HortScience 59(8):1077–1087. 2024. https://doi.org/10.21273/HORTSCI17805-24

Impact of the Plant Growth-promoting Rhizobacterium *Streptomyces saraceticus* Strain 31 on Berry Quality of 'Benifuji' Grape: Improvements through the Reconfiguration of Fine Root Morphology and Vessel Anatomy

Chuang Ma, Yinghua Li, Shufen Tian, Rong Wang, and Chaoxia Wang

College of Horticulture and Landscape, Tianjin Agricultural University, Tianjin 300392, People's Republic of China

Keywords. hydraulic conductivity, root surface area, total soluble solid, vessel lumen area, volatile organic compounds

Abstract. **In an effort to mitigate the environmental impact of chemical fertilizers, plant growth-promoting rhizobacteria (PGPR) have emerged as a more sustainable alternative. *Streptomyces saraceticus* 31 ('SS31'), a new strain of biocontrol bacteria, was inoculated into rhizosphere soils of 'Benifuji' grape to evaluate its impact on grape roots and berries. The results indicated significant improvements in soil fertility, with higher levels of organic matter, phosphorus, potassium, and nitrate nitrogen compared with those of the controls. Moreover, 'SS31' application elicited a notable reduction in soil pH levels, along with a substantial augmentation in the enzymatic activities of both phosphatase and invertase. The grapes treated with 'SS31' exhibited a notable increase in the number, length, surface area, and volume of fine roots in both 0- to 10-cm and 10- to 20-cm soil profiles. The application of 'SS31' resulted in the observation of greater diameter, lower density, and larger lumen area, along with increased specific hydraulic conductivity in the vessels of roots with 1- to 2-mm diameters. Despite a slight reduction in berry weight compared with that of the controls, 'Benifuji' grape berries displayed higher total soluble solids and lower total titratable acidity after 'SS31' application. Furthermore, 'SS31' treatment elevated the levels of volatile compounds in berries, especially fatty acid-derived compounds. A network analysis revealed a robust positive correlation between the observed improvements in grape berry quality and the morphology as well as the hydraulic conductivity of the grape fine roots. In conclusion, these findings suggest that 'SS31' has the potential to enhance grape root function by expanding the root absorption area and facilitating water transportation. This, in turn, may improve the flavor and aroma of 'Benifuji' grape berries.**

The widespread use of synthetic chemical fertilizers in horticultural practices has led to significant environmental issues, including groundwater contamination, soil salinization, and greenhouse gas emissions (Phogat et al. 2014). To mitigate these environmental effects and reduce chemical inputs, it is urgent to explore sustainable and environmentally friendly alternatives as plant nutrient supplements (Mosa et al. 2016). One such alternative is the use of plant growth-promoting rhizobacteria (PGPR) in biofertilizers. These bacteria have been shown to improve soil health and enhance the uptake of mineral nutrients, leading to positive growth benefits for various crop plants (Hafeez et al. 2006). Aslantas et al. (2007) reported that certain rhizobacteria strains enhanced apple tree growth and fruit yield. Similarly, Karakurt et al. (2011) found that *Bacillus subtilis* OSU-142, *Bacillus megaterium* M-3, *Burkholderia cepacia* OSU-7, and *Pseudomonas putida* BA-8 bacteria strains improved fruit set, vegetative growth, and chemical characteristics of sour cherry. Other studies showed that biofertilizers inoculated with *Acidithiobacillus* increased the yield of short-cycle grapes (Stamford et al. 2011). Currently, numerous PGPR strains have been identified and used as biofertilizers, and their impact on plant growth is a key focus of contemporary research.

Root traits are thought to be indicative of the root functional status and demonstrate the root's plasticity in response to horticultural practices (Ruggiero et al. 2012). The beneficial effects of bacteria on roots are often attributed to several mechanisms, including nitrogen (N) fixation, improved nutrient uptake, and phytohormone production (Mitter et al. 2013). It has been estimated that ~80% of bacteria in the rhizosphere are capable of producing indole acetic acid, which promotes cell division and elongation, thereby regulating root development and architecture (Naveed et al. 2015; Spaepen et al. 2008). A recent study by Duan et al. (2021a) reported significant increases in the root length and volume of *Vitis vinifera* when treated with a mixture of PGPR compared with those of untreated controls. In the study by Ramirez-Carino et al. (2023), it was demonstrated that inoculation with *Priestia megaterium*, *Acinetobacter calcoaceticus*, and *Atlantibacter* sp. promoted the formation of secondary roots and root hairs in tomatillo crops, thus providing a larger contact surface for water and nutrient uptake. In addition, the root xylem is a crucial component of the conduit tissue in trees that ensures a continuous supply of water to the shoots (Paul et al. 2012). The conductivity of this tissue is determined by the size, number, and anatomy of vessels (Hacke et al. 2016; Kirfel et al. 2017). According to Hagen-Poiseuille's law, water transport efficiency increases with vessel diameter and the number of vessels per unit cross-section (Gebauer and Volarik 2013; Tyree and Zimmermann 2002). Alsina et al. (2011) reported that the root hydraulic conductance of drought-tolerant grape (*Vitis berlandieri* × *V. rupestris* cv. 1103P) increased during warm summer dry periods. Although many facts have shown that PGPR favor the growth of horticultural crop, it is not yet known whether this is related to their improved roots. An accurate comprehension of alterations in root morphology and function is paramount to clarifying the influence of rhizosphere bacteria on plants.

