



**HAL**  
open science

## Grapevine rootstock and soil microbiome interactions: Keys for a resilient viticulture

Romain Darriaut, Vincent Lailheugue, Isabelle Masneuf-Pomarède, Elisa Marguerit, Guilherme Martins, Stéphane Compant, Patricia Ballestra, Steven Upton, Nathalie Ollat, Virginie Lauvergeat

### ► To cite this version:

Romain Darriaut, Vincent Lailheugue, Isabelle Masneuf-Pomarède, Elisa Marguerit, Guilherme Martins, et al.. Grapevine rootstock and soil microbiome interactions: Keys for a resilient viticulture. Horticulture research, 2022, 9, pp.1-16. 10.1093/hr/uhac019 . hal-03741209

**HAL Id: hal-03741209**

**<https://hal.inrae.fr/hal-03741209>**

Submitted on 1 Aug 2022

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution 4.0 International License

Review Article

# Grapevine rootstock and soil microbiome interactions: Keys for a resilient viticulture

Romain Darriaut<sup>1</sup>, Vincent Lailheugue<sup>1</sup>, Isabelle Masneuf-Pomarède<sup>2,3</sup>, Elisa Marguerit<sup>1</sup>, Guilherme Martins<sup>2,3</sup>, Stéphane Compant<sup>4</sup>, Patricia Ballestra<sup>2</sup>, Steven Upton<sup>3</sup>, Nathalie Ollat<sup>1</sup> and Virginie Lauvergeat<sup>1,\*</sup>

<sup>1</sup>EGFV, Univ. Bordeaux, Bordeaux Sciences Agro, INRAE, ISVV, F-33882, Villenave d'Ornon, France

<sup>2</sup>Université de Bordeaux, UMR Oenologie 1366, INRAE, Bordeaux INP, Bordeaux Sciences Agro, ISVV, Villenave d'Ornon, France

<sup>3</sup>Bordeaux Sciences Agro, 33170 Gradignan, France

<sup>4</sup>AIT Austrian Institute of Technology, Center for Health and Bioresources, Bioresources Unit, Konrad Lorenz Straße 24, Tulln, A-3430, Austria

\*Corresponding author. E-mail: virginie.lauvergeat@inrae.fr

## Abstract

Soil microbiota has increasingly been shown to play an integral role in viticulture resilience. The emergence of new metagenomic and culturomic technologies has led to significant advances in the study of microbial biodiversity. In the agricultural sector, soil and plant microbiomes have been found to significantly improve resistance to environmental stressors and diseases, as well as influencing crop yields and fruit quality thus improving sustainability under shifting environments. Grapevines are usually cultivated as a scion grafted on rootstocks, which are selected according to pedoclimatic conditions and cultural practices, known as terroir. The rootstock connects the surrounding soil to the vine's aerial part and impacts scion growth and berry quality. Understanding rootstock and soil microbiome dynamics is a relevant and important field of study, which may be critical to improve viticulture sustainability and resilience. This review aims to highlight the relationship between grapevine roots and telluric microbiota diversity and activity. In addition, this review explores the concept of core microbiome regarding potential applications of soil microbiome engineering with the goal of enhancing grapevine adaptation to biotic and abiotic stress.

**Keywords:** vine health, terroir, sustainable viticulture, soil diversity, rhizosphere, plant growth-promoting rhizobacteria, microorganisms' interactions, microbiome engineering, grapevine rootstock, Environmental stress

## Introduction

Omics technologies have deepened our knowledge and understanding of telluric and ecosystemic processes; these developments underscore the importance of soil microbiome to plant health. The microbiome has recently been redefined as the microbiota and its theater of activity which combine microbial structural elements such as proteins, peptides, lipids, nucleic acids, polysaccharides, and microbial metabolites as signaling molecules, toxins, (in)organic molecules, and the environmental conditions [1]. Currently, the primary methods used to explore the taxonomic and functional soil microbiome diversity utilize plating methods and computed metagenomics which respectively rely on media composition and high-throughput sequencing [2]. Through the use of these techniques, it has been suggested that plant-associated microorganisms are recruited from the soil microbiota, thus serving as the microorganisms' reservoir of rich microbial diversity [3].

In viticulture, the soil microbiome is now considered as a terroir component that could influence grape berry composition [4]. Studying the microbiome in vineyards, especially fungi and bacteria, is an emerging field of science as it holds the potential to improve grapevine adaptation to climate change and prevention of pathogenic infection. Thus, the study of vineyard microorganisms holds tremendous potential for improving vine resilience and helping vineyards better face increasing environmental stress.

The composition of the soil microbiota, and therefore its related biological activity, is dependent on many factors (e.g. physicochemical characteristics of the soil, plant species and cultivars, climatic conditions, cultural practices ...) [5, 6]. Regardless of the microbiota already present in the soil, the main drivers of the composition of the microbial community associated with the root system (epiphytic and endophytic) are the primary and secondary metabolites exudated by the roots [7]. The composition of the exudates vary depending on

Received: 11 October 2021; Accepted: 17 January 2022; Published: 19 February 2022; Corrected and Typeset: 4 April 2022

© The Author(s) 2022. Published by Oxford University Press on behalf of Nanjing Agricultural University. This is an Open Access article distributed under the terms of the Creative Commons Attribution License (<https://creativecommons.org/licenses/by/4.0/>), which permits unrestricted reuse, distribution, and reproduction in any medium, provided the original work is properly cited.

environmental factors, as well as plant species and cultivars [8, 9], which collectively shape the root microbiome.

Cultivated grapevines are typically grafted plants composed of a scion (*Vitis vinifera* L.), which produces grape berries, and a rootstock (*Vitis* spp., tolerant to phylloxera aphids), which is selected considering pedoclimatic conditions. Grafting is a practice widely used to improve resistance to environmental stresses, yield and quality of the harvested product [10]. The rootstock works as an interface between the soil and the grapevine-associated microbiota, hence modulating the plant holobiont. The scion cultivar is another factor in this complex rootstock  $\times$  scion  $\times$  soil interaction, which may influence the root-associated microbiome. The rootstock's capacity to interact with soil microorganisms differs between genotypes due to their intense breeding and genetic background histories [11]. Rootstocks display contrasting root system in terms of root architecture, as well as synthesis and exudation of metabolites. Some of these compounds are signaling molecules, which shape and attract soil microorganisms. It is therefore essential to understand the role of the rootstock in these interactions that could be further utilized to isolate and promote biofertilizers and bioprotectors. Moreover, the use of rootstocks appears to be an appropriate strategy to conserve wine quality produced by the scion while simultaneously conferring resistance to biotic and abiotic constraints [12]. This review serves to update and expand upon the role of soil microbiome and rootstock dynamics in improving grapevine resilience.

## Close to the roots, a dynamic spot for molecular exchange

### The soil acts as a microbial reservoir for the plant

The grapevine microbiome has been investigated in every compartment using culture-dependent and independent techniques. Independent of soil type and cultivar genotype, the prokaryotic microbiome of *V. vinifera* is mainly composed of *Proteobacteria*, followed by *Firmicutes*, *Actinobacteria*, *Acidobacteria*, and *Bacteroidetes* (Table S1). The grapevine's eukaryotic microbiome consists of *Ascomycota* and *Basidiomycota* on both the above and below-ground parts of the vine (Table S2) while the *Glomeromycota* division is established in the vine roots. Wei et al. (2018) [13] found in their multi-compartment study that *Proteobacteria* and *Firmicutes* are more common to berries, leaves, and grape must, whereas *Bacteroidetes* and *Actinobacteria* adapt better to soil. The authors found that even in the phyllosphere, which is the target of several air-borne pathogens, the relative abundance of bacterial genus and class depends on the plant organs.

The rhizosphere, defined as the tight area of soil enveloping the plant roots, hosts a tremendous number of microorganisms, which interact directly or indirectly with the plant. This soil compartment supports a complex microbiome and is considered as one of the most dynamic ecosystems on Earth. Part of the

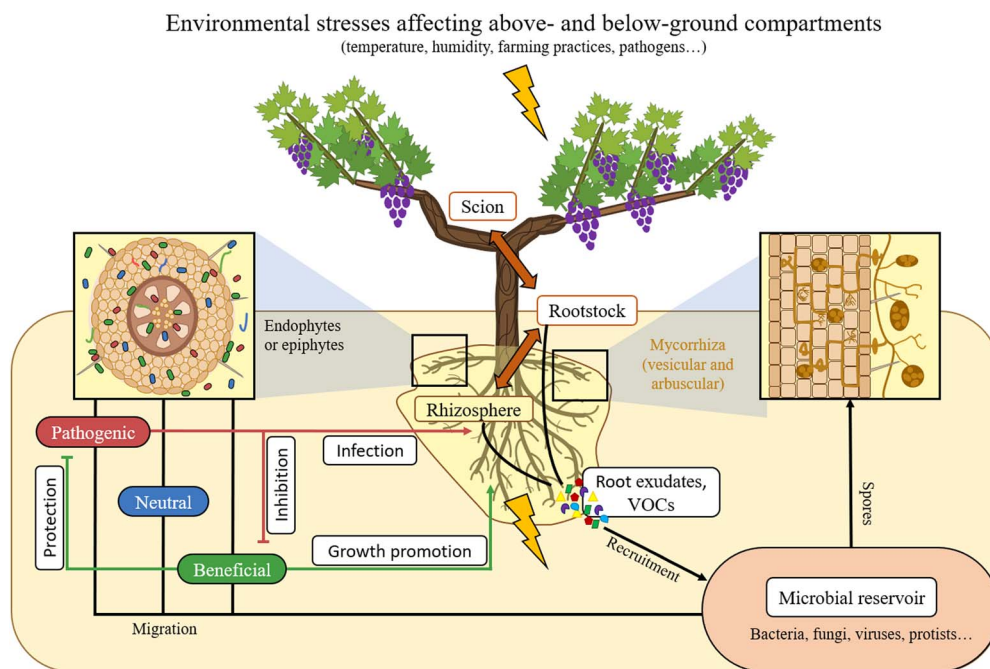
rhizosphere microbiome, also known as rhizomicrobiome, has been shown to provide the host plant with better capacities to adapt to environmental stresses, potentially playing an integral role in plant health [14]. Soil microflora is mainly composed of bacteria, archaea, fungi, protists, and viruses, which have either beneficial, neutral, or pathogenic relationships with the plant (Fig 1). Pathogenic microorganisms participate in the root infection processes whereas beneficial microbiota promote the plant's growth and defense mechanisms [5].

The relative abundance of bacterial and fungal rhizomicrobiome varies with scion/rootstock combination features, soil type, climatic conditions, soil depth, and cultural practices [15–19]. Among fungi, the most encountered taxa in the vineyard soil are principally from the *Ascomycota* and *Basidiomycota* phyla (Table 1). With regard to bacteria, the most abundant genera found in the grapevine rhizosphere belong to *Proteobacteria*, *Actinobacteria*, *Firmicutes*, *Bacteroidetes*, and *Acidobacteria* phyla.

These phyla are keystone taxa that perform a broad range of functions in the soil ecosystem [27]. Zarraonaindia et al. (2015) [18] and Marasco et al. (2018) [15] showed an enrichment of the rhizosphere compared to bulk soil for main phyla such as *Gammaproteobacteria*, *Betaproteobacteria*, and *Actinobacteria*. This increase in bacterial richness might be promoted, through the use of flagella, by chemoattractants (e.g. sugars, amino acids, organic acids, vitamins, phytohormones, flavonoids, terpenes) [28]. Indeed, genes involved in bacterial chemotaxis and motility as well as flagella association, are more present in microbial communities found in root-associated environments, in comparison to bulk soil [29]. Root microbial communities in grapevines were also investigated using 16S/ITS rRNA amplicon sequencing, shotgun metagenomics, and cultivable approaches [30]. It appears that bacterial diversity is lower in the root compartment than in the rhizosphere, and the majority of root-associated bacterial taxa matched the bacteria found in the soil [15, 18], which also occurs with fungal diversity [25, 31], highlighting soil microbial reservoir capacity.

