inoculated with a commercial powdery formulation of mycorrhiza (Micosat F. SEMI, CCS AOSTA S.r.l., Italy), including five different species; *Glomus coronatum* GU 53, *Glomus caledonium* GM 24, *Glomus mosseae* GP 11, *Glomus viscosum* GC 41 and *Rhizophagus irregularis* RI 31. Mycorrhized plants demonstrated notably higher survival rates, enhanced growth, and significantly increased accumulation of 18 essential elements (Cardinale et al., 2022). Similarly, a field study conducted in southeastern Spain found that Crimson grapevines inoculated with *Glomus iranicum* var. *tenuihypharum* exhibited improved water use efficiency, enhanced photosynthetic performance, and increased uptake of nutrients such as phosphorus (P), potassium (K), and calcium (Ca) (Nicolás et al., 2015). These improvements were associated with greater root development, higher yields, and earlier grape maturation. Furthermore, field experiments conducted in hyper-arid environments (Napa Valley, USA) demonstrated that Merlot clones 181 grafted onto 3309 C rootstocks showed enhanced survival and physiological performance under water-stress conditions when inoculated with AMF (*Rhizophagus intraradices, Funneliformis mosseae, Glomus aggregatum*, and *Glomus etunicatum*), compared to their non-inoculated counterparts (Torres et al., 2021a).

In terms of nutrient acquisition, AMF play a critical role in mobilizing and transferring phosphorus (P) —a critical yet often limiting nutrient in soils. AMF hyphae extend into fine soil pores inaccessible to plant roots, significantly enhancing phosphorus availability and uptake (Ferrol et al., 2019; Smith et al., 2011). Numerous greenhouse and field

Table 1
Arbuscular Mycorrhizal Fungi-driven mechanisms for abiotic stress mitigation in grapevine.

Host plant	AMF	Stress type	Observed responses	Reference
Vitis berlandieri × *Vitis rupestris* (1103-Paulsen rootstock)	*Glomus coronatum GU 53, Glomus caledonium GM 24, Glomus mosseae GP 11, Glomus viscosum GC 41, Rhizophagus irregularis RI 31,* + *Bacillus subtilis, Paenibacillus durus, Pseudomonas fluorescens*	Deficit irrigation and elevated temperatures (intentionally late field plantation)	Reduced mortality; increased leaf area, shoot number and shoot length; extension of the vegetative season (later senescence); modulation of chemical element absorption (with higher accumulation of 18 essential elements, including P); enrichment of beneficial bacterial taxa (*Burkholderiaceae, Rhizobiaceae, Methylophilaceae, Bacillus, Massilia, Streptomyces*) in the root endosphere.	Cardinale et al. (2022)
Vitis vinifera L. cv. Tempranillo	*Septglomus deserticola, Funneliformis mosseae, Rhizoglomus intraradices, Rhizoglomus clarum,Glomus aggregatum* + *Bacillus* sp and *Paenibacillus* sp	Deficit irrigation and elevated temperatures	Increased anthocyanin content, modulation of ABA metabolism, and maintenance or improvement of berry quality.	Torres et al. (2018b)
Vitis labrusca L. cv. Niagara Rosada	*Rhizophagus clarus UFSC-14*	Copper	Increased P uptake, reduction in copper toxicity, enhanced growth and physiological traits, increased quantum yield of PSII.	Brunetto et al. (2019)
Vitis vinifera L. cv. Ecolly	*Rhizophagus irregularis, Funneliformis mosseae, G. aggregatum, Claroideoglomus etunicatum*	Drought	Increased the photosynthetic rate, stomatal conductance, and transpiration rate and decreased the intercellular CO_2 concentration.	Ye et al. (2022)
Vitis vinifera L. cv. Merlot (3,309 C rootstock)	*Rhizophagus intraradices, Funneliformis mosseae, Glomus aggregatum, Glomus etunicatum*	Drought	Improved the grapevine vegetative growth, water status, and photosynthetic activity.	Torres et al. (2021a)
Vitis vinifera L. cv. Sultana	*Glomus mosseae* + *Streptomyces rimosus*	Salinity	Improved nutrient uptake, reduced leaf necrosis by increasing osmoregulators, phenolic compounds and antioxidant enzymes.	Karimi & Noori (2022)
Vitis vinifera L. cv. Ercis	*Glomus intraradices* + Whey	Salinity	Enhanced root development, better salt stress tolerance, and higher nutrient content.	Gazioglu & Gazioglu (2022)
Vitis vinifera L. cv. Dogridge rootstock	*Glomus mosseae* + *Bacillus aryabhattai, Pseudomonas taiwanensis, Azobacter tropicalis*	Salinity	Improved root growth, biomass, K+:Na+ ratio, leaf water potential and stress tolerance; increased polyamines, ABA, and cytokinins.	Upreti et al. (2016)
Vitis vinifera L. cv. Touriga Nacional (1103 Paulse rootstock)	*Rhizoglomus irregulare / Funneliformis mosseae*	Heat Stress	Enhanced photosynthesis rate, transpiration, and stomatal conductance under heat stress. The number of differentially expressed miRNAs was higher in mycorrhizal plants (28) compared to non-inoculated plants (17) under heat stress.	Campos et al. (2023)
Vitis vinifera L. cv. Gewurztraminer	*Rhizophagus irregularis*	Biotic and Abiotic Stress	Reprogrammed root metabolism (sugar and fatty acid metabolism), increased defense hormone levels in leaves (jasmonic acid and salicylic acid).	Goddard et al. (2021)
Vitis vinifera L. cv. Tempranillo	*Rhizophagus intraradices*	Elevated temperatures	Improved phenolic and flavonol content in leaves and preserved high levels of phenolic compounds in leaves.	Torres et al. (2015)
Vitis vinifera L. cv. Ecolly	*Funneliformis mosseae, Glomus aggregatum, Claroideoglomus etunicatum*	Drought stress	Increased sucrose, proline, and soluble proteins under drought stress. Enhanced antioxidant activities and reduced oxidative stress markers (e.g., hydrogen peroxide, malonaldehyde). Upregulated drought-responsive genes and improved osmotic regulation.	Ye et al. (2023)

experiments have demonstrated that, in addition to improving P nutrition, AMF enhance the absorption of other essential nutrients, including nitrogen (N), potassium (K), calcium (Ca), zinc (Zn), iron (Fe), sulfur (S), boron (B), copper (Cu) and magnesium (Mg) which are crucial for grapevine metabolism and resilience (Moukarzel et al., 2023; Schreiner, 2005). For example, grapevine rootstock cultivars 101–14, Schwarzmann, and 5C inoculated with AMF communities exhibited significantly higher leaf uptake of K, Mg, P, S, B, Cu, Fe, and Zn when grown in low-P substrates (Moukarzel et al., 2023). Similarly, Schreiner (2007) reported increased levels of P, K, Ca, Mg, Fe, and B in the leaves of *Cabernet Sauvignon* grapevines inoculated by a mix of AMF species (*Glomus mosseae, Glomus intraradices*, and *Scutellospora calospora*) under low-P soil conditions compared to those in high-P soils. This effect was attributed to enhanced P uptake, which in turn stimulated the uptake of other nutrients. Importantly, the AMF-mediated increase in phosphorus uptake by grapevine roots has been widely documented, even under saline stress conditions. Khalil (2013) evaluated the effectiveness of *Glomus intraradices* in mitigating salinity stress in three grapevine rootstocks (*Dogridge*, 1103 Paulsen, and *Harmony*) irrigated with varying concentrations of NaCl. The inoculated rootstocks exhibited increased chlorophyll content, proline levels, total carbohydrates, and leaf concentrations of P and K, highlighting the role of AMF in alleviating salinity-induced stress while improving nutrient acquisition.