The volatile organic compounds (VOCs), which are biochemical and agronomical signatures, of certain horticultural crops play pivotal roles in determining their quality and taste. To enhance VOCs in grape berries, traditional practices have involved rhizospheric and foliar fertilization with minerals. The impact of the N supply on the volatile compounds of Pinot noir berries and *Vitis vinifera* L. cv. Sauvignon Blanc has been well-documented (Lacroux et al. 2008; Yuan et al. 2018). A recent study by Chen et al. (2022a) further explored the effects of foliar fertilization with potassium (K) alone or in combination with girdling on the terpene content in 'Hanxiangmi' grapes. However, recent studies have convincingly demonstrated that PGPR have the potential to enhance plant growth and safeguard against abiotic stress using distinct genetic and protein-based mechanisms (El-Serafy and El-Sheshtawy 2020; Jimenez-Gomez et al. 2020). The plant immune system can be activated through induced systemic resistance mechanisms, leading to enhanced aroma, flavor, and juice qualities of the fruits (Kafi et al. 2021). Additionally, PGPR can promote

Received for publication 5 Mar 2024. Accepted for publication 10 May 2024.
Published online 12 Jul 2024.
This research was funded by the China Agriculture Research System (grant number CARS-29-zp-01).
S.F.T. is the corresponding author. E-mail: sft_tjau@126.com.

photosynthesis and increase the sugar content in fruits, thereby enhancing volatiles such as 3(2H)-Furanone, 4-methoxy-2,5-dimethyl, and phenylalanine-derived compounds (Duan et al. 2021b). Despite these advancements, research of the modulation of grape berry volatiles by PGPR remains limited. Therefore, screening for PGPR that enhance volatile compounds in grape berries represents a promising area of research with significant practical implications.

Streptomyces saraceticus 31 ('SS31'), a strain of biocontrol and growth-promoting bacteria, has been found to significantly enhance the growth of jujube and strawberry plants (Hua et al. 2019; Wu et al. 2021; Zhang et al. 2014). This remarkable capacity highlights the potential of 'SS31' in agricultural applications. Furthermore, our previous research showed that the application of 'SS31' treatment could effectively enhance the metabolic activity and diversity of soil microbial communities in the rhizosphere of grapes (Su et al. 2020). The Benifuji grape cultivar (*Vitis vinifera* × *V. labrusca* cv. Benifuji) is known for its exceptional qualities, including robust flavor, large fruit grains, sweet pulp, and high yield. Thus, studying how 'SS31' affects the 'Benifuji' grape is crucial to understanding its biological properties and optimizing sustainable production methods. To address this knowledge gap, the current study was designed to investigate the impact of 'SS31' on root morphology and vessel anatomy across various soil profiles. The objective of this research was to validate the hypothesis that the PGPR strain has a favorable impact on root growth and function, leading to enhanced quality and volatile compounds of 'Benifuji' grape berries.

Materials and Methods

Plant materials. The 'Benifuji' grape (*V. vinifera* × *V. labrusca* cv. Benifuji), a hybrid descendant of European and American grape cultivars, belongs to the second generation of the 'Kyoho' grape series. This cultivar is renowned for its distinctive traits, which encompass generous clusters and berries exhibiting a range of colors from delicate pink hues to rich purples. The robust growth potential and exceptional germination rates of 'Benifuji' grape are testaments to its remarkable adaptability and viability. However, challenges persist because environmental factors and improper cultivation practices can lead to fruit shedding and inconsistent quality.

This experiment was conducted in the greenhouse of the Grape Research Center at Tianjin Agriculture University, located in Tianjin, China (lat. 39°16′ N, long. 117°4′ E) during the 2020 growing season. This region has a sunshine duration of 2590.5 h and experiences a frost-free period that extends for 189 d, with an average annual temperature of 12.1 °C and annual solar radiation of 129.5 $MJ \cdot cm^{-2}$. Within the greenhouse, 'Benifuji' grapes (5-year-old and self-rooting) were cultivated in 1-m-wide plastic root-restriction containers. Each container housed a single plant. The soil mixture used for planting consisted of a 1:1:1 ratio of sand, loam, and perlite that provided an optimal substrate for grape growth. The grapes were pruned using horizontal double arms placed at 1.0-m × 1.5-m spacing between plants and rows, with the trellis height maintained at 1.8 m. Six grapes with similar growth were selected for the experiment and divided into two groups. Three grapes were treated with 'SS31' biofertilizer, and the other three served as the control group.