### Soil and rhizosphere: A microbial source of inoculum of grape berry microbiota

Must and wine microorganisms belong mainly to the microbial consortia of grape berries [32]. Many studies support that the main source of these microorganisms is the vineyard soil [18, 33], even though the atmospheric microbiome also influences the composition of fungal and bacteria communities associated with leaves, flowers, and fruits [34]. The root endophytes can shape the microbial community of aboveground organs by changing endophytic microbial loads in grapes [18]. A significant input of soil microorganisms to grapes through epiphytic migration during harvest was also suggested [35]. Contrary to the bacterial component, studies on vineyard



**Figure 1.** Schematic representation of the vine-soil interactions. Environmental stresses afflict both below and above ground compartments of vine. Scion and rootstock communicate through long distance signaling compounds. These signaling pathways modulate the root exudates composition (e.g. VOCs, Volatile Organic Compounds) into the soil microbial reservoir. Microorganisms are therefore chemoattracted and present pathogenic, neutral or beneficial functions towards the vine. They can be either epiphytic and/or endophytic (box on the left), such as mycorrhizal fungi (box on the right).

soil contribution to the yeast community of grapes are scarce. A hypothetical endophytic way of colonization was proposed for the fermentative yeast *Saccharomyces cerevisiae* to be transported from the soil via roots and stems to the surface of the grape berry [36] as shown for bacteria [37]. As for bacteria, vineyard soil appears to be a permanent natural reservoir of non-*Saccharomyces* yeasts via possible contamination of grapes with edaphic microorganisms due to deposit of dust from vineyard soil [32]. Microbial communities on grapes could have the potential to influence grape composition and thus the organoleptic properties of the wine, contributing to a regional terroir. Zarraonaindia et al. (2015) [18] showed that the aboveground bacterial community was significantly influenced by soil edaphic factors such as total carbon, moisture, and soil temperature, which would ultimately impact the quality of grapes due to changes in nutrient availability for the plant. Weather and soil properties influence soil and must microbial diversity that will indirectly impact wine aroma profiles [38]. The contribution of the soil microbial component on the berry and the final wine composition should be evaluated in light of other factors including pedoclimatic, human parameters, rootstock and scion genotypes that define the concept of terroir.

### The impact of telluric microbiota on grape berry composition

In agriculture, plant probiotic bacteria significantly impact crop quality and fruit composition by increasing vitamins, flavonoids, and antioxidants content, among

other benefits [39]. For example, the addition of a Plant-Growth Promoting Bacterium (PGPB) *K. radicincitans* modifies amino acid, sugar, and volatile composition of ripened tomato fruits, thus contributing to a more pleasant-tasting fruit [40]. Aoki et al. (2017) [41] investigated the activation in grape berries of the gene expression of stilbene synthase, a key enzyme in resveratrol synthesis, by a *Bacillus cereus* strain. Native microorganisms can exert an accumulation of volatile compounds in grape berries that could be activated by phytopathogens in the case of volatile precursors of volatile thiols (3MH) responsible for grapefruit aroma in white wines [42]. The production of aroma by grape-associated microorganisms could also directly impact grape berry composition [43].

Grape berry endophytic and epiphytic microorganisms are known to activate metabolic pathways leading to an increase in phenolic compounds or other aroma compounds biosynthesis, as reviewed in Otoguro and Suzuki (2018) [42]. Even if the endophytic berry microbial community is largely derived from the soil, very few studies evaluate the impact of telluric microbiota on berry composition and are mainly focused on arbuscular mycorrhizal fungi (AMF).

By using Biolog™ EcoPlates technology, Ji et al. (2019) [44] showed a correlation between metabolic activities and functional diversity of rhizosphere microbial communities and physicochemical indices of grape berry quality. Association of grapevine with AMF facilitates the synthesis of plant secondary metabolites such as resveratrol, flavonol or anthocyanin, which improve

**Table 1.** Examples of the main bacterial and fungal taxa found in the rhizomicrobiome of grafted and ungrafted grapevine, with their relative abundances and associated sequencing target region

Major bacterial taxa (% of relative abundance), and the associated target region	Major fungal taxa (% of relative abundance), and the associated target region	Studied scion/rootstock combination	Reference
	Root / surrounding soil (ITS1): Ascomycota, Mortierellomycota, Basidiomycota. Relative abundances not provided	Pinot noir cv. ( <i>Vitis vinifera</i> ). Presence or absence of rootstock not provided.	(Liu et al., 2021) [20]
Rhizosphere (16S V4-V5): Acidobacteriota (35%), Proteobacteria (22%), Latescibacteriota (15%), Methylomirabilota (6%), Gemmatimonadota (4%)		Ungrafted 1103P, 140 Ru, 161–49 C, and Kober 5BB cv.	(Dries et al., 2021) [21]
Rhizosphere (16S V3-V4): Proteobacteria (~45%), Bacteroidetes (~15%), Firmicutes (~9%), Actinobacteria (~7%), Acidobacteria (~6%)	Rhizosphere (ITS1): Ascomycota (~47%), Basidiomycota (~15%), Mortierellomycota (~10%)	Ungrafted Malbec ( <i>V. vinifera</i> ) and Cabernet Sauvignon cv.	(Aguilar et al., 2020) [22]
Rhizosphere (16S V4): Proteobacteria (~70%), Actinobacteria (~18%), Bacteroidetes (~8%), Firmicutes (~5%)	Rhizosphere (ITS1): Ascomycota (~50%), Basidiomycota (~45%)	Syrah cv. ( <i>V. vinifera</i> ) grafted on 1103P	(Deyett & Rolshausen, 2020) [23]
Rhizosphere (16S V4): Proteobacteria (27%), Actinobacteria (21%), Acidobacteria (15%), Bacteroidetes (6%)	Rhizosphere (ITS2): Ascomycota (67%), Basidiomycota (16%), Zygomycota (12%)	Tempranillo ( <i>V. vinifera</i> ) cv. grafted on 110R, 140 Ru, 1103P (all above are <i>Vitis berlandieri</i> × <i>V. rupestris</i> ), 41 B ( <i>V. vinifera</i> × <i>V. berlandieri</i> ), and 161–49 C ( <i>V. riparia</i> × <i>V. berlandieri</i> )	(Berlanas et al., 2019) [24]
	Rhizosphere (ITS2): Ascomycota (61%), Basidiomycota (21%)	Tempranillo cv. grafted on 110R	(Martínez-Diz et al., 2019) [25]
Root and Rhizosphere (16S V3-V4): Proteobacteria (53%), Actinobacteria (24%), Bacteroidetes (5%), Chloroflexi (4%), Acidobacteria (4%)		Barbera cv., ungrafted ( <i>V. vinifera</i> ) and grafted on SO4, 420A, 161-49C and 157-11C (all are <i>Vitis riparia</i> × <i>V. berlandieri</i> )	(Marasco et al., 2018) [15]
Rhizosphere (16S V1-V4): Actinobacteria (52%), Proteobacteria (36%), Gemmatimonadetes (2%), Bacteroidetes (~2%)		Pinot noir cv. Presence or absence of rootstock not provided.	(Novello et al., 2017) [26]
Rhizosphere (16S V5-V7): Actinobacteria (47%), Proteobacteria (22%), Bacteroidetes (13%)		Zweigelt cv. clone GU4 ( <i>V. vinifera</i> ) grafted on Kober 5BB ( <i>V. berlandieri</i> × <i>Vitis riparia</i> )	(Samad et al., 2017) [17]

berry quality and plant tolerance to environmental stresses [45]. Wine produced from a vineyard with cv. Sangiovese had better oxidative stability and a significantly higher level of bioactive compounds such as gallic acid, resveratrol, caffeic acid and, quercetin, when treated with a consortium of *Glomus* species plus soil bacteria, fungi and, yeast to a lesser extent, compared to the wine produced by control vines [46]. The protective role of AMF against warming effects on berries on three clones of Tempranillo was shown to improve their antioxidant properties and anthocyanin content [47]. The inoculation of eight ancient grapevine

varieties with a mixture of five AMF species reduced the berry mass and increased the soluble sugars and anthocyanin contents for most of the cultivars [48]. The intensity of these variations on berries was different among the cultivars, suggesting a genotype dependent effect. These studies do not take into account the effect of the rootstock genotype as almost all were performed with ungrafted cultivars. Therefore, the functional potential of the rootstocks to impact the soil microbiota effect on fruit physiology, susceptibility to pathogen and grape berry quality remains to be explored.

**Table 2.** Non-exhaustive list of common biological control products used in the wine-growing industry to apply on the grapevine’s foliar part

Microorganism as active ingredient	Target pathogen	Tradename (manufacturer)	Mode of action	Reference
<i>Bacillus subtilis</i>	<i>Botrytis cinerea</i>	Rhapsody® Serenade Max® (Bayer)	Antimicrobial, eliciting plant defense	(Thomidis et al., 2016) [89]
<i>Bacillus pumilus</i>	<i>Uncinula necator</i>	Sonata® (Bayer)	Antimicrobial, antibiosis	(Serrano et al., 2013) [90]
<i>Streptomyces griseoviridis</i>	<i>Botrytis cinerea</i> , <i>Fusarium</i> , <i>Alternaria</i>	Mycostop® (Verdera)	Competition	(Lahdenperä et al., 1991) [91]
<i>Ampelomyces quisqualis</i>	<i>Uncinula necator</i>	AQ10® (Ecogen)	Competition, antibiosis	(Hofstein et al., 1996) [92]
<i>Trichoderma harzianum</i>	<i>Botrytis cinerea</i>	Trichodex® (Makhteshim-Agan)	Competition	(O’Neill et al., 1996) [93]
<i>T. atroviride</i>	<i>Phaeoacremonium minimum</i> , <i>Phaeoconiella chlamyospora</i> , <i>Botrytis cinerea</i>	Vintec® (Belchim Crop Protection)	Antibiosis	(Pertot et al., 2017) [100], (Pertot et al., 2016) [111]
<i>Saccharomyces cerevisiae</i>	<i>Botrytis cinerea</i>	Julietta® (Agrauxine)	Antibiosis	(São-José et al., 2017) [94]
<i>Metschnikowia fructicola</i>	<i>Botrytis cinerea</i>	Noli® (Koppert Biological Systems)	Antimicrobial, eliciting plant defense	(Sipiczki et al., 2006) [95]
<i>Aureobasidium pullulans</i>	<i>Botrytis cinerea</i>	Botector® (Nufarm)	Competition	(Calvo-Garrido et al., 2019) [96]

**Root-associated and rhizosphere microbiomes are regulated by grapevine genotype and possess useful plant growth-promoting features**

Plant species and genotypes play determinant roles in selecting the telluric microorganisms that will surround the host. As most cultivated grapevines are chimeric plants composed by *V. vinifera* cultivars grafted on American *Vitis* species and hybrids, it is essential to consider the effect of the scion/rootstock combination. To date, only one study analyzed the bacterial community structure in the rhizosphere of 4 cultivars x 4 rootstocks combinations [49]. Authors showed that the diversity of rhizosphere bacteria is impacted first by the cultivar followed by rootstock genotypes, but the effect was dependent on the diversity index used. The distinct genetic component and capacity to produce photosynthate components of the cultivars might alter the exudate composition and could explain this difference in bacterial diversity. Bacterial microbiomes in the rhizosphere of five different rootstocks grafted with the same Barbera cv. were significantly different in terms of richness, diversity, and community networking, within the same vineyard [15]. Biget et al. (2021) [50] demonstrated through their multi-site analysis within a vineyard that vine age was one of the main drivers of bacterial and fungal root endophytes, even though the genetic background of rootstock was not investigated. Considering this, Berlanas et al. (2019) [24] highlighted that rootstock genotype had a greater impact than millesimal or sampling date on bacterial and fungal microbiome structure in the rhizosphere exclusively in mature vineyards. Predominant amounts of *Proteobacteria* and *Actinobacteria* were found in all samples of rhizosphere, but bacterial genera varied depending on the rootstocks. With regard to fungi,

the Ascomycota and Basidiomycota phyla varied greatly among rootstocks. Specific genera were affiliated to distinct rootstock genotypes, such as *Geopyxis* for the 110R rootstock, or *Clonostachys* for 1103P and 140 Ru rootstocks.