AMF also enhance soil enzyme activity, particularly under conditions of low phosphorus availability. For instance, in the AL-420A rootstock subjected to low soil Olsen-P levels, AMF colonization increased the enzymatic activities of β-glucosidase and N-acetyl-β-glucosaminidase by 30 % and 25 %, respectively, compared to grafted vines without AMF colonization (Catalani et al., 2024). These enzymes play a crucial role in biogeochemical cycling, organic matter decomposition, and nutrient mobilization, serving as key indicators of soil health and "sensors" of changes in soil management or fertility practices (Neemisha and Sharma, 2022). The activity of these enzymes not only increases the availability of critical nutrients but also stimulates soil enzyme activation, further enhancing soil fertility (El-Sawah et al., 2021). Interestingly, recent studies highlight that AMF alone often lack the enzymatic machinery to mobilize complex organic nutrients directly from the soil. Instead, this function is supported by hyphosphere bacteria, which

produce enzymes such as phosphatases and phytases to liberate nutrients like phosphorus from organic complexes (Zhang et al., 2022). This highlights the need for a more nuanced understanding of the synergistic mechanisms driving AMF-mediated nutrient acquisition.

5.2. Osmotic adjustment, water relations, and modulation of stress-related pathways

In conditions of drought, AMF can significantly enhance plant tolerance by supporting osmotic adjustment, improving water relations, and mitigating oxidative stress. By accumulating osmolytes such as sugars, proline, and glycine betaine, AMF reduce osmotic and leaf water potentials, enabling plants to maintain higher turgor pressure and sustain cellular functions during water deficits (Abdalla et al., 2023; Tang et al., 2022). Additionally, AMF facilitate greater nutrient uptake, particularly nitrogen, which promotes osmolyte synthesis and reinforces osmotic balance. Recent studies have highlighted the critical role of these mechanisms. For example, Ye et al. (2023) demonstrated that *Vitis vinifera* cv. Ecolly plants inoculated with *Funneliformis mosse*ae, *Glomus aggregatum*, and *Claroideoglomus etunicatum* accumulated significantly higher levels of sucrose and proline under drought stress compared to non-inoculated plants, thus ensuring better maintenance of leaf water potential and cellular integrity. Beyond osmotic regulation, AMF play a pivotal role in enhancing water transport by modulating the expression of aquaporin genes, which regulate water movement across cell membranes. Notably, Ye et al. (2023) reported significant upregulation of key aquaporin genes, including *VvPIP1;2* and *VvTIP2;1*, in AMF-colonized grapevines under both well-watered and drought conditions. This modulation enhances aquaporin activity, ensuring efficient water transport and maintaining homeostasis, thereby improving the plant's ability to cope with water scarcity or salinity. Similarly, Braidotti et al. (2024) conducted a study on two new PIWI (fungus-resistant) grapevine varieties, Merlot Kanthus and Sauvignon Kretos, and found that aquaporins such as *VvPIP2;1* and *VvTIP2;1* may significantly influence hydraulic behavior under water stress. These findings underscore the critical role of AMF in regulating aquaporin expression and improving water management in grapevines, particularly under drought conditions.

Hormonal signaling also plays a key role in AMF-mediated drought tolerance. AMF regulate ABA pathways, a critical hormonal response to drought stress. Increased ABA levels promote stomatal closure, reducing water loss through transpiration, while encouraging adaptive root architecture changes, such as enhanced root growth and branching, to improve water foraging (Singh, 2020). Additionally, AMF interact with other hormones, including auxins and gibberellins, to modulate growth responses and further support plant adaptation to stress (Liao et al., 2018). These hormonal adjustments highlight the multifaceted role of AMF in orchestrating physiological and molecular responses that bolster drought resilience.

AMF also mitigate the oxidative stress commonly associated with drought stress. Drought-induced accumulation of reactive oxygen species (ROS), such as hydrogen peroxide (H_2O_2) and superoxide anions (O_2^-), can damage cellular structures and impair plant functions. AMF-inoculated plants exhibit lower levels of oxidative stress markers, including malondialdehyde (MDA), which reflects reduced lipid peroxidation and improved membrane stability (Tang et al., 2022). Ye et al. (2023) demonstrated that AMF-inoculated grapevines had reduced concentrations of MDA, H_2O_2, and O_2^- under drought conditions, alongside higher activity of antioxidant enzymes such as superoxide dismutase (SOD) and peroxidase (POD), which neutralize ROS and protect cellular integrity. This enhanced antioxidant capacity ensures the delicate balance between photosynthesis, transpiration, and root water movement during drought and recovery (Chandrasekaran, 2022a). A recent study conducted over a two-year greenhouse trial tested the hypothesis that AMF can alleviate virus-induced oxidative stress in grapevines (Radić et al., 2024). Specifically, the 'Merlot' cultivar, was infected with three grapevine-associated viruses and subjected to either AMF inoculation or a control treatment. At five and fifteen months post-inoculation, AMF inoculation resulted in reduced levels of ascorbic acid and superoxide dismutase, both indicators of antioxidative responses, across both years. During the mature phase of symbiosis, guaiacol peroxidases, which emerged as a critical mechanism for scavenging H_2O_2, were enhanced in AMF inoculated plants. Furthermore, the downregulation of stilbene synthase (*STS1*) genes, along with the upregulation of enhanced disease susceptibility (*EDS1*) genes, indicated efficient ROS scavenging in AMF-colonized plants.

The combined effects of AMF on osmotic regulation, water transport, and oxidative stress highlight their critical role in maintaining plant resilience under drought stress. By improving water relations, AMF-colonized plants sustain higher relative water content and leaf water potential, ensuring the stability of cellular functions even under prolonged water scarcity.

5.3. Improved photosynthesis and growth

The cumulative impact of AMF on plant water relations, osmotic adjustment, and stress resilience translates into a marked improvement of photosynthetic processes and overall plant growth, particularly under stress conditions. By stabilizing water availability and reducing oxidative damage, AMF-inoculated grapevines can maintain photosynthetic activity during periods of drought and salinity stress. This sustained photosynthetic performance directly contributes to enhanced plant health, increased biomass, and improved fruit yields, even in challenging environmental conditions (Biasi et al., 2023; Kozikova et al., 2024). Recent studies reinforce these findings: Ye et al. (2022), for instance, observed that AMF inoculation (*Rhizophagus irregularis, Funneliformis mosseae, G. aggregatum*, and *Claroideoglomus etunicatum*) significantly improved chlorophyll concentration, photosynthetic rate, and chlorophyll fluorescence in *Vitis vinifera* cv. Ecolly under drought stress. In this study, AMF-colonized plants exhibited higher maximal photochemical efficiency (Fv/Fm) and actual photosystem efficiency (ΦPSII), demonstrating enhanced photosynthetic performance and energy use efficiency during water-deficient conditions. These benefits were accompanied by increased dry biomass of both shoots and roots, reflecting the positive impact of AMF on overall growth and resource allocation.