Preparation of 'SS31' biofertilizer. The strain of bacteria, *Streptomyces saraceticus* 31, was originally isolated by the Department of Plant Pathology of Chung Hsing University in Taiwan, which is a member of the biocontrol and growth-promoting bacteria (Tong'an Agricultural Technology Co., Ltd.). Before the experiments, the bacteria were fermented using soybeans and white granulated sugar under aerobic conditions at 28 °C. This process yielded a mixture containing 3% to 5% organic matter, less than 5 $g \cdot L^{-1}$ water insoluble matter, 16 types of amino acids, and 156 to 167 $g \cdot L^{-1}$ free amino acids. The stock solution was characterized by a concentration more than 2.5×10^{10} $cfu \cdot L^{-1}$ of single effective viable bacteria with a density of 1.23 $g \cdot cm^{-3}$ at 25 °C.

Experimental design. In a controlled greenhouse study, the stock solution of 'SS31' was diluted 300-fold with distilled water. To evaluate its effect on grapes, three plastic root-restriction containers were irrigated with the 'SS31' dilution containing 120 L of diluted solution per container at a concentration of 8.3×10^7 $cfu \cdot L^{-1}$. The treatment was administered during the following four critical growth stages in 2020: budbreak (5 Apr), fruit set (23 May), pea-sized berries (23 Jun), and veraison period (7 Jul) (Coombe 2010). Beyond the four previously mentioned periods, daily water management primarily comprised limited hanging spray irrigation, thus ensuring precise consistency in water volume and duration across both the control and 'SS31' treatments. For each grape, regardless of treatment, an additional standardized fertilizer application of 0.1 kg of a N-phosphorus-K compound was used. Other cultivation practices, including short pruning, fruit thinning, pest control, and

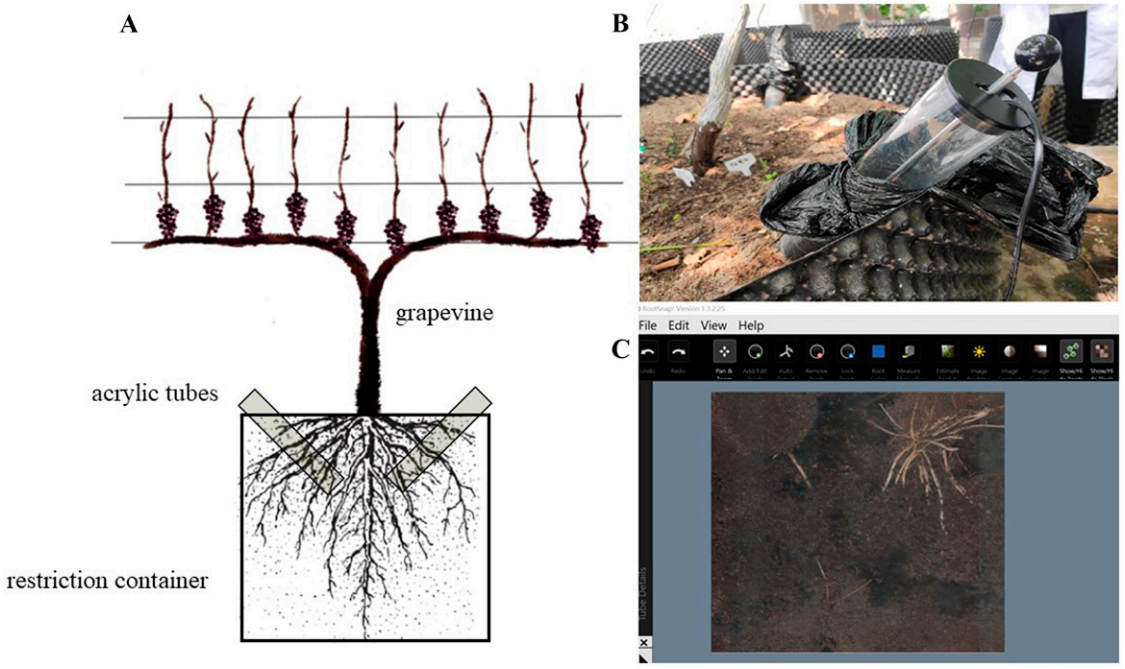

Fig. 1. Root morphology detected by the minirhizotron method. Tubes are positioned in the restriction container (**A**, **B**). Root image scanned by the CI-600 System (**C**).