Regarding functional screening of indigenous isolates, Samad et al. (2017) [17] and Marasco et al. (2018) [15] confirmed the significant enrichment of *Proteobacteria* in grapevine root tissues (Kober 5BB rootstock, and ungrafted/grafted Barbera cv. on 402A, 157-11C, SO4, 161-49C, respectively), while *Actinobacteria* and *Bacteroidetes* remained at relatively constant levels in both rhizosphere and root compartments. Conversely, *Gemmatimonadetes* and *Firmicutes* were less abundant in roots than the surrounding soils. In both studies, Plant-Growth Promoting (PGP) activities of strains belonging to the *Enterobacteriaceae* and *Pseudomonadaceae* families were tested for production of hydrogen cyanide, ACC deaminase (ACCd), siderophores, indole acetic acid (IAA), and for phosphate solubilization. It has been shown by Marasco et al. (2018) [15] that PGP functional genes were conserved in both the rhizosphere and root endosphere despite selecting different bacterial communities, and therefore that the frequencies of these PGP traits were not dependent on the rootstock genotype. For Syrah cv. grafted on 1103P rootstock, Deyett and Rolshausen (2020) [23] observed a different enrichment composed mainly of *Rhizobium*, *Devosia*, *Streptomyces*, and *Pseudomonas* genera in the rhizosphere. This study also revealed that fungal and bacterial richness in roots accounted for 64% of the amplicon sequence variants (ASVs) found in the rhizosphere and soil compartments. *Streptomyces* and *Pseudomonas* genera are often associated with PGP activities but also inhibit the colonization of pathogens in grapevine woods [51]. Using a disruptive approach based

on metaproteomic, Bona *et al.* (2019) [52] confirmed that the high biochemical activity (*i.e.* phosphorus metabolic processes and regulation of nitrogen compounds) in the rhizosphere of ungrafted *V. vinifera* cv. Pinot noir was largely attributed to bacteria belonging to the *Proteobacteria* phylum. To another extent, D'Amico *et al.*, (2018) [53], observed a depletion and sometimes a total absence of potassium (K) solubilizing bacterial members from the *Micrococcaceae*, *Comamonadaceae*, *Cytophagacea*, *Sphingomonadaceae*, *Rhizobiaceae*, *Xanthomonadaceae*, and *Microbacteriaceae* in the rhizosphere and roots of 1103P rootstock, whereas they were detected in 5BB rootstock with the same Lambrusco cultivar. This dysregulation of the functional microbiome was linked to the problem of K absorption observed in the studied *Vitis berlandieri* × *Vitis rupestris* rootstocks. Except for AMF, more studies have been focused on the bacterial communities of grapevine roots and rhizosphere compared to studies of fungal communities. Given the importance of rhizosphere functions, it is relevant and crucial to examine the link between rootstock agronomic features and rhizosphere microbiome traits.

### Case of the famous symbiont, the arbuscular mycorrhizal fungi

AMF symbioses are endomycorrhizal associations with obligate biotrophic fungi belonging to the *Glomeromycota* division. This is the most frequently encountered mycorrhizal form encompassing grapevines as approximately 80% of terrestrial plants are able to associate with AMF [37, 38, 39]. AMF symbioses are mainly induced in soil where P availability is low, and play a key role in providing P and N to plant root cells, which can be attributed to increased soil exploration surface due to extra-radicular hyphae proliferation [55]. In return, fungi receive photosynthetically fixed carbon assimilated from plant cells. AMF do not only affect plant growth traits, water and nutrient uptake, but also protect their host from pathogens. Since the first description of two AMF species by Tulasne *et Tulasne* in 1845, more than 260 *Glomeromycota* species have been discovered [56]. The most common species identified using culture-dependent approaches are included in the *Glomeraceae* order such as *G. intraradices* or *G. mosseae*. New technologies based on molecular approaches provided deeper insights about AMF diversity in vineyards by sequencing ribosomal Internal Transcribed Spacers (ITS) or their small subunit (SSU) rRNA fragments [57, 58]. Drain *et al.* (2019) [59] proposed a standardized protocol to study AMF communities from root samples of vines. The authors amplified the D2 domain from the Large Subunit Region (LSU) and revealed the predominance of the *Rhizophagus* and *Glomus* genera coupled to eight other genera from the *Glomeromycota* division. However, a clear picture of how AMF diversity colonizes grapevine roots in different parts of the world is incomplete, especially since the classification of AMFs remains controversial

and molecular techniques for their identification have not been standardized [60].

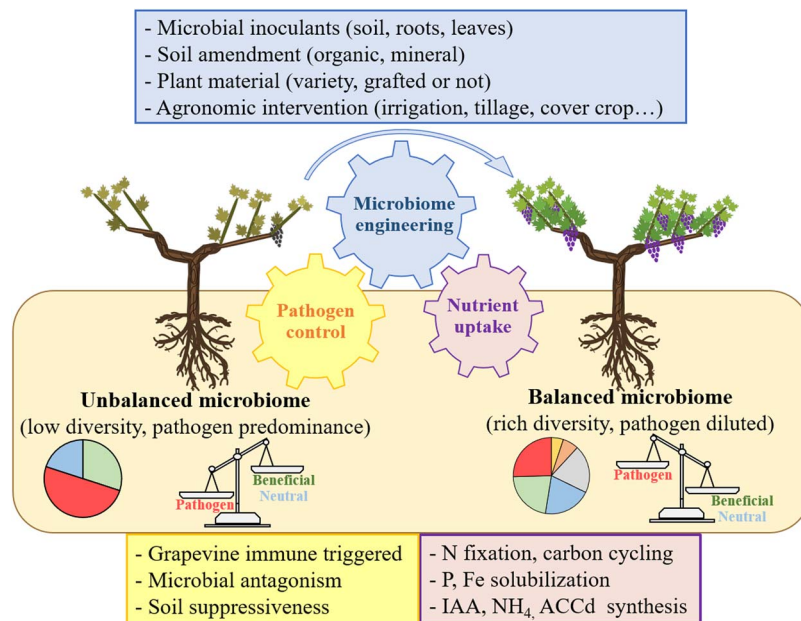
Although it is assumed that sustainable practices enhance the spore abundance and diversity of AMF [61], they are influenced by several factors including edaphic parameters and grapevine genotype. Moukarzel *et al.* (2021) [62] demonstrated a significant difference in the AMF community associated with nine rootstocks grafted or not with Pinot noir cv. using denaturing gradient gel electrophoresis (DGGE) and trap cultures. Nerva *et al.* (2021) identified the influence of the rootstock genotype in activating distinct defense pathways by young cuttings, grafted on either 1103P or SO4 rootstock, when treated with *Rhizophagus irregularis* and *F. mosseae* [63]. While studies of citrus have shown scions to be more influential to the AMF community structure than on rootstock [64], the role that scion genotype could play in AMF diversity in grapevines has yet to be explored. The selection of rootstock and scion genotype are important in determining grapevine capacity to form mycorrhizal associations that could enhance host mineral uptake and increase grapevine sustainability.

### Microbiome engineering, a tool to promote plant health

#### The concept of compositional and functional core microbiome

The concept of core microbiome relies on operational taxonomic units (OTUs), and to some extent on ASVs, shared between different individuals of the same species, as was first proposed in humans [65]. Despite its complexity, the concept of core microbiome is gaining support and several definitions have been made with regard to either microbiome's functionality, temporal stability, taxonomy, plant-adapted, or ecology [66]. Most of the time, core microbiome is referred to as the compositional core based on taxonomy or functional core. Indeed, this core concept is not only considered as the microorganism's diversity, but also as the core interactions that are used to maintain an individuals' health, and on a larger scale the ecosystem. Crops and plants in general, are associated with distinct soil microbiomes which are influenced, independent of temporal factors, by biotic and abiotic components [67].

Swift *et al.* (2021) [68] suggested, subsequently to a multi-compartment analysis submitted to irrigation stress, that the core microbiome is quite conserved in the different analyzed rootstocks (cv. Chambourcin grafted on 1103P, 3309C, and SO4). The different irrigations lead to microbial changes in aerial compartments such as different amounts of *Acetobacterales* and *Saccharomycetes* in berries which could affect wine quality. Carbone *et al.* (2021) [69] recently pointed out this shift in fungal communities under three distinct irrigation regimes (25%, 50%, or 100% of field capacity) with 22.3% of fungal OTUs shared in roots among those conditions, while



**Figure 2.** Schematic representation of grapevine health affected by soil microbiome services, pathogen control (yellow box) and nutrient uptake (purple box), which are enhanced by microbiome engineering (blue box). Unbalanced microbiome comes along with a low microbial diversity with predisposition to pathogen predominance, while high microbial diversity is found in balanced microbiome and inhibits the pathogen capacity to afflict grapevine.

66.8% and 55.6% OTUs were found to be common in rhizosphere, and bulk soil compartments, respectively. Despite neglecting the role of rootstock, Liu & Howell (2021) [20] unveiled the fungal core microbiome in Merlot cv. which displays 32.75% of shared OTUs between roots and soil, fluctuating in abundance across the season. This supports the idea that the grapevine core microbiome relies on the composition of microbial soil reservoir, which is recruited differently according to the rootstock.

Core functions such as biogeochemical processes in the soil appear to be related to taxonomically distinct patterns but with similar metabolic functions, hence confirming that the theater of microbiota activity can be distinguished into taxonomy and functioning that interact with the terroir [38]. Terroir is a broad concept that can be described as the components driving the aromas and wine typicity within a defined geographical region with specific soil topology, and viticultural practices including cultivar variety [70]. As discussed previously, different rootstocks are able to be associated with different microbial communities sharing similar functional traits [15, 53]. Functional redundancy is indeed the idea that more than one taxon can exert the same function within a microbial community [71]. Unravelling the core species recruited through rootstocks could be a powerful tool in determining microbiome responses to environmental constraints. Therefore, microbiome functioning must be understood in order to predict plant health in response to various stresses, even though microbiome-plant partnerships are complex belowground-based interactions linked with the soil.