AMF also indirectly support photosynthesis by ensuring an efficient nutrient supply, especially phosphorus, which is essential for ATP production and chlorophyll synthesis, both critical components of the photosynthetic process (Jian et al., 2024). Enhanced photosynthesis driven by AMF inoculation allows for better carbon assimilation, resulting in more robust plant growth and greater above-ground biomass (Betancur-Agudelo et al., 2020). As a result, AMF-colonized plants exhibit a more efficient conversion of resources into growth and productivity, a feature that is especially valuable for crops under adverse environmental conditions.

Furthermore, AMF improve stomatal conductance (gs) and intercellular CO_2 concentration, optimizing gas exchange processes that are vital for sustained photosynthetic activity under stress (Zhu et al., 2018). Torres et al. (2021a) reported that AMF-inoculated grapevines under reduced irrigation conditions maintained higher stomatal conductance and net photosynthesis rates compared to non-inoculated controls. This effect was particularly pronounced when AMF colonization was combined with efficient water management practices, highlighting the synergy between biological and agronomic strategies for stress mitigation. In addition to enhancing photosynthetic efficiency, arbuscular mycorrhizal fungi influence carbon distribution within the plant, facilitating an increased allocation of resources to leaves and other photosynthetically active tissues. This optimized carbon allocation enables grapevines to develop and maintain a larger leaf area, thereby improving their capacity for light capture and photosynthesis. Gaši et al. (2023) demonstrated that AMF significantly enhance net photosynthesis

rates, chlorophyll concentration, and total carotenoid content, even in grapevines under biological stress. Specifically, higher net photosynthesis rates, conductance to H_2O, chlorophyll *a* concentration, total carotenoid concentration, and dry matter content were observed in Kober 5BB rootstock (*Vitis berlandieri* Planch. × *Vitis riparia* Michx.) grafted with *Vitis vinifera* cv. Merlot scions infected with various combinations of Grapevine Rupestris Stem Pitting Virus, Grapevine Leafroll-Associated Virus 3, and/or Grapevine Pinot Gris Virus, following AMF inoculation.

Together, these benefits reinforce the capacity of AMF to support plant growth under suboptimal conditions, positioning them as a promising component in sustainable agriculture for enhancing photosynthetic efficiency and productivity in stress-prone environments. By synergistically improving water relations, increasing nutrient availability, and optimizing carbon allocation, AMF contribute to a comprehensive enhancement of plant physiological performance, enabling better adaptation and resilience to environmental stressors.

5.4. Improving tolerance to heavy metals

Arbuscular mycorrhizal fungi have been shown to significantly alleviate heavy metal stress in plants by sequestering metals within their fungal structures, producing glomalin to bind and stabilize metals, and redistributing them within plant tissues to minimize toxicity (Akhtar et al., 2024). Additionally, AMF enhance antioxidant enzyme activities, such as superoxide dismutase and catalase, to combat oxidative stress in some plants exposed to heavy metals (Bano and Ashfaq, 2013). The extensive use of copper (Cu)-based fungicides in viticulture has led to significant Cu accumulation in vineyard soils, often reaching toxic levels, with concentrations as high as 3216 mg kg^{-1} in some regions (Trouvelot et al., 2015). This contamination negatively affects soil biodiversity and creates risks for young grapevines with shallow root systems (Vršič et al., 2023).

Studies have shown that AMF inoculation can significantly enhance grapevine growth and physiological traits in Cu-contaminated soils. For instance, Betancur-Agudelo et al. (2020) found that grapevines inoculated with native AMF from Cu-rich soils showed improved photosynthetic activity and nutrient uptake. Specifically, *Rhizophagus clarus* was found to increase carbon assimilation in grapevine rootstocks.

Future research should aim to better understand the cellular mechanisms underlying AMF-mediated metal tolerance, optimize the selection of AMF strains for specific environmental conditions, and integrate AMF inoculation with sustainable practices such as organic amendments and reduced tillage. These strategies could enhance vineyard resilience, mitigate heavy metal stress, and promote long-term soil and plant health.

5.5. Mycorrhiza-Induced resistance and biocontrol role of AMF

Arbuscular mycorrhizal fungi are increasingly recognized as natural biocontrol agents, offering sustainable solutions to mitigate plant pathogens and pests. This role has gained importance as climate change exacerbates the prevalence and severity of plant diseases. Rising temperatures, altered precipitation patterns, and shifting growing seasons significantly impact grapevine cultivation, intensifying the threat of fungal diseases such as downy mildew (*Plasmopara viticola*), powdery mildew (*Erysiphe necator*), and botrytis (*Botrytis cinerea*). Climate models predict that these pathogens will adapt to changing conditions (Juroszek and von Tiedemann, 2015). For instance, Francesca et al. (2006) and Salinari et al. (2007) projected increased severity and earlier onset of downy mildew epidemics across regions like Italy, Argentina, Australia, Chile, and the USA due to rising temperatures and the polycyclic nature of the pathogen. Similarly, Lalic et al. (2013) noted earlier downy mildew outbreaks in Serbia, although reduced humidity during later growing stages might temper disease risks.

AMF play a critical role in alleviating these pathogen pressures, particularly under climate change. By enhancing nutrient uptake, water-use efficiency, and root health, AMF improve plant resilience while inducing systemic resistance to pathogens. A study involving three rootstock varieties (101–14, 5C, and Schwarzmann) infected with a mixture of *black foot* pathogen species demonstrated that AMF inoculation increased vine growth parameters by 60 % to 80 % and reduced both disease incidence and severity by 40 % to 50 % compared to vines inoculated with the pathogen mixture alone (Moukarzel et al., 2022). Similarly, Petit & Gubler (2006) investigated the effects of the arbuscular mycorrhizal fungus *Glomus intraradices* (INVAM CA 501) on *black foot* disease caused by the fungus *Cylindrocarpon macrodidymum* in *Vitis rupestris* cv. St. George under controlled conditions. Their findings revealed that mycorrhizal plants exhibited significantly fewer leaf and root symptoms compared to non-mycorrhizal plants.

One key mechanism by which AMF enhance plant defense is through mycorrhiza-induced resistance (MIR). MIR activates complex plant defense pathways, boosting resistance to both biotic and abiotic stresses. AMF-colonized plants exhibit systemic protection against diverse threats, including soilborne pathogens, root-attacking insects, and foliar fungi. MIR involves the priming of defense signaling pathways, such as the salicylic acid (SA) and jasmonic acid (JA) pathways, which are central to resistance against biotrophic and necrotrophic pathogens, respectively (Cameron et al., 2013). In grapevines, studies have highlighted MIR's effectiveness in combating root pathogens. Mycorrhization has been shown to reduce symptoms of diseases like black foot vascular disease (Moukarzel et al., 2022; Petit and Gubler, 2006) and root rot caused by *Armillaria mellea* (Dey and Ghosh, 2022). These findings underscore the potential of AMF inoculation to reduce disease severity in grapevines, particularly when applied to young plants before planting.