Table 1. Effects of the control (CK) and *Streptomyces saraceticus* 31 ('SS31') treatments on soil physicochemical properties and enzyme activities.

	Soil profile 0–10 cm				Soil profile 10–20 cm			
	CK	SS31	*t* value	*P*	CK	SS31	*t* value	*P*
Available phosphorus ($mg \cdot kg^{-1}$)	70.54 ± 13.04[i]	87.43 ± 13.10	3.17	**[ii]	67.70 ± 10.29	80.09 ± 10.87	2.86	**
Available potassium ($mg \cdot kg^{-1}$)	43.60 ± 8.02	67.80 ± 4.83	8.95	***	34.44 ± 6.33	56.27 ± 4.01	10.09	***
Ammonium nitrogen ($mg \cdot kg^{-1}$)	6.89 ± 1.43	7.60 ± 1.46	1.20	NS	5.44 ± 1.13	6.31 ± 1.21	1.82	NS
Nitrate nitrogen ($mg \cdot kg^{-1}$)	1.05 ± 0.22	1.85 ± 0.41	5.96	***	0.83 ± 0.17	1.53 ± 0.34	6.38	***
Organic matter ($mg \cdot kg^{-1}$)	17.54 ± 1.37	20.97 ± 0.45	8.24	***	13.86 ± 0.88	17.41 ± 0.37	12.88	***
pH	8.04 ± 0.07	7.72 ± 0.07	11.19	***	7.75 ± 0.06	7.61 ± 0.06	5.71	***
Urease activity ($\mu mol \cdot g^{-1} \cdot d^{-1}$)	0.67 ± 0.28	0.73 ± 0.18	0.62	NS	0.42 ± 0.09	0.49 ± 0.11	1.71	NS
Phosphatase activity ($mg \cdot g^{-1} \cdot d^{-1}$)	7.44 ± 0.54	9.01 ± 0.37	8.31	***	5.96 ± 0.17	7.09 ± 0.39	9.20	***
Invertase activity ($mg \cdot g^{-1} \cdot d^{-1}$)	5.32 ± 0.45	6.28 ± 0.51	4.89	***	4.65 ± 0.43	5.28 ± 0.37	3.84	***

[i] Values were presented as means ± *SD*.
[ii] NS, *, **, *** indicate nonsignificant or significant at $P < 0.05$, 0.01, or 0.001 according to the *t* test, respectively.

disease control, were executed according to strict operational guidelines to maintain uniformity across all treatment groups. Additionally, environmental variables such as lighting and temperature were meticulously maintained at uniform levels within the same greenhouse, thus mitigating any potential confounding factors during the comparison between the control and 'SS31' fertilizer treatment.

Root minirhizotron and morphology analyses. Four transparent acrylic tubes (each had a length of 100 cm and inner diameter of 7-cm) were installed at a 45° angle to the ground in four intersecting directions within each plastic container (Fig. 1). The upper sections of the tubes at the aboveground level were shielded from light using black tape and rubber covers. On 13 Sep 2020, images were obtained using a root scanner system (CI-600 Growth Monitoring System; CID, Camas, WA, USA). Then, the captured images were analyzed separately for both soil profiles of 0 to 10 cm and 10 to 20 cm. The split image of each soil profile had a size of 19.56 cm × 14.14 cm. Using an image analysis program (WinRHIZO Tron MF; Regent, Quebec, Canada), the number, length, surface area, and volume of fine roots with diameters ≤1 mm and 1 to 2 mm on the collected images were measured (Tarin et al. 2020).

Root sampling and anatomy analyses. On 15 Sep 2020, root sample collection was performed. At a distance of 20 cm from the main stem of the grape, soil blocks (0.2 m × 0.2 m × 0.1 m) were excavated at two soil profiles (0–10 cm and 10–20 cm) in four intersecting directions. The roots, still embedded in soil, were carefully placed in plastic bags, labeled, and transported to the laboratory in a 4 °C icebox. Upon arrival at the laboratory, the soil was removed from the root samples using a 0.25-mm mesh sieve under running water. Then, the fine roots were categorized based on their diameter using a caliper. For the purpose of the analysis, they were divided into the following two categories: ≤1 mm and 1 to 2 mm (including 2 mm but excluding 1 mm) (Zadworny et al. 2018).