### Microbial diversity as a biological marker for grapevine fitness

Many biotic and abiotic stresses occur in vineyards and can lead to plant decline or dieback if not managed properly. Grapevine dieback afflict viticulture worldwide and can be defined as a pluriannual decrease in vine productivity linked to its sudden premature or gradual death due to environmental causes and/or agronomic practices [72]. Despite evidence of negative impact on microbial communities in young replanted vines due to long-term monoculture and intense replanting management, replacing the dead vines with young vines remains sometimes the only solution to palliate this problematic dieback [73, 74]. Grapevines are a perennial plant which require significant time-consuming cultivation; at least three years are needed for the new plant to harbor productive grapes [75]. To this end, accelerating the growth of young cuttings with plant growth-promoting rhizobacteria (PGPR) or AMF may be an interesting approach to compensate for the lack of productivity during the beginning of replantation, however this approach has not been widely studied in vineyards [76]. However, this strategy may increase the incidence and severity of grapevine trunk diseases (GTDs) symptoms due to the predisposition of GTD to affect such vineyards managed using training and pruning techniques which promote vine growth [77]. On that account, microbiome engineering which is an actual trend which encompasses crops and numerous cultivars [78], appears to be a promising strategy against environmental stressors. Microbiome engineering often refers to a set of tools which strengthen the soil microbiome and hence the plant-associated microbiome through nutrient



**Table 3.** List of inocula used for their biological control properties on grapevine and applied on the soil or root system

Target pathogen (Disease)	Inoculum identification (Origin)	Observations	Plant material (Type of application)	Reference
Botrytis cinerea (Gray mold)	<i>Bacillus subtilis</i> PTA-271, (Grapevine rhizosphere)	Systemic resistance. Accumulation of stilbenic phytoalexins, <i>trans</i> -resveratrol and $\epsilon$ -viniferin in leaves and berries.	Field, 15 years-old cv. Chardonnay-41B (Soil drenching)	(Aziz et al., 2016) [107]
	<i>Pseudomonas fluorescens</i> PTA-CT2, and (Grapevine stem)			
	<i>Pantoea agglomerans</i> PTA-AF2 (Grapevine leaf)			
	<i>P. agglomerans</i> Pa-AF2, (Grapevine leaf)	Local and systemic resistance. Early oxidative burst and stilbenic phytoalexins ( <i>trans</i> -resveratrol and <i>trans</i> - $\epsilon$ -viniferin) accumulation in leaves.	<i>In vitro</i> , 4 weeks-old cv. Chardonnay (Root dipping)	(Verhagen et al., 2011) [104]
Botrytis cinerea (Gray mold)	<i>Acinetobacter lwoffii</i> Al-113, (Grapevine roots)			
	<i>Bacillus subtilis</i> Bs271, and (Grapevine rhizosphere)			
	<i>P. fluorescens</i> PfCT2 (Grapevine stem)			
Botrytis cinerea (Gray mold)	<i>B. subtilis</i> PTA-271, <i>A. lwoffii</i> PTA-113, <i>P. agglomerans</i> PTA-AF1 and PTA-AF2, and <i>P. fluorescens</i> PTA-268 and PTA-CT2 (All isolated from grapevine rhizosphere)	Systemic resistance. Accumulation of chitinase and $\beta$ -1,3-glucanase in leaves and berries.	Field, 10 years-old cv. Chardonnay-41B (Soil drenching)	(Magnin-Robert et al., 2007) [105]
	<i>Burkholderia</i> sp. BE17 and BE24	Systemic resistance. H <sub>2</sub> O <sub>2</sub> accumulation and upregulations of PR5 and PR10 in leaves.	<i>In vitro</i> , 4 weeks-old cv. Chardonnay (Root dipping)	(Esmaeel et al., 2020) [106]
Botrytis cinerea (Gray mold)	<i>Paraburkholderia phytofirmans</i> PsJN	Systemic resistance. H <sub>2</sub> O <sub>2</sub> accumulation and upregulations of PR1, PR2, PR5, WRKY, and JAZ in leaves.	<i>In vitro</i> , 4 weeks-old cv. Chardonnay (Root dipping)	(Miotto-Vilanova et al., 2016) [107]
	<i>Plasmopara viticola</i> (Downy mildew) and <i>B. cinerea</i> (Gray mold)	<i>Pseudomonas fluorescens</i> PTA-CT2 (Grapevine rhizosphere)	Systemic resistance. <i>P. viticola</i> : Stilbenes accumulation. Upregulations of PR1, PR2, GST, ACO, and HSR. <i>B. cinerea</i> : Stilbenes and resveratrol accumulation. Upregulations of ACO, PR1, GST genes and HSR downregulation.	Greenhouse, 2 years-old cv. Pinot noir-5BB and Solaris30-5BB (Soil drenching)
<i>E. necator</i> (Powdery mildew)	<i>T. harzianum</i> 5R (Citrus rhizosphere, <i>Trichoderma viride</i> F-01812 (sugarcane soil), and F-01951 (forest soil), and <i>T. asperellum</i> F-01769 (soil)	Systemic resistance. Increase in total phenol contents, chitinase, and $\beta$ -1,3-glucanase in leaves.	Field, 8 years-old cv. Centennial Seedless (Soil drenching)	(Sawant et al., 2020) [109]
<i>Phaeoconiella chlamydospora</i> (Esca)	<i>Pythium oligandrum</i> Oth-2, Oth-3, Sto-1, Oth-4, Sto-7, and Sto-11 (Grapevine rhizosphere)	Systemic resistance. Oligandrin synthesis <i>in vitro</i> . PR10, <i>Glu</i> , <i>Gst</i> , and <i>Lox</i> upregulations.	Greenhouse, 4 months-old cv. Cabernet Sauvignon (Collar inoculation)	(Yacoub et al., 2016) [110]
<i>Neofusicoccum parvum</i> (Botryosphaeria dieback)	<i>B. subtilis</i> PTA-271 (Grapevine rhizosphere), and <i>Trichoderma atroviride</i> SC1 (Hazelnut wood)	Decrease of salicylic acid (SA)-dependent defenses compared to symptomatic non plants. LOX9, PR2, PAL, and STS upregulation in leaves.	Culture chamber, 1 year-old cv. Chardonnay and Tempranillo. Soil drenching ( <i>B. subtilis</i> PTA-271) and wound painting ( <i>T. atroviride</i> SC1).	(Leal et al., 2021) [111]
<i>Agrobacterium tumefaciens</i> (Crown gall)	<i>Pseudomonas kilonensis</i> Sn48, (Grapevine roots) and <i>P. agglomerans</i> Sa14 (Wild-grapevine stem)	Systemic resistance. Stilbenic phytoalexins ( <i>trans</i> -resveratrol, <i>trans</i> -piceid, and $\epsilon$ -viniferin) global accumulation in leaves, roots, and stems. PR1, PR2, and PR4 genes upregulation in leaves.	Greenhouse, 4 weeks-old cv. Chardonnay (Root dipping)	(Asghari et al., 2020) [112]

**Table 4.** List of inocula used for their beneficial effect on grapevine submitted to abiotic stress and applied on the soil or root system

Abiotic stress (Factor to counter)	Inoculum identification (Origin)	Observations	Plant material (Type of application)	Reference
Arsenic	<i>Bacillus licheniformis</i> Rt4M10, <i>Micrococcus luteus</i> Rz2M10 and <i>P. fluorescens</i> Rt6M10 (Grapevine root endosphere and rhizosphere)	Reduction of arsenic toxicity indicators with enhanced ascorbate peroxidase activity ( <i>B. licheniformis</i> ) and increased peroxidase activity ( <i>Micrococcus luteus</i> and <i>P.</i> <i>fluorescens</i> )	Greenhouse, 2 years-old cv. Malbec (Leaf sprayed and stem-based inoculation)	(Funes Pinter et al., 2018) [117]
Drought	<i>Acinetobacter</i> and 2 <i>Pseudomonas</i> spp. (Grapevine root endosphere)	Higher tolerance to water deficit by maintaining photosynthetic activity and growth which was rootstock dependent. Positive effect on evapotranspiration and stomatal conductance.	Greenhouse, 1 year-old cv. SO4, 420A, 5BB (Roots dipping) Field, 1 year-old cv. Barbera (Roots dipping)	(Rolli et al., 2015) [118]
Drought	<i>Glomus mosseae</i> (not specified)	Higher tolerance to water deficit by maintaining photosynthetic activity and growth which was rootstock dependent. Positive effect on evapotranspiration and stomatal conductance. Increase of phosphorus content in leaves.	Greenhouse, 1 year-old cv. Cabernet-Sauvignon grafted on 110R, 41B, 1103P, 5BB, 44–53 Malegue, 140R and 101–14MGt (Soil inoculation)	(Nikolaou et al., 2003) [119]

uptake and pathogen control (Fig 2). Among these tools, agricultural practices (e.g. cover crop, irrigation, tillage), soil amendment, and plant material choice (i.e. grafted rootstock or not) can interfere with microbial diversity which is considered as a key biomarker in plant protection and growth strategies [79]. The greatest microbial diversity was found in organic vineyards compared to conventional ones [80] but with a lower soil microbial biomass [81]. This difference in diversity may be related to the abundance of organic matter which are a rich source of exogenous microbial inoculants which can colonize the vines. A meta-analysis made by Karimi et al. (2020) [82] highlighted the effect of viticultural practices on soil microbiological diversity and showed that tillage, absence of cover crop, and mineral fertilization all contributed significantly to reductions in soil biodiversity. Microbiome inoculation is another interesting tool that directly modify the soil and/or rootstock microbiome functionalities and compositions.

### Biological control agents (BCAs) as limited but efficient disease management strategies

Nurseries have proposed to winegrowers the possibility of inoculating rootstocks with specific microorganisms such as AMF prior to planting, in an effort to improve grapevine resilience to abiotic and biotic stresses. Biological control provides tools for disease management which are partly based on soil microbial properties that promote plant health and fruit quality. This strategy called biocontrol, has been exploited recently as an alternative to synthetic or chemical pesticides [83]. The most common BCAs in viticulture are used in spray application and are partly efficient, compared to the synthetic solutions,

against powdery, downy mildew or gray mold, caused by *Erysiphe necator*, *Plasmopara viticola*, and *Botrytis cinerea* respectively [84]. Currently, commercial microbial fungicides sprayed on the grapevine aerial part can be derived from bacteria, yeast, and multicellular fungi (Table 2). Those listed microorganisms are present in a variety of habitats worldwide, and can naturally be found in vineyard soils [85–88], hence comforting the vineyard soil studies for BCA screening.

Usually, spray applications are applied on the aerial part of the vine, targeting the leaves and berries where the first symptoms of the disease occur. However, the vine architecture and dense foliage may reduce the efficiency of the product, allowing the pathogen to sporulate on the untreated part of the crop. One solution to counteract the pathogen growth in viticulture is to leverage the microbe-associated molecular patterns (MAMPs) from beneficial microbes through belowground host-specific receptors, which prime grapevine immune response [97]. This strategy is referred to as induced systemic resistance (ISR) and can benefit both the aboveground parts of the plant and the roots via BCAs when applied to the soil or grapevine root system (Table 3). ISR leads to the production of phytoalexins and/or pathogenesis-related (PR) proteins in the distal parts. Phytoalexins are low weight metabolites synthesized after microbial recognition and signaling in plant cells acting as defense compounds. In grapevines, these molecules (Table 3) are mainly stilbenes and encompasses *trans*-resveratrol, *trans*- $\epsilon$ -viniferin, and its derivative *trans*-piceid [98]. Moreover, it has been shown that the BCA oomycete *Pythium oligandrum* inoculated at

the root level can modulate the transcriptome of the grapevine but also of the *Phaeoconiella chlamydospora* virulence factors, a GTD ascomycota fungus, even when the two microorganisms are not in direct contact [99]. Among the GTDs, black-foot and Petri diseases are the most common and are present in nurseries and young vineyards. Their symptoms in fields include overall reduced growth, dysregulation in the budbreak and sprouting, with chlorotic leaves and necrosis on the rootstock [100]. *Trichoderma* spp., *Bacillus*, and *Pseudomonas*-based commercialized products as well as two potential BCAs (i.e. *P. oligandrum* Po 37, *Streptomyces* sp. E1 and R4) reduced the Black-foot and Petri diseases by dipping the roots before planting under field conditions [101]. Stempien et al. (2020) unveiled the grapevine defense activation triggered by *Trichoderma atroviride* (T-77 and USPP T1) drenching and its colonization on rootstock cultivars 110R, US 8–7, 1103P. It appeared that the level of expression of genes such as *VvSTS* and *VvChit4c* encoding proteins involved in stilbene synthesis and chitinase, respectively, was dependent on the rootstock genotype and *Trichoderma* strain used. Recently Jaarsveld et al. (2021) [102] showed the higher colonization capacity by six *Trichoderma* products on graftlings (Sauvignon blanc cv. Grafted onto Ramsey) basal ends compared to middle or root tip part, even though *Trichoderma* spp. treatments were not sufficient to prevent fungal infections. Clear evidence of the biocontrol effects was observed *in vitro*, in greenhouse and in field (Table 3). These findings suggest that preventive application by soil drenching or root inoculation could be a promising strategy for disease management since the molecular mechanisms underlying the biocontrol effects of the inoculum are deciphered.