Local and systemic MIR has been demonstrated against the ectoparasitic nematode *Xiphinema index*, the vector of grapevine fanleaf virus, which causes gall formation and severe damage to the grapevine root system (Hao et al., 2012). This study highlights the priming of defense responses in grapevine rootstock SO4 by the arbuscular mycorrhizal fungus *Rhizophagus irregularis* BEG141, as well as the transmission of a plant-mediated signal to non-mycorrhizal tissues. Interestingly, this bioprotective effect was not associated with an enhanced P status in the plant but was instead attributed to an as-yet unidentified induced systemic factor. Another investigation on white root rot disease, caused by *Armillaria mellea*, showed that the disease progressed more slowly in *Glomus intraradices* BEG72-inoculated grapevine plants of the 110R rootstock, which also exhibited greater root and shoot growth compared to non-inoculated plants (Nogales et al., 2010). These findings suggest that mycorrhizal plants display higher tolerance to *A. mellea* than their non-mycorrhizal counterparts. An interesting and recent study investigated the effect of *Vitis vinifera* cv. Gewürztraminer colonization by the arbuscular mycorrhizal fungus *Rhizophagus irregularis* on plant tolerance to wood inoculation with *Neofusicoccum parvum* Bt67, one of the most aggressive fungi associated with Botryosphaeria dieback (Belval et al., 2024). The results revealed that mycorrhization led to a modest yet significant reduction in wood necrosis size and less severe necrosis symptoms on the leaves. Using a non-targeted metabolomic approach, the authors found that both mycorrhization and *N. parvum* infection induced metabolite reprogramming in roots, particularly affecting sugars and stilbenes, which were downregulated in response to both AMF symbiosis and pathogen infection. Additionally, *N. parvum* infection caused a marked decrease in fatty acids and oxylipins in the leaves of non-mycorrhizal plants, whereas these compounds were maintained or increased in plants colonized by *R. irregularis*. These findings further suggest that AMF symbiosis may serve as a valuable tool for enhancing the health of young grapevines and mitigating the effects of trunk disease fungi by modulating lipid metabolism.

Beyond addressing biotic challenges, MIR offers substantial protection against abiotic stressors such as drought and salinity, which can

exacerbate plant susceptibility to pathogens. By enhancing water and nutrient uptake, AMF mitigate physiological strain and lower infection risks (Ye et al., 2022). The priming effect triggered by AMF equips plants to respond more effectively to subsequent stressors, fostering a dynamic and adaptive defense system (Cameron et al., 2013). Notably, MIR mechanisms extend beyond biochemical and physiological changes to include structural adaptations. AMF colonization improves root architecture, enhancing resource acquisition and forming physical barriers to pathogen invasion. For example, such structural enhancements have been shown to suppress root rot fungi and nematode vectors in grapevine soils (Petit and Gubler, 2006; Trouvelot et al., 2015). The broad-spectrum protection conferred by MIR underscores its potential as a valuable tool in sustainable agriculture.

6. Challenges and strategies for enhancing mycorrhizal applications in viticulture

The prospect of using AMF inoculants as a tool to support grapevine growth under challenging environmental conditions aligns well with the goals of eco-friendly and resilient viticulture, especially as climate change continues to impact traditional grape-growing regions. However, while the theoretical benefits of AMF inoculants are well-documented in research, translating these findings into reliable field applications presents a host of challenges. The shift from controlled experimental settings to diverse vineyard environments has shown limitations in achieving consistent root colonization and stress mitigation effects. Despite significant advances in AMF research, the practical application of these inoculants in viticulture requires careful consideration of various biological, ecological, and market-related factors. Without addressing these barriers, the widespread adoption of AMF inoculants in viticulture remains limited, and the potential of AMF to contribute meaningfully to sustainable viticulture is constrained. A schematic summary of the main limitations affecting the practical use of AMF inoculants in viticulture is presented in Fig. 3, which categorizes the constraints into four main areas: colonization failure, field performance, ecological impacts, and market-related challenges.

Additionally, a detailed overview of widely used AMF inoculants, highlighting their formulations, application methods, and observed results in different grapevine systems is provided in Table 2. This compilation underscores the diversity of approaches being employed globally to enhance the efficacy of AMF applications in viticulture. The table also illustrates the varied success rates of these products, reflecting the complexity of optimizing AMF use in diverse viticultural environments.

6.1. *Colonization and performance variability in mycorrhizal application*

A key challenge in the application of AMF inoculants is selecting fungal strains that exhibit optimal efficacy in specific environmental conditions and grapevine varieties. While AMF are not strictly host-specific, they display host preferences, with certain strains conferring greater benefits to specific grapevine cultivars or soil types (Berruti et al., 2016). Commercial AMF formulations vary in application methods and dosages, emphasizing the necessity of tailored inoculation strategies. For instance, Symplanta's *Funneliformis mosseae* is manually applied at a dose of 8000 spores per vine, whereas Agronutrition's *Rhizophagus irregularis* suspension is applied at 1000 spores per plant at