For the root anatomy analyses, 30 meticulously selected root segments, all within the same diameter class, were gathered from each soil profile of the respective treatment groups. A total of 720 segments were stained using safranin-fast green solution. Then, the samples were dehydrated in a series of alcohol solutions (70%, 85%, 95%, and 100%) and embedded in paraffin. Microtome sections with a thickness of 18 μm were prepared for each sample (Gu et al. 2014). These slides were observed under a compound microscope (Leica DM4000B), and images were captured using a Leica DFC450 CCD camera (Leica Microsystems, Wetzlar, Germany). Using the Motic 3000 Imaging System (Motic Co., Fujian, China), root cross-sections for each root segment were used to measure root anatomical parameters, including the maximum (d_{max}) and minimum (d_{min}) vessel diameter, the number of vessels per stele (*VD*), and the lumen area of vessels (A_{lum}).

The specific conductivity (K_s) was calculated using Hagen-Poiseuille's law (Tyree and Ewers 1991).

$$K_{th} = \sum_1^n \frac{\pi\rho}{8\eta} r^4_{lum} \left[kg \cdot m \cdot s^{-1} \cdot MPa^{-1}\right]$$

and

$$r^4_{lum} = \frac{d^3_{max}\, d^3_{min}}{8d^2_{max} + 8d^2_{min}}$$

where ρ is the density of water at 20 °C (998.205 $kg \cdot m^{-3}$), η is the dynamic viscosity of water (1.002×10^{-9} $MPa \cdot s^{-1}$), d is the diameter of the ith vessel, and n is the number of the vessel in the xylem.

The root specific theoretical conductivity (K_s) was calculated as the sum of all of the K_{th} values in the root divided by the xylem area of a particular root (A_{xyl}).

$$K_s = \Sigma K_{th} / A_{xyl} \left[kg \cdot m \cdot s^{-1} \cdot MPa^{-1}\right]$$

Soil sampling and determination. During root sampling on 15 Sep, soil samples were collected from both soil profiles (0–10 cm and 10–20 cm) in four intersecting directions. To complete testing, 12 soil samples were collected from each soil layer for each treatment, resulting in a total of 48 soil samples. The pH of the soil was measured in soil:water suspension (1:5) using a pH meter (PHS-3C; Shanghai Leici Instrument, Shanghai, China). The concentrations of soil organic matter, ammonium N, nitrate N, available phosphorus, and available K were determined according to the method established by Anderson and Ingram (1993). The alkaline phosphatase activity in the soil was measured using the disodium phenyl phosphate method (Guan et al. 1986). To assess the soil urease activity, sodium phenolate–sodium hypochlorite colorimetry was used (Gosewinkel and Broadbent 2008). The invertase activity in soil was determined using the 3,5-dinitrosa-licylic acid method (Frankeberger and Johanson 1983).

Table 2. Effect of the control (CK) and *Streptomyces saraceticus* 31 ('SS31') treatments on fine root morphologies of 'Benifuji' grapes.

		Soil profile 0–10 cm				Soil profile 10–20 cm			
Root diam	Root morphologies	CK	SS31	*t* value	*P*	CK	SS31	*t* value	*P*
0–1 mm	Root number ($ind \cdot m^{-2}$)	342.94 ± 40.86[i]	618.81 ± 38.33	17.05	***[ii]	288.53 ± 26.39	441.83 ± 33.99	12.34	***
	Root length ($m \cdot m^{-2}$)	10.11 ± 0.71	12.31 ± 0.86	6.83	***	8.43 ± 0.55	12.52 ± 0.79	14.74	***
	Root volume ($cm^3 \cdot m^{-2}$)	3.89 ± 0.39	5.43 ± 0.54	6.19	***	3.98 ± 0.36	5.06 ± 0.36	7.35	***
	Root surface area ($cm^3 \cdot m^{-2}$)	222.24 ± 29.65	289.79 ± 28.56	5.68	***	215.85 ± 11.57	283.1 ± 20.61	9.86	***
1–2 mm	Root number ($ind \cdot m^{-2}$)	186.97 ± 26.03	265.21 ± 24.59	11.43	***	128.72 ± 13.38	189.46 ± 17.35	9.60	***
	Root length ($m \cdot m^{-2}$)	4.43 ± 0.33	5.27 ± 0.40	6.18	***	4.23 ± 0.26	5.36 ± 0.47	7.31	***
	Root volume ($cm^3 \cdot m^{-2}$)	9.83 ± 0.36	12.68 ± 1.45	6.72	***	9.41 ± 0.36	12.29 ± 1.08	8.76	***
	Root surface area ($cm^3 \cdot m^{-2}$)	231.31 ± 31.46	289.79 ± 30.01	4.66	***	219.11 ± 9.04	289.61 ± 20.61	10.85	***

[i] Values were presented as means ± *SD*.
[ii] NS, *, **, *** indicate nonsignificant or significant at $P < 0.05$, 0.01, or 0.001 according to the *t* test, respectively.