### Microbiome can enhance abiotic stress tolerance

By mitigating abiotic stresses, microbiome × rootstock interactions could be a relevant way to contribute to adaptation in the global climate change context. Up to now, the mechanisms developed by the plants to recruit their microbiomes in response to specific abiotic stresses remain poorly understood.

The root microbiome can enhance water deficit tolerance by acting in hormone regulation or by increasing plant antioxidant activity [113]. To this end, trends in microorganisms' biomass, diversity, and activity under water deficit conditions have been explored [113, 114]. Exopolysaccharides (EPS) allow beneficial microbes to efficiently colonize the rhizosphere by increasing the percentage of stable soil aggregates and thus by increasing water and nutrient uptake [114]. It was also demonstrated that microorganisms from more fluctuating environments have a higher functional acclimatization [115]. In addition, plants benefit from their associated microbiome to tolerate water deficit, especially when the microbiome has been previously exposed to water deficit with the host plant in years before [116]. In grapevines, few studies

have been made on the microbiome impact on abiotic stress [30]. However all the microorganisms tested were originated from root endosphere compartment and some of them vary in their effect depending on the rootstock genotype (Table 4). This comforts the hypothesis that microbiota from resistant rootstock in stressed environment might be an interesting strategy to investigate.

In addition, several microorganisms isolated from grapevine roots were studied for their capacity to synthesize protective molecules that might alleviate abiotic stresses. Carotenoids, known for their antioxidant activities and as precursors of abscisic acid (ABA), were produced by *Microbacterium imperial* Rz19M10, *Kocuria erythromyxa* Rt5M10, and *Terribacillus saccharophilus* Rt17M10 [120] but also by *Bacillus licheniformis* Rt4M10 [121]. The metabolism of ABA could be modulated in the advantage of inoculated grapevines with arbuscular mycorrhizal symbiosis [45]. Among the protective molecules, the melatonin allows to counteract the negative effects of abiotic stresses and it has been shown that inoculated grapevines with *Bacillus amyloliquefaciens* SB-9 [122] or with *Pseudomonas fluorescens* RG11 [123] accumulate more melatonin. Additionally to bacterial endophytes, water deficit stress can be alleviated by the presence of AMF thanks to their external mycelium that increase water use efficiency even though there is no current evidence of direct water transfer to the plant [54].

Besides the issues surrounding water deficit, the problem of soil salinization impacts a large percentage of irrigated vineyards worldwide [124]. AMF are known to improve growth related traits in saline conditions. Khalil (2013) [125] demonstrated on three rootstocks genotypes (1103P, Harmony, and Dogridge) that AMF addition contributes to increase plant height, stem diameter, leaf area, total leaf number, and total dry weight even if the effects were not significant. The total carbohydrates, leaf free proline content, and total leaf chlorophyll content were higher in inoculated seedlings than in uninoculated ones, suggesting a higher osmoprotection coupled to a photosynthesis maintenance. Moreover, mycorrhizal inoculation tends to decrease the Na and Cl concentrations while increasing P and K leaves content. A relevant choice of rootstock with mycorrhizal inoculation could be one way to avoid salinity problems in a vineyard.

The complexity of the interactions between the plant, the microbiome, and the surrounding environment is an issue that must be overcome to understand the beneficial associations between plants and microbes. It appears more relevant to isolate plant growth-promoting microbe (PGPM) that can promote tolerance to a specific abiotic stress from environments in which this stress occurs [126]. It could be outstanding to study the plasticity of the PGPM to rootstock × scion × interactions at the field level, hence the importance of including the microbiome in grapevine breeding programs [127]. As suggested for the tree species, association of rootstocks with different

beneficial microbiota could be a relevant way to share the benefits of the microbiota from one individual to another to get a “microbial complementarity” [128].

### Are soil microbial inoculum a safe and relevant process to increase grapevine resilience?

The establishment and persistence of the BCAs in the soil and root compartments remain one of the most important concerns in microbial inoculant preparation [129]. Although the transfer of inoculation to different climatic regions can be a success, the effect may not be the same depending on pedoclimatic features [130]. Aside from these technical aspects, the BCAs legislation among EU, USA, and worldwide markets are quite different but remain important for their biosafety which are based on molecular identification coupled to pathogenicity, toxicological, and 37°C-growth tests [131]. While the biosafety issue has always been evaluated for human healthcare and plant health, the mass application of PGPM in the environment is never considered during the BCAs development. What if the PGPM application provokes soil or plant microbiome dysbiosis and lately its degradation [132]? What if a BCA turns out to become pathogenic, due to horizontal gene transfer from other surrounding microbes or because of the evolution or speciation?

In grapevine wood tissues, Haidar et al. (2021) [132] unveiled the synergistic effect of some bacterial strains with the basidiomycete *Fomitiporia mediterranea* involved in esca complex, to degrade wood components. The interesting part is the capacity of some of these bacterial strains to inhibit the pathogen growth *in vitro*, while having cellulose and xylan degradation properties. In grapevines, colonization process by inoculating beneficial endophytes such as *Paraburkholderia phytofirmans* strain PsJN or strains of *Enterobacter ludwigii* and *Pantoea vagans* have been studied in young plants [134, 135], and among the PGPR inoculated on grapevine roots, they are mainly composed from *Pseudomonas*, *Bacillus*, *Pantoea*, and *Burkholderia* genera (Table 3). However, depicting the PGPR inoculation impact on the soil microbiome remains a challenge and should combine both culture-dependent and independent approaches. Indeed, exogenous microorganisms might affect soil quality negatively by modifying soil capacity to process bio-geochemical cycles and hence, its potential to promote vine growth.

Soil exhibits the natural ability to suppress disease through its microbiome composition which is enhanced by agricultural processes that positively influence microbial diversity [136, 137]. For instance, Nerva et al. (2019) [138] investigated the microbial profile of both Esca-symptomatic and asymptomatic soils which suggested that higher proportions of *Curvularia*, *Coprinopsis*, *Bacillus*,

and *Streptomyces* genera could suppress disease symptoms. These studies further support the idea that bulk soils are a major source of inoculum for pathogens. Microbial transplant is now assumed in medical research as a solution to modulate the human microbiota coupled to therapeutic effects [139]. While not conducted in a vineyard, Siegel-Hertz et al. (2018) [140] used soil transplants from suppressive soil to show inhibiting effects on Fusarium wilt conducive soils. Exclusive bacterial and fungal genera were found in Fusarium wilt-suppressive soils compared to conducive soils which suggest that microbiome transplant could be an efficient and promising way to promote microbiome diversity. This strategy within a vineyard could counteract the microbiome dysbiosis and the problematic effect of the inoculum survival since the soils possess quite similar abiotic features.

Biocontrol is assumed to be less efficient in disease management compared to chemical and synthetic products. One biotechnology-based tool that must be mentioned for increasing the microorganisms' efficiency in pathogen control is the protoplast fusion technique, which is mainly studied for genetic transformation and somatic hybridization. This approach is quite difficult in grapevines and has recently been used for whole grapevine generation from protoplasts [141]. Protoplast fusion technique is also used in PGP and biocontrol bacteria to merge distinct traits. For instance, Gaziea et al. (2020) [142] attempted to merge, the biocontrol ability of *Bacillus thuringiensis* 1977 against *Meloidogyne* spp. and the PGP capacity of *Pseudomonas aeruginosa* in grapevine seedlings and successfully controlled the root-knot nematode while promoting the plant growth. While this approach has not been tested on the field, it has already been considered against root-knot nematodes [143] and remains an interesting solution for BCA or biofertilizer products. *Trichoderma* spp., which are one of the most famous BCAs worldwide, have also been subjected to capacity enhancement for soil-borne disease suppressiveness [144]. Strains engineered via protoplast fusion are not affiliated to genetically modified organisms' regulations since this technique is a form of natural homologous recombination [145], hence giving the possibility for BCAs to have more positive impacts on grapevine health.

### Conclusions and future prospects

Altogether, these findings demonstrate that the grapevine is able, via rootstock and scion genotypes, to select distinct but potentially beneficial microorganisms close to the roots. Although there is no consensus regarding the choice of hypervariable regions to amplify and sequence (Table 1), it is still possible to make comparable taxonomic descriptions between studies at the phyla level. However, it may be quite difficult to compare at the genera or species level since bias, in addition to “universal primers” choice, can occur until data processing [146]. The rhizosphere and root-associated microbiome, which

are a balance between stress and fitness, would be relevant biological indicators of plant health status. The rhizosphere could be considered as an extended root phenotype, presented by Dawkins (1982) [147], which is a trait that may also reflect the agronomic properties of the rootstock as well as its health status. To this end, soil microbial diversity could explain many dysbiosis and symbiosis observed in the grapevine organs since most of them are recruited from the surrounding soil. Until now, no research of soil virome in vineyards has been done even though it is known that the viruses are playing important roles in ecological processes and microorganism evolution [148], whereas the grapevine associated virome has been well investigated in leaf and trunk tissues [149].

Given increasing environmental constraints, improving viticulture sustainability is currently a major challenge. One important area of study to improve sustainability includes better understanding soil microbiome functionalities and its effects on the grapevine metabolism and agronomic responses. Based on the current literature, the soil microbiome could offer new engineering solutions to palliate intensive phytosanitary use and climate change issues. To this end, molecular and microbial dialogues between the scion and the soil through the rootstock must be considered. The core microbiome of the grape should be preserved as it represents a sensitive balance for the plant protection, growth, nutrition, and health.

## Acknowledgements

This work received support from the FranceAgrimer/CNIV and was funded as part of the program “Plan National Dépérissement du Vignoble” within the project Vitirhizobiome.

## Conflict of interests statement

The authors declare no competing interests.

## Supplementary data

Supplementary data is available at *Horticulture Research Journal* online.