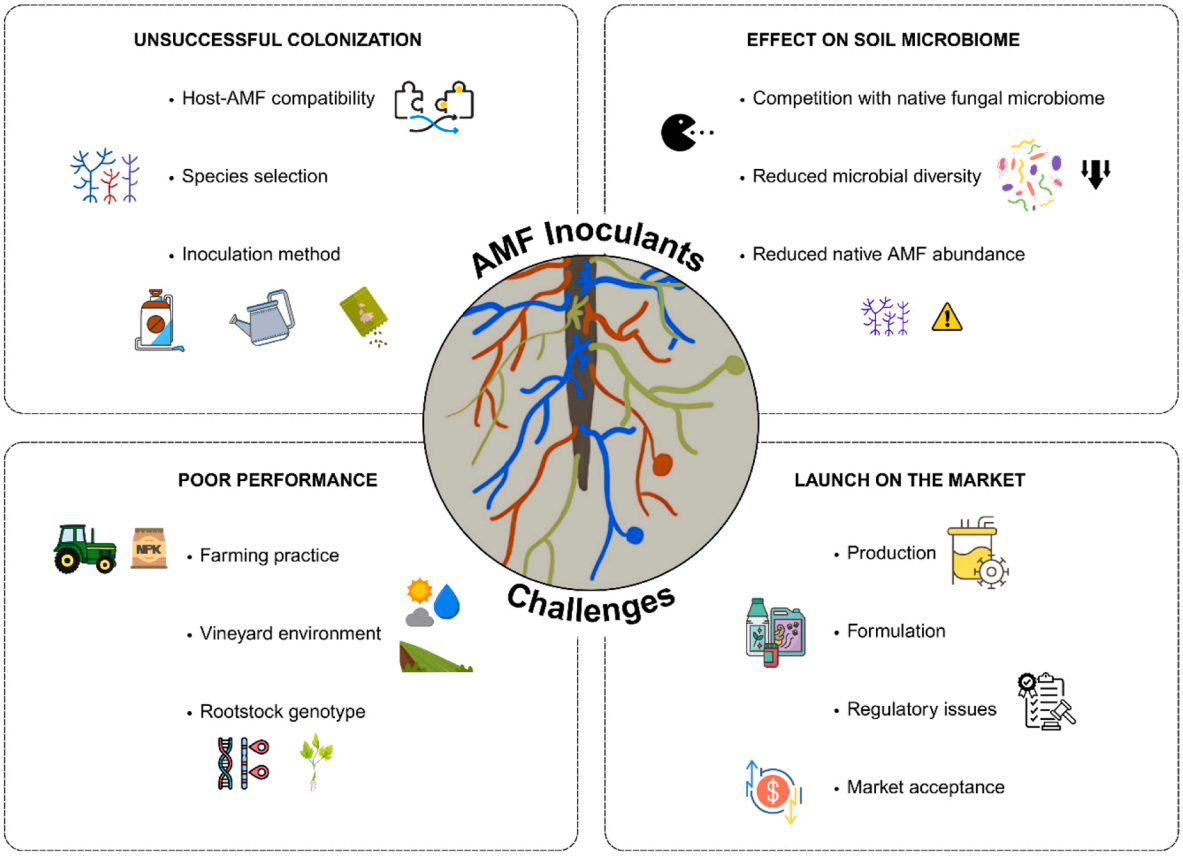

Fig. 3. Challenges associated with the application of AMF inoculants in viticulture. These challenges include: (i) Unsuccessful colonization, often due to poor host–AMF compatibility, inadequate species selection, or suboptimal inoculation methods; (ii) Poor field performance, influenced by farming practices, vineyard environmental conditions, and rootstock genotype; (iii) Negative effects on the soil microbiome, including competition with native fungal communities, reduced microbial diversity, and a decrease in native AMF abundance; and (iv) Market-related constraints, such as production complexity, formulation challenges, regulatory hurdles, and limited market acceptance.

Table 2
Commercial AMF inoculants for grapevine cultivation: Applications and outcomes.

Brand / Country	AMF Species	Concentration of inoculum	Formulation	Application mode	Dose	Plant studied	Country of experiment / Type of experiment	Main results	Reference
Symbiom, / Czech Republic	*Funneliformis mosseae* BEG95	Not specified	Carrier material consisting of expanded clay	Manual application in a ditch beneath each grapevine, covered with soil and rye seeds sown above	10 g of inoculum per vine	*Vitis vinifera* L. cv. White Viosinho and 1103 Paulsen rootstock	Portugal / Field experiment	Improved photochemical indices post-heat wave. Partial production loss compensation due to berry sunburn reduction. Inoculation did not lead to a replacement of native AMF communities.	Nogales et al. (2021)
Symbiom / Czech Republic	*Rhizophagus irregularis*	4000 spores/g	Not specified	Irrigation of the soil with a fungal spore suspension	1500 spores per cutting	*Vitis vinifera* cv Cabernet Sauvignon grapevine, SO4 rootstock	Portugal / Pot experiment	Altered pathogen effector expression (*Plasmopara viticola*). Enhanced resistance to pathogens. Mycorrhizal inoculation significantly increased the biomass of grapevine plants.	Cruz-Silva et al. (2021)
MYKE® PRO GR (Premier Tech, Inc) / Canada	*Rhizoglomus irregulare* DAOM 197198	2130 spores per 15 g	Vermiculite as spore carrier	Added to pots	15 g per pot	Riparia Gloire (*Vitis riparia*), Schwarzmann (*Vitis riparia Vitis rupestris*), and Salt Creek (*Vitis champinii*)	Canada / Greenhouse and field experiments	In the greenhouse, AM fungal inoculation increased biomass production in Riparia Gloire and Salt Creek rootstocks but not in Schwarzmann. In the field, the inoculant colonized roots but did not increase biomass production. The inoculant persisted but did not provide growth benefits.	Rosa et al. (2020)
Symplanta LLC and Inoq LLC / Germany	*Rhizophagus irregularis* (Ri) and *Rhizophagus irregularis, Funneliformis mosseae, Funneliformis caledonium* (Mix)	Symplanta: 10,000 spores per gram Inoq: 2,700 spores per gram	Spore-based inoculum	Inoculum added to the sterile grapevine substrate	8,000 spores per 6 L pot	*Vitis vinifera* L. Merlot and Kober 5BB rootstock *Vitis berlandieri Planch.* × *Vitis riparia Michx*	Croatia / Greenhouse experiment	AMF inoculation, particularly with the Mix inoculum, significantly influenced virus concentration in grapevine tissues. Increased GRSPaV concentration in roots and decreased GRSPaV concentration in young leaves.	Gaši et al. (2023)
Advantage Grade II—INOQ GmbH / Germany	*Rhizophagus irregularis*, *Funneliformis mosseae*	Not specified	Not specified	Inoculation at the young cutting stage	Not specified	*Vitis vinifera* cv Glera, 1103 Paulsen (1103P) and SO4 rootstocks	Italy / Field experiment	Improved photosynthetic performance and water use efficiency. Enhanced growth-defense balance. Increased concentration of IAA and viniferin in AMF-inoculated plants.	Nerva et al. (2022)
Agronutrition, / France	*Rhizophagus irregularis* DAOM 197198	50 spores/ml	Suspension	Gently poured at the base of the plant stem	1000 spores (20 ml)	*Vitis vinifera* cv. Gewurztraminer	France / Pot experiment	AMF colonization led to significant changes in primary metabolism, especially in sugar and fatty acid metabolism in roots. Enhanced levels of defense hormones (JA and SA) were observed in leaves.	Goddard et al. (2021)
GLOMYGEL® vid, olivo, frutales /	*Rhizophagus intraradices*	2000 propagules per mL	Inert pieces of roots colonized by AMF, spores, and	Diluted with distilled water near roots	8 mL of diluted inoculum	*Vitis vinifera* L. cv. Tempranillo, different accessions	Spain / Greenhouse experiment	Improved phenolic content and antioxidant activity in leaves.	Torres et al. (2015)

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Table 2 (*continued*)