Table 3. F value of the effects of the treatment, soil profile, and root diameter on the 'Benifuji' grape root anatomy through a mix-level three-way analysis of variance.

Factors	d_{max}	d_{min}	A_{lum}	VD	K_s
Treatment	25.642***[i]	0.043^{NS}	160.821***	16.137***	77.808***
Soil profile	21.938***	11.535**	9.240**	18.057***	33.084***
Root diameter	18.758***	39.907***	29.660***	57.755***	138.143***
Treatment × soil profile	1.578^{NS}	1.709^{NS}	20.484***	0.106^{NS}	0.536^{NS}
Treatment × root diameter	1.003^{NS}	2.326^{NS}	26.463***	1.609^{NS}	84.604***
Soil profile × root diameter	2.220^{NS}	1.139^{NS}	15.934***	0.371^{NS}	2.510^{NS}
Treatment × soil profile × root diameter	5.011*	0.465^{NS}	10.298**	0.265^{NS}	0.974^{NS}

[i] NS, *, **, *** indicate nonsignificant or significant at $P < 0.05$, 0.01, or 0.001, respectively.

Berry quality and volatile organic compounds analyses. On 15 Sep, 30 healthy grape berries that had attained full industrial ripeness were randomly chosen from diverse locations within the clusters of the identical treatment. This process was repeated three times, resulting in a total of 180 grape berries. Then, these berries were divided into the control and 'SS31' groups based on their assigned experimental conditions. The fresh weight of each berry was accurately measured using an electronic balance (ES20K-1D; Shenyang Longteng Electronic Co. Ltd., Liaoning, China). The berries were squeezed to extract the juice, which was then filtered using a Whatman filter 520 A 1/2. The juice was centrifuged for 5 min at 3 500 rpm in a 15-mL Falcon tube to remove any solid particles. The total soluble solids (TSS) content of the clarified juice was determined using an electronic refractometer (PAL-1; ATAGO, Saitama, Japan). The total titratable acidity (TA) was determined using the sodium hydroxide (NaOH) titration method. Finally, the TSS-to-TA ratio was calculated by dividing the TSS and TA values (Jia et al. 2023).

On 15 Sep, a meticulous sampling procedure was performed; six berries (~50 g) were delicately gathered from diverse clusters within the same grapevine. This sampling process was replicated three times within the same treatment group. These berries were promptly stored in a freezer to ensure their preservation in a state that retained their original characteristics. To obtain a clear juice for further analyses, the hand-peeled fruit samples were pulverized in liquid N, centrifuged, and filtered. The gas chromatography-mass spectrometry analysis was performed using an Agilent 7890B–5977A system equipped with a HP–5MS chromatographic column (Agilent Technologies, Santa Clara, CA, USA). The chromatographic conditions were meticulously controlled as follows (Chen et al. 2022a; Sasaki et al. 2020): the sample inlet temperature was set at 250 °C; helium, which served as the carrier gas, was circulated at a constant flow rate of 1 mL·min^{-1}; the gas chromatography inlet was set in the splitless mode to ensure an optimal sample injection; and the column temperature was programmed to initially heat to 35 °C and hold for 2 min. Then, it was increased to 200 °C at a rate of 4 °C·min^{-1} and held for 5 min. Afterward, the temperature was increased by 30 °C·min^{-1} for another 5 min until it reached 250 °C. For mass spectrometry, the ion source temperature was set at 230 °C, whereas the quadrupole temperature was maintained at 250 °C. The ionization mode was electron ionization with an ionization energy of 70 eV. The mass spectrometric data range was set from 30 to 300 m·z^{-1}.

The sample vial was equilibrated at 45 °C for 5 min. Subsequently, a solid phase microextraction fiber (50/30 μm DVB/CAR/PDMS; Supelco, Bellefonte, PA, USA) was used to extract volatile compounds from the sample at 45 °C for 50 min. Immediately after extraction, the fiber was inserted in the gas chromatograph (Agilent 7890B GC; Agilent Technologies) injection port. The fiber was desorbed in the splitless mode at 250 °C for 2 min. The gas chromatography system was equipped with a 5977A mass-selective detector (Agilent Technologies) to facilitate compound identification. For compound identification, the NIST library along with the mass spectrum and retention times of chromatographic standards (Sigma-Aldrich, Burlington, MA, USA) were used (Sun et al. 2022).