## References

- Berg G, Rybakova D, Fischer D et al. Microbiome definition re-visited: old concepts and new challenges. *Microbiome*. 2020;**8**:103.
- Sarhan MS, Hamza MA, Youssef HH, Patz S. Culturomics of the plant prokaryotic microbiome and the dawn of plant-based culture media – a review. *J Adv Res*. 2019;**19**:15–27.
- Hardoim PR, van Overbeek LS, Berg G et al. The hidden world within plants: ecological and evolutionary considerations for defining functioning of microbial endophytes. *Microbiol Mol Biol Rev*. 2015;**79**:293–320.
- White RE. The value of soil knowledge in understanding wine terroir. *Front Environ Sci*. 2020;**8**:1–6.
- Compant S, Samad A, Faist H, Sessitsch A. A review on the plant microbiome: ecology, functions, and emerging trends in microbial application. *J Adv Res*. 2019;**19**:29–37.
- Fierer N. Embracing the unknown: disentangling the complexities of the soil microbiome. *Nat Rev Microbiol*. 2017;**15**:579–90.
- Pascale A, Proietti S, Pantelides IS, Stringlis IA. Modulation of the root microbiome by plant molecules: the basis for targeted disease suppression and plant growth promotion. *Front Plant Sci*. 2020;**10**:1–23.
- Ghatak A, Schindler F, Bachmann G et al. Root exudation of contrasting drought-stressed pearl millet genotypes conveys varying biological nitrification inhibition (BNI) activity. *Biol Fertil Soils*. 2021. <https://doi.org/10.1007/s00374-021-01578-w>.
- Herz K, Dietz S, Gorzolja K et al. Linking root exudates to functional plant traits. *PLoS One*. 2018;**13**:e0204128.
- Williams B, Ahsan MU, Frank MH. Getting to the root of grafting-induced traits. *Curr Opin Plant Biol*. 2021;**59**:101988.
- Marín D, Armengol J, Carbonell-Bejerano P et al. Challenges of viticulture adaptation to global change: tackling the issue from the roots. *Aust J Grape Wine Res*. 2021;**27**:8–25.
- Ollat N, Bordenave L, Tandonnet JP et al. Grapevine rootstocks: origins and perspectives. *Acta Hort*. 2016;**1136**:11–22.
- Wei Y, Wu Y, Yan Y-Z et al. High-throughput sequencing of microbial community diversity in soil, grapes, leaves, grape juice and wine of grapevine from China. *PLoS One*. 2018;**13**:e0193097.
- Qu Q, Zhang Z, Peijnenburg WJGM et al. Rhizosphere microbiome assembly and its impact on plant growth. *J Agric Food Chem*. 2020;**68**:5024–38.
- Marasco R, Rolli E, Fusi M et al. Grapevine rootstocks shape underground bacterial microbiome and networking but not potential functionality. *Microbiome*. 2018;**6**:3.
- Mezzasalma V, Sandionigi A, Guzzetti L et al. Geographical and cultivar features differentiate grape microbiota in northern Italy and Spain vineyards. *Front Microbiol*. 2018;**9**:1–13.
- Samad A, Trognitz F, Compant S et al. Shared and host-specific microbiome diversity and functioning of grapevine and accompanying weed plants. *Environ Microbiol*. 2017;**19**:1407–24.
- Zarraonaindia I, Owens SM, Weisenhorn P et al. The soil microbiome influences grapevine-associated microbiota. *MBio*. 2015;**6**:1–10.
- Nerva L, Moffa L, Giudice G et al. Microscale analysis of soil characteristics and microbiomes reveals potential impacts on plants and fruit: vineyard as a model case study. *Plant Soil*. 2021;**462**:525–41.
- Liu D, Howell K. Community succession of the grapevine fungal microbiome in the annual growth cycle. *Environ Microbiol*. 2021;**23**:1842–57.
- Dries L, Bussotti S, Pozzi C et al. Rootstocks shape their microbiome—bacterial communities in the rhizosphere of different grapevine rootstocks. *Microorganisms*. 2021;**9**:822.
- Aguilar MO, Gobbi A, Browne PD et al. Influence of vintage, geographic location and cultivar on the structure of microbial communities associated with the grapevine rhizosphere in vineyards of San Juan Province, Argentina. *PLoS One*. 2020;**15**:e0243848.
- Deyett E, Rolshausen PE. Endophytic microbial assemblage in grapevine. *FEMS Microbiol Ecol*. 2020;**96**:fiaa053.

24. Berlanas C, Berbegal M, Elena G et al. The fungal and bacterial rhizosphere microbiome associated with grapevine rootstock genotypes in mature and young vineyards. *Front Microbiol.* 2019;**10**:1142.
25. Martínez-Diz M D P, Andrés-Sodupe M, Bujanda R et al. Soil-plant compartments affect fungal microbiome diversity and composition in grapevine. *Fungal Ecol.* 2019;**41**:234–44.
26. Novello G, Gamalero E, Bona E et al. The rhizosphere bacterial microbiota of *Vitis vinifera* cv. Pinot noir in an integrated pest management vineyard. *Front Microbiol.* 2017;**8**.
27. Banerjee S, Schlaeppi K, van der Heijden MGA. Keystone taxa as drivers of microbiome structure and functioning. *Nat. Rev. Microbiol.* 2018;**16**:567–76.
28. Musilova L, Ridl J, Polivkova M et al. Effects of secondary plant metabolites on microbial populations: changes in community structure and metabolic activity in contaminated environments. *Int J Mol Sci.* 2016;**17**:1205.
29. Trivedi P, Leach JE, Tringe SG et al. Plant-microbiome interactions: from community assembly to plant health. *Nat Rev Microbiol.* 2020;**18**:607–21.
30. Pacifico D, Squartini A, Crucitti D et al. The role of the endophytic microbiome in the grapevine response to environmental triggers. *Front Plant Sci.* 2019;**10**:1256.
31. Zahid MS, Li D, Javed HU et al. Comparative fungal diversity and dynamics in plant compartments at different developmental stages under root-zone restricted grapevines. *BMC Microbiol.* 2021;**21**:317.
32. Ramírez M, López-Piñeiro A, Velázquez R et al. Analysing the vineyard soil as a natural reservoir for wine yeasts. *Food Res Int.* 2020;**129**:108845.
33. Belda I, Ruiz J, Esteban-Fernández A et al. Microbial contribution to wine aroma and its intended use for wine quality improvement. *Molecules.* 2017;**22**:189.
34. Abdelfattah A, Sanzani SM, Wisniewski M et al. Revealing cues for fungal interplay in the plant-air interface in vineyards. *Front Plant Sci.* 2019;**10**:1–10.
35. Martins G, Lauga B, Miot-Sertier C et al. Characterization of epiphytic bacterial communities from grapes, leaves, bark and soil of grapevine plants grown, and their relations. *PLoS One.* 2013;**8**:e73013.
36. Mandl K, Schieck J, Silhavy-Richter K et al. Through the vine to the stem and skins of grapes. *Ithaka J.* 2015;349–55.
37. Compant S, Mitter B, Colli-Mull JG et al. Endophytes of grapevine flowers, berries, and seeds: identification of cultivable bacteria, comparison with other plant parts, and visualization of niches of colonization. *Microb Ecol.* 2011;**62**:188–97.
38. Griggs RG, Steenwerth KL, Mills DA et al. Sources and assembly of microbial communities in vineyards as a functional component of winegrowing. *Front Microbiol.* 2021;**12**:673810.
39. Jiménez-Gómez A, Celador-Lera L, Fradejas-Bayón M, Rivas R. Plant probiotic bacteria enhance the quality of fruit and horticultural crops. *AIMS Microbiol.* 2017;**3**:483–501.
40. Berger B, Baldermann S, Ruppel S. The plant growth-promoting bacterium *Kosakonia radicincitans* improves fruit yield and quality of *Solanum lycopersicum*. *J Sci Food Agric.* 2017;**97**:4865–71.
41. Aoki T, Aoki Y, Ishiai S et al. Impact of *Bacillus cereus* NRKT on grape ripe rot disease through resveratrol synthesis in berry skin. *Pest Manag Sci.* 2017;**73**:174–80.
42. Otoguro M, Suzuki S. Status and future of disease protection and grape berry quality alteration by micro-organisms in viticulture. *Lett Appl Microbiol.* 2018;**67**:106–12.
43. Verginer M, Leitner E, Berg G. Production of volatile metabolites by grape-associated microorganisms. *J Agric Food Chem.* 2010;**58**:8344–50.
44. Ji W, Han K, Cai Y et al. Characterization of rhizosphere bacterial community and berry quality of Hutai no. 8 (*Vitis vinifera* L.) with different ages, and their relations. *J Sci Food Agric.* 2019;**99**:4532–9.
45. Torres N, Goicoechea N, Zamarreño AM, Carmen Antolín M. Mycorrhizal symbiosis affects ABA metabolism during berry ripening in *Vitis vinifera* L. cv. Tempranillo grown under climate change scenarios. *Plant Sci.* 2018;**274**:383–93.
46. Gabriele M, Gerardi C, Longo V, Lucejko JJ. The impact of mycorrhizal fungi on Sangiovese red wine production: phenolic compounds and antioxidant properties. *LWT - Food Sci Technol.* 2016;**72**:310–6.
47. Torres N, Goicoechea N, Morales F, Antolín MC. Berry quality and antioxidant properties in *Vitis vinifera* cv. Tempranillo as affected by clonal variability, mycorrhizal inoculation and temperature. *Crop Pasture Sci.* 2016;**67**:961.
48. Antolín MC, Izurdiaga D, Urmeneta L et al. Dissimilar responses of ancient grapevines recovered in Navarra (Spain) to arbuscular mycorrhizal symbiosis in terms of berry quality. *Agronomy.* 2020;**10**:473.
49. Vink SN, Dini-Andreote F, Höfle R et al. Interactive effects of scion and rootstock genotypes on the root microbiome of grapevines (*Vitis* spp. L.). *Appl Sci.* 2021;**11**:1615.
50. Biget M, Mony C, Aubry M et al. The drivers of vine-plant root microbiota endosphere composition include both abiotic and plant-specific factors. *OENO One.* 2021;**55**:299–315.
51. Niem JM, Billones-Baaijens R, Stodart B, Savocchia S. Diversity profiling of grapevine microbial endosphere and antagonistic potential of endophytic *Pseudomonas* against grapevine trunk diseases. *Front Microbiol.* 2020;**11**:1–19.
52. Bona E, Massa N, Novello G et al. Metaproteomic characterization of *Vitis vinifera* rhizosphere. *FEMS Microbiol Ecol.* 2018;**95**:1–16.
53. D'Amico F, Candela M, Turroni S et al. The rootstock regulates microbiome diversity in root and rhizosphere compartments of *Vitis vinifera* cultivar Lambrusco. *Front Microbiol.* 2018;**9**:1–11.
54. Trouvelot S, Bonneau L, Redecker D, van Tuinen D. Arbuscular mycorrhiza symbiosis in viticulture: a review. *Agron Sustain Dev.* 2015;**35**:1449–67.
55. Popescu GC. Arbuscular mycorrhizal fungi—an essential tool to sustainable vineyard development : a review. *Curr Trends Nat Sci.* 2016;**5**:107–16.
56. Likar M, Regvar M. Arbuscular mycorrhizal fungi and dark septate endophytes in grapevine: the potential for sustainable viticulture? In: *Mycorrhiza - Function, Diversity, State of the Art*. Springer International Publishing, 2017,275–89.
57. Lanfranco L, Fiorilli V, Gutjahr C. Partner communication and role of nutrients in the arbuscular mycorrhizal symbiosis. *New Phytol.* 2018;**220**:1031–46.
58. Öpik M, Davison J. Uniting species- and community-oriented approaches to understand arbuscular mycorrhizal fungal diversity. *Fungal Ecol.* 2016;**24**:106–13.
59. Van Geel M, Erik Verbruggen MDB, Rennes G, Bart Lievens OH. High soil phosphorus levels overrule the potential benefits of organic farming on arbuscular mycorrhizal diversity in northern vineyards. *Agric Ecosyst Environ.* 2017;**248**:144–52.
60. Schreiner RP. Depth structures the community of arbuscular mycorrhizal fungi amplified from grapevine (*Vitis vinifera* L.) roots. *Mycorrhiza.* 2020;**30**:149–60.