Brand / Country	AMF Species	Concentration of inoculum	Formulation	Application mode	Dose	Plant studied	Country of experiment / Type of experiment	Main results	Reference
Mycovitro S.L. / Spain			vegetative mycelium		(2000 propagules)			Effects varied with intra-varietal diversity.	
Myco Apply Endo Maxx / Mycorrhizal Applications LLC / USA	*Rhizophagus intraradices, Funneliformis mosseae, Glomus aggregatum, Glomus etunicatum*	5625 propagules/g	Suspendable powder	Drenched around the trunk for 50 seconds	10 g/1000 plants, drenched for 50 seconds	Merlot (clone 181) grafted onto 3309C rootstock	USA / Field experiment	Fungal communities were more responsive to treatments in terms of alpha diversity, while bacterial communities showed more changes in beta diversity. Inoculation with AMF increased positive associations between vineyard-soil-living microbes.	Torres et al. (2021a)
Agronutrition / France	*Rhizophagus irregularis* DAOM197198	1000 spores in 20 mL aqueous suspension	Aqueous suspension	Poured at the base of the plant stem	1000 spores per plant	Syrah, *Vitis vinifera* cv. Mondeuse blanche B x Duzera N.	France / Controlled conditions in a climatized chamber	Developed RT-qPCR method for mycorrhization intensity estimation. Strong correlations found between fungal genes and symbiosis vitality.	Duret et al. (2022)
Bioradis Gel / Bioera SLU / Spain	*Septoglomus deserticola, Funneliformis mosseae, Rhizoglomus intraradices, Rhizoglomus clarum, Glomus aggregatum*	100 spores per gram	A mixture of five AMF species and Bacillus and Paenibacillus (2 × 10ˆ6 CFU gˆ-1)	Submerging roots in the inoculum for 15 minutes	1 gram per plant	*Vitis vinifera* cv. Tempranillo CL-843	Spain / Greenhouse experiment	Improved fruit quality in Tempranillo under warming conditions. Maintained sugar to organic acid balance. Mycorrhizal association favored the accumulation of certain minerals (Mg, Zn) in leaves under elevated temperatures.	Goicoechea et al. (2023).
MycoApply Ultrafine Endo / Compostwerks Company / USA	*Rhizophagus irregularis, Funneliformis mosseae, Glomus aggregatum, Claroideoglomus etunicatum*	Not specified	Not specified	A hole was dug in the pot, and 5 g of inoculum was placed in the hole and covered with soil	5 g per pot	*Vitis vinifera* L. cv. Ecolly	China / Greenhouse experiment	AMF alleviated the negative effects of drought stress on grapevines, improving leaf water status, chlorophyll concentration, and photosynthetic capacity.	Ye et al. (2022)
Micoflow, Radimix advance / Filnova / Italy MycoApply DR / Sumitomo Chemical Italia / Italy MycoUp / Biogard® / Italy Overground ST-Plus / Overtis / Italy Team mix / Hello Nature® / Italy Tricoveg / Chemia S.p.a. / Italy Vici Rhyzoteam WG / Koppert / Italy	Micoflow: *Rhizophagus irregularis* Radimix advance: *Rhizophagus* ssp. MycoApply DR: *R. irregularis, Claroideoglomus luteum, Claroideoglomus etunicatum, Claroideoglomus claroideum* MycoUp: *Rhizophagus iranicus* var. tenuihypharum Overground ST-Plus: *Rhizoglomus* spp. Team mix: *R. irregularis, Funneliformis mosseae* Tricoveg: *Rhizophagus* spp.	Micoflow: 1% Radimix advance: 0.005% MycoApply DR: 1% MycoUp: 120 propagules/g Overground ST-Plus: 0.004% Team mix: 500 spores/g Tricoveg: 0.2% Vici Rhyzoteam WG: 4%	Micoflow: Liquid Radimix advance: Powder MycoApply DR: Granular MycoUp: Granular Overground ST-Plus: Powder Team mix: Granular Tricoveg: Powder Vici Rhyzoteam WG: Granular	Applied once per year for three consecutive years	Followed label instructions for each product	Grapevine (*Vitis vinifera* L.), Kober 5BB rootstocks	Italy / Field experiment	Higher photosynthetic efficiency and better PSII functioning in biostimulant-treated vines. Decrease in photoinhibition compared to untreated plants. Significant reprogramming of primary (lipids) and secondary (alkaloids and terpenoids) metabolites in treated plants. Improved contents of polyphenols and sugars in berries from treated plants. Yield remained unchanged.	Ganugi et al. (2023)

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Table 2 (*continued*)

Brand / Country	AMF Species	Concentration of inoculum	Formulation	Application mode	Dose	Plant studied	Country of experiment / Type of experiment	Main results	Reference
MycAgro Lab and MICOSAT F Vite / Italy	Vici Rhyzoteam WG: *Rhizophagus* spp. *Glomus mosseae* *Trichoderma viride, T. harzianum, Pochonia chlamidosporia, Streptomyces* spp. ST60, SB14 and SA51, *Bacillus subtilis* BA41, *Pseudomonas fluorescens* PN53, *Pseudomonas* sp. PT65, *Glomus* sp. GB67, *G. mosseae* GP11, *G. viscosum* GC41	Not specified	Spores, extraradical mycelium, sorghum mycorrhizal roots, and sorghum growth substrate	Soil supplementation	FMOS; 30% inoculum/soil for each plant MICO; 30 g for each plant About 1,000 propagules per plant	Pinot noir grafted on Richter 110 rootstock	Italy / Greenhouse experiment	The single AM fungus (*F. mosseae*) led to significant colonization of grapevine roots and upregulation of several AM marker genes. The mixed microbial inoculum resulted in only traces of AM fungal colonization but elicited significant transcriptional regulation. Both treatments altered the expression of genes related to nutrient transport, transcription factors, and cell wall-related genes, though the specific genes affected differed between the two conditions.	Balestrini et al. (2017)
AGTIV / Canada	*Rhizophagus irregularis*	12,000 spores per g	Wettable powder	Dipping roots in a slurry	12.5 g of inoculum in 25 mL water	*Vitis riparia* 'Riparia gloire'	Canada / Greenhouse experiment	AMF did not suppress *Ilyonectria* infection in grapevine rootstocks. Instead, it increased the abundance of *Ilyonectria*. Mycorrhizal rootstocks did not show enhanced growth effects compared to non-mycorrhizal rootstocks.	Taylor et al. (2019)
Unibiotis / France	*Rhizophagus irregularis*	Not specified	Not specified	Coated	10 mL 10% v/v	*V. vinifera* cv. Pinot Noir, Chasselas hybrid Divico (Gamaret x Bronner), rootstock 41 B MGt (V. vinifera x V. berlandieri),	France / Greenhouse experiment	AMF root colonization potentiates grapevine stilbenoid defenses in response to the aerial pathogens *Plasmopara viticola* and *Botrytis cinerea*. Stimulated transcription of key genes in the phenylpropanoid pathway. Mycorrhized plants accumulated larger amounts of stilbenoid phytoalexins and pterostilbene.	Bruisson et al. (2016).
MycoApply / USA	*Funneliformis mosseae, Glomus aggregatum, Claroideoglomus etunicatum*	Not specified	Not specified	Added to soil and watered	5 g per plant	*Vitis vinifera* cv. Ecolly	China / Greenhouse experiment	Increased proline and sucrose concentration under drought. Enhanced antioxidant activity and gene expression.	Ye et al. (2023)

the base of the stem (Gaši et al., 2023; Goddard et al., 2021). The efficacy of an AMF inoculant is contingent on its compatibility with the host plant and the environmental conditions of application. A given AMF strain may perform well in one vineyard but offer limited benefits in another due to variations in soil composition, climate, and microbial community structure (Biasi et al., 2023).