Statistical analysis. To assess the differences in variables between the control and 'SS31' treatments, such as soil characteristics, root morphology, root anatomy, and berry quality, Student's t test (independent samples t test) was used (significance level = 0.05). The interactions among the treatment, soil profile, and root diameter on root vessel anatomy and hydraulic conductivity were conducted by a mixed-level three-way analysis of variance with IBM SPSS Statistics data processing software (version 24.0; IBM, Armonk, NY, USA). Multivariate correlations between anatomical characteristics of vessels and specific hydraulic conductivity were analyzed using the Pearson method. Network analysis methods were used to visualize the intricate relationships among variables with the 'igraph' package in the R programming environment. All diagrams were meticulously constructed using

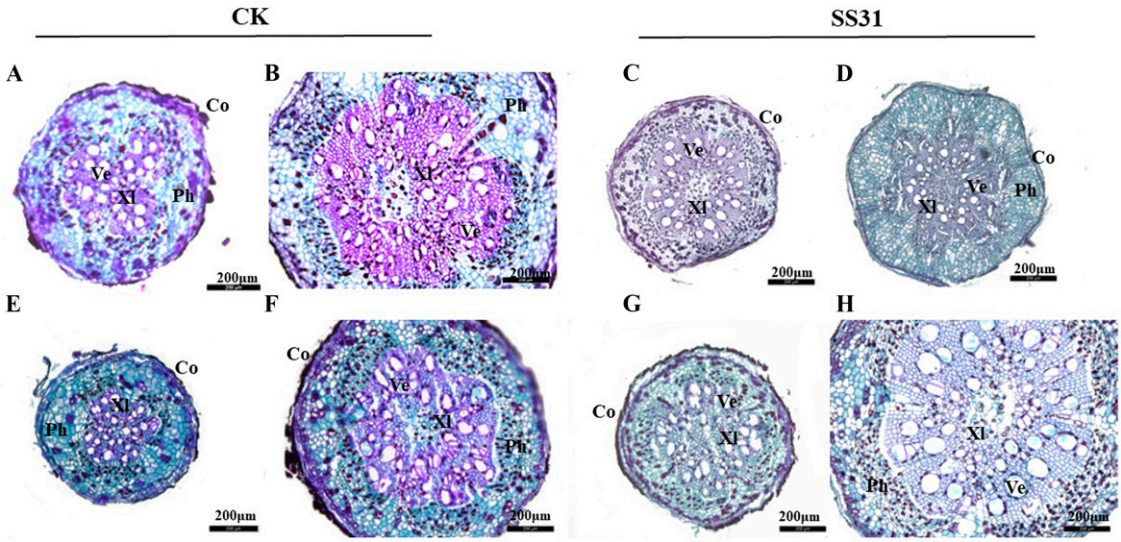

Fig. 2. Effects of the control (CK) and *Streptomyces saraceticus* 31 ('SS31') treatments on the root anatomy of 'Benifuji' grapes in the 0- to 10-cm soil profile (**A**–**D**) and the 10- to 20-cm soil profile (**E**–**H**). The 0- to 1-mm root diameter (**A**, **C**, **E**, **G**) and 1- to 2-mm root diameter (**B**, **D**, **F**, **H**). Co = cork layer; Ph = phloem; Ve = vessel; Xl = xylem.