61. Drain A, Bonneau L, Recorbet G, van Tuinen D. Characterization of arbuscular mycorrhizal communities in roots of vineyard plants. In: Reinhardt D, Sharma A, eds. *Methods in Rhizosphere Biology Research*. Springer: Singapore, 2019;27–34.
62. Kryukov AA, Gorbunova AO, Machs EM et al. Perspectives of using Illumina MiSeq for identification of arbuscular mycorrhizal fungi. *Vavilov J Genet Breed*. 2020;**24**:158–67.
63. Radić T, Likar M, Hančević K et al. Occurrence of root endophytic fungi in organic versus conventional vineyards on the Croatian coast. *Agric Ecosyst Environ*. 2014;**192**:115–21.
64. Moukarzel R, Ridgway HJ, Guerin-Laguette A, Jones EE. Grapevine rootstocks drive the community structure of arbuscular mycorrhizal fungi in New Zealand vineyards. *J Appl Microbiol*. 2021;**131**:2941–56.
65. Nerva L, Giudice G, Quiroga G et al. Mycorrhizal symbiosis balances rootstock-mediated growth-defence tradeoffs. *Biol Fertil Soils*. 2022;**58**:17–34.
66. Song F, Pan Z, Bai F et al. The scion/rootstock genotypes and habitats affect arbuscular mycorrhizal fungal community in citrus. *Front Microbiol*. 2015;**6**:1–11.
67. Turnbaugh PJ, Ley RE, Hamady M et al. The human microbiome project. *Nature*. 2007;**449**:804–10.
68. Risely A. Applying the core microbiome to understand host-microbe systems. *J Anim Ecol*. 2020;**89**:1549–58.
69. Thakur MP, Geisen S. Trophic regulations of the soil microbiome. *Trends Microbiol*. 2019;**27**:771–80.
70. Swift JF, Hall ME, Harris ZN et al. Grapevine microbiota reflect diversity among compartments and complex interactions within and among root and shoot systems. *Microorganisms*. 2021;**9**:92.
71. Carbone MJ, Alaniz S, Mondino P et al. Drought influences fungal community dynamics in the grapevine rhizosphere and root microbiome. *J Fungi*. 2021;**7**:686.
72. Van Leeuwen C, Roby J-P, De Ressaiguier L. Soil-related terroir factors: a review. *OENO One*. 2018;**52**:173–88.
73. Louca S, Polz MF, Mazel F et al. Function and functional redundancy in microbial systems. *Nat Ecol Evol*. 2018;**2**:936–43.
74. Riou C, Agostini D, Aigrain P, Barthe M. Action plan against declining vineyards: an innovative approach. *BIO Web Conf*. 2016;**7**:01040.
75. Liu Q, Wang S, Li K et al. Responses of soil bacterial and fungal communities to the long-term monoculture of grapevine. *Appl Microbiol Biotechnol*. 2021;**105**:7035–50.
76. Westphal A, Browne GT, Schneider S. Evidence for biological nature of the grape replant problem in California. *Plant Soil*. 2002;**242**:197–203.
77. Sanmartin C, Venturi F, Taglieri I, Ferroni G. Restoration of an old vineyard by replanting of missing vines: effects on grape production and wine quality. *Agrochimica*. 2017;**61**:154–63.
78. Rolli E, Marasco R, Saderi S et al. Root-associated bacteria promote grapevine growth: from the laboratory to the field. *Plant Soil*. 2017;**410**:369–82.
79. Hrycan J, Hart M, Bowen P et al. Grapevine trunk disease fungi: their roles as latent pathogens and stress factors that favour disease development and symptom expression. *Phytopathol Mediterr*. 2020;**59**:395–424.
80. Orozco-Mosqueda M D C, Rocha-Granados MDC, Glick BR, Santoyo G. Microbiome engineering to improve biocontrol and plant growth-promoting mechanisms. *Microbiol Res*. 2018;**208**:25–31.
81. Berg G, Köberl M, Rybakova D et al. Plant microbial diversity is suggested as the key to future biocontrol and health trends. *FEMS Microbiol Ecol*. 2017;**93**:1–9.
82. Vega-Avila AD, Gumiere T, Andrade PAM et al. Bacterial communities in the rhizosphere of *Vitis vinifera* L. cultivated under distinct agricultural practices in Argentina. *Antonie Van Leeuwenhoek*. 2015;**107**:575–88.
83. Ostandie N, Giffard B, Bonnard O et al. Multi-community effects of organic and conventional farming practices in vineyards. *Sci Rep*. 2021;**11**:11979.
84. Karimi B, Cahurel J-Y, Gontier L et al. A meta-analysis of the ecotoxicological impact of viticultural practices on soil biodiversity. *Environ Chem Lett*. 2020;**18**:1947–66.
85. Pertot I, Giovannini O, Benanchi M, Caffi T. Combining biocontrol agents with different mechanisms of action in a strategy to control *Botrytis cinerea* on grapevine. *Crop Prot*. 2017;**97**:85–93.
86. Dagostin S, Schärer H-J, Pertot I, Tamm L. Are there alternatives to copper for controlling grapevine downy mildew in organic viticulture? *Crop Prot*. 2011;**30**:776–88.
87. Angeli D, Pellegrini E, Pertot I. Occurrence of *Erysiphe necator* *Chasmothecia* and their natural parasitism by *Ampelomyces quisqualis*. *Phytopathology*. 2009;**99**:704–10.
88. Andreazza R, Pieniz S, Okeke B, Camargo FA. Evaluation of copper resistant bacteria from vineyard soils and mining waste for copper biosorption. *Brazilian J Microbiol*. 2011;**42**:66–74.
89. Nally MC, Pesce VM, Maturano YP et al. Biocontrol of *Botrytis cinerea* in table grapes by non-pathogenic indigenous *Saccharomyces cerevisiae* yeasts isolated from viticultural environments in Argentina. *Postharvest Biol Technol*. 2012;**64**:40–8.
90. Salunkhe VP, Sawant IS, Banerjee K et al. Biodegradation of profenofos by *Bacillus subtilis* isolated from grapevines (*Vitis vinifera*). *J Agric Food Chem*. 2013;**61**:7195–202.
91. Thomidis T, Pantazis S, Konstantinou K. Evaluation of serenade max to control fruit rot of grapes. *J Agric Sci*. 2016;**8**:212.
92. Serrano L, Manker D, Brandi F, Cali T. The use of *Bacillus subtilis* QST 713 and *Bacillus pumilus* QST 2808 as protectant fungicides in conventional application programs for black leaf streak control. *Acta Hort*. 2013;**986**:149–55.
93. Lahdenperä M-L, Simon E, Uoti J. Mycostop—a novel biofungicide based on *Streptomyces* bacteria. In: *Developments in agricultural and managed forest ecology*. Vol. **23**. 1991;258–63.
94. Hofstein R, Daoust RA, Aeschlimann JP. Constraints to the development of biofungicides: the example of “AQ10”, a new product for controlling powdery mildews. *Entomophaga*. 1996;**41**:455–60.
95. O’neill TM, Elad Y, Shtuenberg D, Cohen A. Control of grapevine Grey Mould with *Trichoderma harzianum* T39. *Biocontrol Sci Tech*. 1996;**6**:139–46.
96. Pertot I, Prodorutti D, Colombini A, Pasini L. *Trichoderma atroviride* SC1 prevents *Phaeoemoniella chlamydospora* and *Phaeoacremonium aleophilum* infection of grapevine plants during the grafting process in nurseries. *BioControl*. 2016;**61**:257–67.
97. São-José C, Santos MA, Schmitt MJ. Viruses of wine-associated yeasts and bacteria. In: König H, Uden G, Fröhlich J, eds. *Biology of Microorganisms on Grapes, in Must and in Wine*. Springer International Publishing, 2017;133–54.
98. Sipiczki M. *Metschnikowia* strains isolated from botrytized grapes antagonize fungal and bacterial growth by iron depletion. *Appl Environ Microbiol*. 2006;**72**:6716–24.
99. Calvo-Garrido C, Roudet J, Aveline N et al. Microbial antagonism toward *botrytis* bunch rot of grapes in multiple field tests using