AMF function is highly dependent on fungal strain diversity and their functional traits, which vary across environmental contexts. Different AM fungal species recruit distinct microbial communities in the hyphosphere, influencing nutrient cycling and stress mitigation capacities (Zhang et al., 2022; Kuyper and Jansa, 2023). This heterogeneity underscores the importance of selecting AM fungal species or strains suited to specific viticultural conditions to maximize their role in mitigating abiotic stress. However, predicting inoculant success remains challenging without extensive field trials. Research suggests that grapevines derive greater benefits from inoculants comprising multiple AMF species, as multispecies formulations provide a broader range of functional benefits under varying environmental conditions (Basiru et al., 2020). For example, Symplanta's mixed inoculum of *Rhizophagus irregularis, Funneliformis mosseae*, and *Funneliformis caledonium* significantly reduced virus concentrations in grapevine tissues when applied at 8000 spores per 6 L pot. Conversely, the single-species product MYKE® PRO GR enhanced biomass in specific rootstocks but lacked consistent efficacy across all tested varieties (Gaši et al., 2023; Rosa et al., 2020). These findings highlight the necessity of carefully selecting and testing AMF strains to optimize inoculation efficacy and enhance grapevine resilience and productivity. Such efforts require collaboration among researchers, AMF manufacturers, and vineyard managers to ensure tailored inoculant applications that maximize viticultural benefits.

Effective colonization of grapevine roots by AMF in field conditions presents an additional challenge. Colonization success depends on multiple factors, including soil health, competition with native microorganisms, and environmental stresses such as drought or salinity (Biasi et al., 2023). AMF require specific conditions to establish symbiosis, which may not be uniformly present across vineyards. Soil disturbances, such as tillage and chemical fertilization, can further inhibit AMF colonization (Balzergue et al., 2013; Brito et al., 2012). Excessive nitrogen fertilization, for example, reduces AMF colonization by decreasing the plant's dependence on mycorrhizal networks for nutrient acquisition (Aguilera et al., 2022). Similarly, significant soil disruption can damage hyphal networks critical for AMF function, thereby diminishing inoculant efficacy (Van der Heyde et al., 2017). These findings underscore the need for vineyard management practices that support AMF colonization and optimize symbiotic benefits.

A major limitation to the widespread adoption of AMF inoculants is their inconsistent performance across diverse environmental settings. While AMF have been shown to enhance grapevine growth and stress resilience in controlled conditions, field results remain highly variable. Differences in soil composition, climate, and native microbial communities contribute to this inconsistency (Torres et al., 2018b). In vineyards with well-established native AMF populations, commercial inoculants may provide minimal additional benefits, as pre-existing mycorrhizal networks may already fulfill nutrient cycling and plant health functions (Basiru and Hijri, 2022b). Furthermore, the successful establishment and persistence of introduced AMF strains are not guaranteed in all vineyard environments, with studies documenting cases where commercial strains failed to persist or exert significant effects (Rosa et al., 2020). This variability complicates the reliable use of AMF inoculants for consistent stress management and growth enhancement in vineyard systems.

Recent research highlights the critical influence of rootstock genotype on the composition and dynamics of bacterial and fungal communities in the grapevine rhizosphere and root endosphere (Bettenfeld et al., 2022; Darriaut et al., 2022; Dries et al., 2021; Vink et al., 2021). For instance, Moukarzel et al. (2021) identified rootstock cultivar as a key determinant of AMF composition across three vineyards and nine rootstock types. Similarly, metabarcoding analyses of ten grapevine scion-rootstock combinations demonstrated that rootstock genotype significantly shapes AMF diversity and community structure in both the rhizosphere and root compartments (Lailheugue et al., 2024). These findings suggest that rootstock-specific microbiomes regulate plant physiological processes, including nutrient uptake and stress tolerance. However, the underlying mechanisms governing genotype-dependent microbiota interactions remain poorly understood. One hypothesis posits that variations in root exudate profiles among different rootstock genotypes influence microbial recruitment and selection. Root exudates, consisting of a complex mixture of nutrients and signaling molecules, play a crucial role in microbial community structuring and are influenced by both environmental conditions and plant genetic factors (Afridi et al., 2024; Canarini et al., 2019). Thus, distinct genetic characteristics among rootstocks may drive differences in exudate profiles, leading to variations in below-ground microbial associations (Francioli et al., 2024). Strigolactones, a specific class of root exudates, function as both plant hormones and signaling molecules essential for AMF symbiosis. Variations in strigolactone composition and quantity among grapevine rootstocks may influence AMF recruitment and colonization in the rhizosphere (Lailheugue et al., 2024). Indeed, differential production of strigolactones among grapevine rootstocks has been reported (Cochetel et al., 2018; Lailheugue et al., 2023). These findings underscore the decisive role of rootstock genotype in shaping AMF communities, with significant implications for sustainable viticulture. However, despite these insights, research on grapevine root exudates remains limited, constraining our understanding of rootstock-microbe interactions. Addressing this knowledge gap is crucial for optimizing rootstock selection to enhance microbial symbioses and improve resource acquisition, presenting a promising avenue for future research.

6.2. *Effect of AMF inoculation on the soil microbiome*

The introduction of AMF inoculants has the potential to influence existing soil microbial communities, potentially shifting the balance of beneficial microbes. Research has demonstrated that AMF inoculants can alter soil microbial diversity by promoting the growth of other microorganisms, such as nitrogen-fixing bacteria, thereby increasing nutrient availability for the host plant (Basiru et al., 2023). For instance, AMF inoculation has been associated with a significantly reduced soil N and P losses, with the most pronounced reduction occurring in soil NO_3^--N (−32 %), followed by total P (−21 %), available P (−16 %) and N_2O (−10 %) (Qiu et al., 2022), thereby highlighting the supportive role of AMF in nutrient cycling.

However, the introduction of non-native AMF strains may disrupt indigenous AMF communities, particularly when commercial inoculants include strains that are functionally divergent or highly competitive. Studies have reported that the introduction of non-native AMF into soils with pre-existing AMF populations can reduce native AMF abundance, likely due to competitive interactions (Basiru and Hijri, 2022a). Conversely, field inoculation with AMF has been shown to alter microbial community composition in vineyards by reducing the prevalence of certain plant pathogenic fungi with high mycorrhizal growth response, highlighting AMF's role in improving soil and plant health (Torres et al., 2021b).

The potential displacement of native AMF and the resulting alterations in microbial community composition raise concerns about the long-term ecological impacts of AMF inoculation. Such changes could result in unintended consequences, including reduced microbial diversity or shifts in nutrient cycling dynamics, ultimately affecting soil health and vineyard sustainability. Therefore, further research is critical to evaluating the ecological risks and benefits of AMF inoculation in vineyard ecosystems. These studies are essential for ensuring long-term soil productivity, particularly in managed environments where microbiome stability is a key factor. Regarding plant-associated bacterial microbiota, a field trial in southern Italy demonstrated that AMF

inoculation with proven beneficial effects on grapevines did not significantly alter alpha diversity in the rhizosphere or root endosphere of cuttings of 1103-Paulsen (*Vitis berlandieri* × *Vitis rupestris*) (Cardinale et al., 2022); however, AMF inoculation did influence the abundance of specific bacterial taxa, with more pronounced effects observed in the root endosphere, where nearly 20 % of the total bacterial microbiota was affected, compared to only ~2.5 % in the rhizosphere. A recent study conducted in a three-year-old vineyard planted with Merlot (clone 181) grafted onto 3309C rootstock during its first productive year (Fresno, CA, USA) evaluated the effects of AMF inoculation and irrigation management (fully irrigated vs. half irrigated) on the vineyard soil microbiome (Torres et al., 2021b). The study revealed that bacterial and fungal communities in vineyard soils were significantly influenced by both treatments, while edaphic factors had minimal impact. Notably, microbial network analyses indicated that AMF inoculation enhanced positive interactions among vineyard soil microbes, suggesting that the addition of AMF to vineyard systems can have beneficial effects on the soil microbiota by strengthening microbial networks. These improvements may contribute to better soil quality and enhanced crop performance.

6.3. Challenges in production, scalability, and regulatory market integration of AMF inoculants

The adoption of mycorrhizal fungi inoculants in viticulture faces several interconnected challenges related to production, scalability, regulatory hurdles, and market acceptance. The production of AMF inoculants is inherently complex due to their obligate symbiotic nature, requiring a host plant for propagation (Basiru et al., 2020). Unlike other microbial inoculants that can be cultured independently, AMF must be cultivated under conditions that replicate their natural symbiotic environment. This dependency significantly increases production costs and introduces technical challenges in maintaining the viability of AMF propagules (spores, hyphae, and root fragments) during storage and transportation (Salomon et al., 2022a).

Large-scale AMF production methods include pot cultivation in sterilized soil, in vitro systems (root organ cultures and aeroponics), and substrate-based approaches, each with distinct advantages and limitations in terms of cost, scalability, and propagule quality (Kumar et al., 2017). While in vitro systems offer greater environmental control and reduced contamination risk, scaling up remains a challenge. The preservation of propagule viability is critical for inoculant efficacy in the field, with factors such as temperature, humidity, and storage duration significantly influencing performance (Salomon et al., 2022a). Various formulations—including granular, powder, and liquid—are designed to enhance viability and stress tolerance (Delaeter et al., 2024). However, any lapse in storage conditions can compromise colonization success and diminish the benefits of inoculation. Moreover, achieving consistent performance across diverse environmental conditions remains a major obstacle to widespread AMF adoption in commercial viticulture (Salomon et al., 2022b).

Beyond production constraints, regulatory and market barriers further limit the use of AMF inoculants. Regulatory frameworks for microbial inoculants vary widely across countries, often requiring lengthy and costly approval processes. These inconsistencies create significant obstacles for companies seeking to commercialize AMF products, particularly in international markets where compliance with diverse and stringent regulations is necessary (Ghorui et al., 2024). The absence of harmonized standards further complicates trade and market development, introducing uncertainty and delaying innovation in AMF-based solutions (Basiru et al., 2020).

Market acceptance remains another key challenge. Growers often express skepticism regarding AMF inoculants due to inconsistent field performance and variable commercial results. This skepticism is exacerbated by the lack of standardized quality control measures, making it difficult for end-users to assess product efficacy and reliability. Variability in propagule viability, formulation stability, and overall effectiveness across different products further undermines market confidence (Salomon et al., 2022a). Additionally, the absence of standardized methodologies for quantifying AMF colonization and evaluating functional benefits in diverse cropping systems hampers adoption.

Addressing these challenges requires a multifaceted approach. Advancements in bioengineering and storage technologies could improve AMF cultivation efficiency, enhance scalability, and reduce production costs while maintaining high-quality standards. Streamlining regulatory approval processes and establishing clear, consistent guidelines would facilitate market entry and international trade. Furthermore, implementing standardized quality control measures would enhance grower confidence by ensuring product efficacy and reliability. These combined efforts are essential for expanding the use of AMF inoculants in viticulture and broader agricultural applications.

7. AMF in sustainable viticulture: future directions

The role of arbuscular mycorrhizal fungi inoculants in promoting sustainable viticulture is becoming increasingly recognized as vineyards worldwide grapple with the intensifying challenges posed by climate change. The integration of AMF inoculants into vineyard management practices offers a multitude of benefits, including enhanced plant resilience, optimized nutrient uptake, and a reduced reliance on chemical inputs. However, the successful adoption of AMF in viticulture necessitates the resolution of existing challenges while the exploration of new research avenues to maximize their potential.

Moving forward, research into AMF in viticulture should focus on several key areas to enhance their effectiveness and promote their broader adoption:

- Strain selection and customization:
  Identifying and developing AMF strains that are specifically adapted to the unique conditions of individual vineyards, such as soil type, stress type, climate, and grapevine variety, is essential (Holland et al., 2018; Rosa et al., 2020). This tailored approach to AMF inoculation could improve the consistency of results and maximize the benefits of AMF in viticulture. In addition, compatibility testing between AMF strains and grapevine rootstocks plays a critical role in ensuring successful colonization and optimal symbiotic relationships. Rootstock-specific compatibility can influence the efficiency of nutrient uptake, disease resistance, and overall plant health, making this testing a key factor in customizing AMF applications for different vineyard conditions and improving grapevine resilience under abiotic stress.
- Field trials and long-term studies:
  Further long-term field trials are required to evaluate the efficacy of AMF inoculants under realistic vineyard conditions. These trials should assess the long-term impact of AMF on soil health, plant growth, and grape quality, as well as the interactions between introduced AMF strains and native microbial communities.
- Integration with other sustainable practices:
  Future research should also explore the integration of AMF inoculants with other sustainable viticulture practices, such as organic farming, reduced tillage, mulching, and cover cropping (George and Ray, 2023). Combining these practices with AMF inoculation could create synergistic effects to enhance vineyard sustainability and resilience.
- Prediction:
  Future research should leverage advancements in ecological modeling and data analytics to predict AMF performance under various environmental scenarios, including projected climate change conditions. This could involve developing models that integrate data on soil properties, climate variables, grapevine physiology, and AMF community dynamics to forecast the impact of AMF inoculation on vineyard productivity and resilience. Furthermore, the use of meta-

analysis and systematic reviews to synthesize existing data on AMF effects in viticulture can provide valuable insights and identify knowledge gaps.

- Omics technologies and functional ecology:

  The application of omics- (genomics, transcriptomics, proteomics, metabolomics) and meta-omics technologies will provide a deeper understanding of the molecular mechanisms underlying AMF-grapevine interactions. This includes investigating the genes and metabolic pathways involved in nutrient exchange, stress tolerance, and plant defense responses. Combining omics and meta-omics approaches with functional ecology studies will enable researchers to link AMF genetic diversity to specific ecosystem functions and services in vineyards. This knowledge can be used to select and develop AMF inoculants with enhanced functional traits.

- Technology and innovation:

  Advances in biotechnology could play a role in improving the production, scalability, and delivery of AMF inoculants. Research into new methods for producing high-quality AMF inoculants with greater consistency and viability will be critical for meeting the growing demand for biofertilizers in the agricultural sector (Basiru et al., 2020). Additionally, precision agriculture technologies could help optimize the application of AMF inoculants, ensuring they are delivered where they are most needed in the vineyard.

Funding sources

This work was supported by grants from Der Forschungsring des Deutschen Weinbaus (FDW) bei der Deutschen Landwirtschafts-Gesellschaft (DLG), associated with the RhizosphereRebe project (53114301).

CRediT authorship contribution statement

Brenda Valenzuela-Aragon: Writing – review & editing, Writing – original draft, Conceptualization. **Massimiliano Cardinale:** Writing – review & editing. **Eleonora Rolli:** Writing – review & editing. **Laura Rustioni:** Writing – review & editing. **Davide Francioli:** Writing – review & editing, Supervision, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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