- one bacillus ginsengihumi strain and formulated biological control products. *Front Plant Sci.* 2019;**10**:105.
100. Héloir M-C, Adrian M, Brulé D et al. Recognition of elicitors in grapevine: from MAMP and DAMP perception to induced resistance. *Front Plant Sci.* 2019;**10**:1–17.
  101. Jeandet P, Hébrard C, Deville M-A et al. Deciphering the role of phytoalexins in plant-microorganism interactions and human health. *Molecules.* 2014;**19**:18033–56.
  102. Yacoub A, Magnin N, Gerbore J et al. The biocontrol root-oomycete, *Pythium oligandrum*, triggers grapevine resistance and shifts in the transcriptome of the trunk pathogenic fungus, *Phaeomoniella chlamydospora*. *Int J Mol Sci.* 2020;**21**:6876.
  103. Gramaje D, Armengol J. Fungal trunk pathogens in the grapevine propagation process: potential inoculum sources, detection, identification, and management strategies. *Plant Dis.* 2011;**95**:1040–55.
  104. del Pilar Martínez-Diz M, Díaz-Losada E, Andrés-Sodupe M et al. Field evaluation of biocontrol agents against black-foot and petri diseases of grapevine. *Pest Manag Sci.* 2021;**77**:697–708.
  105. Stempien E, Jean R, Pierron G, Jaarsveld WJVAN. Host defence activation and root colonization of grapevine rootstocks by the biological control fungus *Trichoderma atroviride*. *Phytopathol Mediterr.* 2020;**59**:615–26.
  106. Jaarsveld WJ, Halleen F, Bester MC et al. Investigation of *Trichoderma* species colonization of nursery grapevines for improved management of black foot disease. *Pest Manag Sci.* 2021;**77**:397–405.
  107. Aziz A, Verhagen B, Magnin-Robert M et al. Effectiveness of beneficial bacteria to promote systemic resistance of grapevine to gray mold as related to phytoalexin production in vineyards. *Plant Soil.* 2016;**405**:141–53.
  108. Verhagen B, Trotel-Aziz P, Jeandet P et al. Improved resistance against *Botrytis cinerea* by grapevine-associated bacteria that induce a prime oxidative burst and phytoalexin production. *Phytopathology.* 2011;**101**:768–77.
  109. Magnin-Robert M, Trotel-Aziz P, Quantinet D et al. Biological control of *Botrytis cinerea* by selected grapevine-associated bacteria and stimulation of chitinase and  $\beta$ -1,3 glucanase activities under field conditions. *Eur J Plant Pathol.* 2007;**118**:43–57.
  110. Esmaeel Q, Jacquard C, Sanchez L et al. The mode of action of plant associated Burkholderia against grey mould disease in grapevine revealed through traits and genomic analyses. *Sci Rep.* 2020;**10**:19393.
  111. Miotto-Vilanova L, Jacquard C, Courteaux B et al. Burkholderia phytofirmans PsJN confers grapevine resistance against *Botrytis cinerea* via a direct antimicrobial effect combined with a better resource mobilization. *Front Plant Sci.* 2016;**7**:1–15.
  112. Lakkis S, Trotel-Aziz P, Rabenoelina F et al. Strengthening grapevine resistance by *Pseudomonas fluorescens* PTA-CT2 relies on distinct defense pathways in susceptible and partially resistant genotypes to downy mildew and gray mold diseases. *Front Plant Sci.* 2019;**10**:1–18.
  113. Sawant IS, Wadkar PN, Ghule SB et al. Induction of systemic resistance in grapevines against powdery mildew by *Trichoderma asperelloides* strains. *Australas Plant Pathol.* 2020;**49**:107–17.
  114. Yacoub A, Gerbore J, Magnin N et al. Ability of *Pythium oligandrum* strains to protect *Vitis vinifera* L., by inducing plant resistance against *Phaeomoniella chlamydospora*, a pathogen involved in esca, a grapevine trunk disease. *Biol Control.* 2016;**92**:7–16.
  115. Leal C, Richet N, Guise J-F et al. Cultivar contributes to the beneficial effects of *Bacillus subtilis* PTA-271 and *Trichoderma atroviride* SC1 to protect grapevine against *Neofusicoccum parvum*. *Front Microbiol.* 2021;**12**:1–17.
  116. Asghari S, Harighi B, Ashengroph M et al. Induction of systemic resistance to *agrobacterium tumefaciens* by endophytic bacteria in grapevine. *Plant Pathol.* 2020;**69**:827–37.
  117. de la Fuente Cantó C, Simonin M, King E et al. An extended root phenotype: the rhizosphere, its formation and impacts on plant fitness. *Plant J.* 2020;**103**:951–64.
  118. Caddell DF, Deng S, Coleman-Derr D. Role of the plant root microbiome in abiotic stress tolerance. In: *Seed Endophytes*. Springer International Publishing, 2019,273–311.
  119. Hawkes CV, Keitt TH. Resilience vs. historical contingency in microbial responses to environmental change. *Ecol Lett.* 2015;**18**:612–25.
  120. Zolla G, Badri DV, Bakker MG et al. Soil microbiomes vary in their ability to confer drought tolerance to *Arabidopsis*. *Appl Soil Ecol.* 2013;**68**:1–9.
  121. Funes Pinter I, VictoriaSalomon M, Berli F et al. Plant growth promoting rhizobacteria alleviate stress by AsIII in grapevine. *Agric Ecosyst Environ.* 2018;**267**:100–8.
  122. Rolli E, Marasco R, Viganì G et al. Improved plant resistance to drought is promoted by the root-associated microbiome as a water stress-dependent trait. *Environ Microbiol.* 2015;**17**:316–31.
  123. Nikolaou N, Angelopoulos K, Karagiannidis N. Effects of drought stress on mycorrhizal and non-mycorrhizal cabernet sauvignon grapevine, grafted onto various rootstocks. *Exp Agric.* 2003;**39**:241–52.
  124. Salomon MV, Purpora R, Bottini R, Piccoli P. Rhizosphere associated bacteria trigger accumulation of terpenes in leaves of *Vitis vinifera* L. cv. Malbec that protect cells against reactive oxygen species. *Plant Physiol Biochem.* 2016;**106**:295–304.
  125. Cohen AC, Dichiara E, Jofré V et al. Carotenoid profile produced by bacillus licheniformis Rt4M10 isolated from grapevines grown in high altitude and their antioxidant activity. *Int J Food Sci Technol.* 2018;**53**:2697–705.
  126. Jiao J, Ma Y, Chen S et al. Melatonin-producing endophytic bacteria from grapevine roots promote the abiotic stress-induced production of endogenous melatonin in their hosts. *Front Plant Sci.* 2016;**7**:1–13.
  127. Ma Y, Jiao J, Fan X et al. Endophytic bacterium *Pseudomonas fluorescens* RG11 may transform tryptophan to melatonin and promote endogenous melatonin levels in the roots of four grape cultivars. *Front Plant Sci.* 2017;**07**:1–15.
  128. Aragüés R, Medina ET, Zribi W et al. Soil salinization as a threat to the sustainability of deficit irrigation under present and expected climate change scenarios. *Irrig Sci.* 2015;**33**:67–79.
  129. Khalil HA. Influence of vesicular-arbuscula mycorrhizal fungi (*glomus* spp.) on the response of grapevines rootstocks to salt stress. *Asian J Crop Sci.* 2013;**5**:393–404.
  130. Rodriguez RJ, Henson J, Van Volkenburgh E et al. Stress tolerance in plants via habitat-adapted symbiosis. *ISME J.* 2008;**2**:404–16.
  131. Gómez-Bellot MJ, Ortuño MF, Nortes PA et al. Protective effects of *Glomus iranicum* var. *tenuihypharum* on soil and *Viburnum tinus* plants irrigated with treated wastewater under field conditions. *Mycorrhiza.* 2015;**25**:399–409.



132. Bettenfeld P, Fontaine F, Trouvelot S et al. Woody plant declines. What's wrong with the microbiome? *Trends Plant Sci.* 2020;**25**: 381–94.
133. Verbruggen E, Heijden MGA, Rillig MC, Kiers ET. Mycorrhizal fungal establishment in agricultural soils: factors determining inoculation success. *New Phytol.* 2013;**197**:1104–9.
134. Chibeba AM, Kyei-Boahen S, Guimarães MF et al. Feasibility of transference of inoculation-related technologies: a case study of evaluation of soybean rhizobial strains under the agro-climatic conditions of Brazil and Mozambique. *Agric Ecosyst Environ.* 2018;**261**:230–40.
135. Velivelli SLS, De Vos P, Kromann P et al. Biological control agents: from field to market, problems, and challenges. *Trends Biotechnol.* 2014;**32**:493–6.
136. Keswani C, Prakash O, Bharti N et al. Re-addressing the biosafety issues of plant growth promoting rhizobacteria. *Sci Total Environ.* 2019;**690**:841–52.
137. Haidar R, Yacoub A, Vallance J et al. Bacteria associated with wood tissues of esca-diseased grapevines: functional diversity and synergy with *Fomitiporia mediterranea* to degrade wood components. *Environ Microbiol.* 2021;**23**:6104–21.
138. Compant S, Reiter B, Sessitsch A et al. Endophytic colonization of *Vitis vinifera* L. by plant growth-promoting bacterium *Burkholderia* sp. strain PsJN. *Appl Environ Microbiol.* 2005;**71**: 1685–93.
139. López-Fernández S, Compant S, Vrhovsek U et al. Grapevine colonization by endophytic bacteria shifts secondary metabolism and suggests activation of defense pathways. *Plant Soil.* 2016;**405**:155–75.
140. Cook RJ. Plant health management: pathogen suppressive soils. In: *Encyclopedia of Agriculture and Food Systems*. Vol. 4. 2014, 441–55.
141. Richards A, Estaki M, Úrbez-Torres JR et al. Cover crop diversity as a tool to mitigate vine decline and reduce pathogens in vineyard soils. *Diversity.* 2020;**12**:128.
142. Nerva L, Zanzotto A, Gardiman M et al. Soil microbiome analysis in an ESCA diseased vineyard. *Soil Biol Biochem.* 2019;**135**:60–70.
143. Smits LP, Bouter KEC, de Vos WM et al. Therapeutic potential of fecal microbiota transplantation. *Gastroenterology.* 2013;**145**: 946–53.
144. Siegel-Hertz K, Edel-Hermann V, Chapelle E et al. Comparative microbiome analysis of a fusarium wilt suppressive soil and a fusarium wilt conducive soil from the Châteaurenard region. *Front Microbiol.* 2018;**9**:1–16.
145. Bertini E, Tornielli GB, Pezzotti M, Zenoni S. Regeneration of plants from embryogenic callus-derived protoplasts of Garganega and Sangiovese grapevine (*Vitis vinifera* L.) cultivars. *Plant Cell Tissue Organ Cult.* 2019;**138**:239–46.
146. Gaziea SM, Shereen MAH, Laila HF, Eman EHS. Efficiency of biological control of root-knot nematodes in infected grapevines seedling by genetic improved bacteria. *Plant Arch.* 2020;**20**: 951–61.
147. Abdel-Salam MS, Ameen HH, Soliman GM et al. Improving the nematicidal potential of *Bacillus amyloliquefaciens* and *Lysinibacillus sphaericus* against the root-knot nematode *Meloidogyne incognita* using protoplast fusion technique. *Egypt J Biol Pest Control.* 2018;**28**:31.
148. Lakhani HN, Vakharia DN. Influence of protoplast fusion in *Trichoderma* Spp. on controlling some soil borne diseases. *J Plant Pathol Microbiol.* 2016;**7**.
149. Zhang Y-X, Perry K, Vinci VA et al. Genome shuffling leads to rapid phenotypic improvement in bacteria. *Nature.* 2002;**415**: 644–6.
150. Pollock J, Glendinning L, Wisedchanwet T, Watson M. The madness of microbiome: attempting to find consensus “best practice” for 16S microbiome studies. *Appl Environ Microbiol.* 2018;**84**:e02627–17.
151. Dawkins R, Barnett SA. *The Extended Phenotype*. Vol. 18. Oxford Univ Press; 1982:253–9.
152. Pratama AA, van Elsas JD. The ‘neglected’ soil virome – potential role and impact. *Trends Microbiol.* 2018;**26**:649–62.
153. Martelli GP. An overview on grapevine viruses, viroids, and the diseases they cause. In: *Grapevine Viruses: Molecular Biology, Diagnostics and Management*. Springer International Publishing, 2017,31–46.
154. Vitulo N, Lemos WJF Jr, Calgaro M et al. Bark and grape microbiome of *Vitis vinifera*: influence of geographic patterns and agronomic management on bacterial diversity. *Front Microbiol.* 2019;**9**.
155. Faist H, Keller A, Hentschel U, Deeken R. Grapevine (*Vitis vinifera*) crown galls host distinct microbiota. *Appl Environ Microbiol.* 2016;**82**:5542–52.
156. Portillo M D C, Franquès J, Araque I et al. Bacterial diversity of Grenache and Carignan grape surface from different vineyards at Priorat wine region (Catalonia, Spain). *Int J Food Microbiol.* 2016;**219**:56–63.
157. Bokulich NA, Thorngate JH, Richardson PM, Mills DA. Microbial biogeography of wine grapes is conditioned by cultivar, vintage, and climate. *Proc Natl Acad Sci.* 2014;**111**:139–48.
158. Perazzolli M, Antonielli L, Storari M et al. Resilience of the natural phyllosphere microbiota of the grapevine to chemical and biological pesticides. *Appl Environ Microbiol.* 2014;**80**: 3585–96.
159. Pinto C, Pinho D, Sousa S et al. Unravelling the diversity of grapevine microbiome. *PLoS One.* 2014;**9**:e85622.
160. Gramaje D, Eichmeier A, Spetik M et al. Exploring the temporal dynamics of the fungal microbiome in rootstocks, the lesser-known half of the grapevine crop. *Res Sq.* 2021.
161. Kraus C, Voegelé RT, Fischer M. Temporal development of the culturable, endophytic fungal community in healthy grapevine branches and occurrence of GTD-associated fungi. *Microb Ecol.* 2019;**77**:866–76.
162. Carmichael PC, Siyoum N, Chidamba L, Korsten L. Exploring the microbial communities associated with *Botrytis cinerea* during berry development in table grape with emphasis on potential biocontrol yeasts. *Eur J Plant Pathol.* 2019;**154**:919–30.
163. Dissanayake AJ, Purahong W, Wubet T et al. Direct comparison of culture-dependent and culture-independent molecular approaches reveal the diversity of fungal endophytic communities in stems of grapevine (*Vitis vinifera*). *Fungal Divers.* 2018;**90**:85–107.
164. Eichmeier A, Pečenka J, Peňázová E et al. High-throughput amplicon sequencing-based analysis of active fungal communities inhabiting grapevine after hot-water treatments reveals unexpectedly high fungal diversity. *Fungal Ecol.* 2018;**36**:26–38.