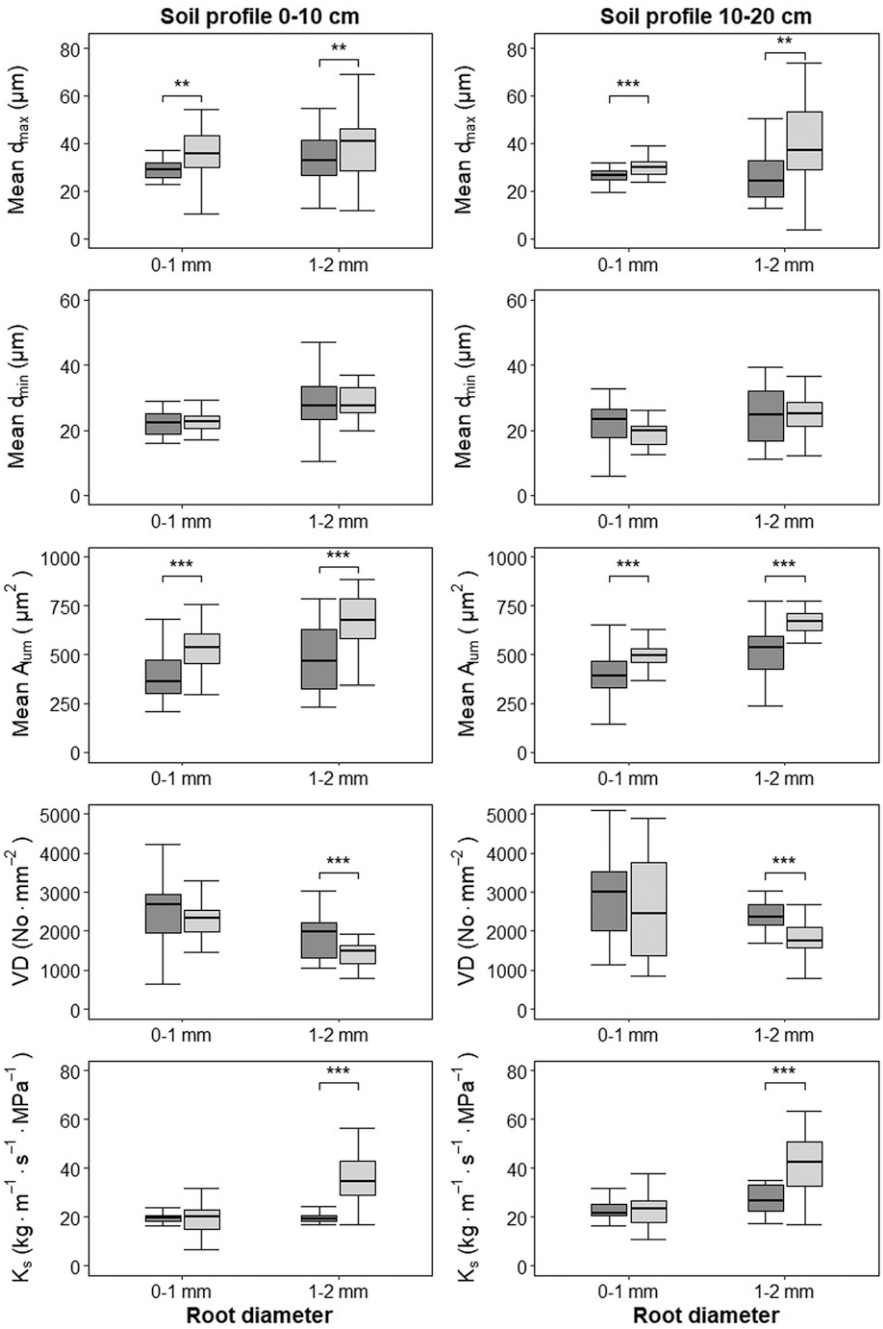

Fig. 3. Effects of the control (CK; gray boxplot) and *Streptomyces saraceticus* 31 ('SS31'; light gray boxplot) treatments on the root vessel characteristics of 'Benifuji' grapes with 0- to 1-mm and 1- to 2-mm root diameters in both soil profiles. Significance levels with Student's *t* test: $^{**}P < 0.01$; $^{***}P < 0.001$.

R software (version 4.3.2) and the ggplot2 package to ensure high-quality visual representations.

Results

Soil physicochemical properties and enzyme activities. Upon the application of 'SS31', significant changes were observed in the physicochemical properties and enzyme activities of the rhizosphere soil of 'Benifuji' grapes (Table 1). In comparison with the control, the 'SS31' treatment increased the amounts of available phosphorus by 23.9% and 18.3% in the 0- to 10-cm and 10- to 20-cm soil profiles, respectively. Additionally, the available K levels increased significantly by 55.5% and 63.4% in the 0- to 10-cm and 10- to 20-cm soil profiles, respectively. The nitrate N also experienced substantial increases of 76.1% and 84.3% in the 0- to 10-cm and 10- to 20-cm soil profiles, respectively. However, 'SS31' had no notable impact on the ammonia N in both soil profiles. In comparison with the control, the levels of organic matter increased by 19.5% and 25.6% in the 0- to 10-cm and 10- to 20-cm soil profiles, respectively, after the application of 'SS31'. Notably, the pH of both soil profiles was lower in the 'SS31' treatment than in the control treatment. The urease activity was not significantly affected by 'SS31' in either soil profile. In contrast to the control, the phosphatase activity of soil increased significantly by 21.1% and 18.9% in the 0- to 10-cm and 10- to 20-cm soil profiles, respectively, after applying 'SS31'. A similar increasing trend was observed for soil invertase activity after the application of 'SS31', and statistical significance was detected in both soil profiles.

Fine root morphologies. The application of 'SS31' had a profound impact on the 'Benifuji' grapes; it significantly enhanced the number, length, volume, and surface area of their fine roots (Table 2). In the 'Benifuji' grape roots with diameters between 0 and 1 mm, those treated with 'SS31' in the 0- to 10-cm soil profile exhibited 80.4%, 21.7%, 39.7%, and 30.3% increases in the number, length, volume, and surface area, respectively, compared with the control. Similarly, in the 10- to 20-cm soil profile, these parameters increased by 53.1%, 48.5%, 27.2%, and 31.6%, respectively. The same trend was observed in the roots with a diameter of 1 to 2 mm. In the 0- to 10-cm soil profile, the number, length, volume, and surface area of 'Benifuji' grape roots treated with 'SS31' increased by 78.2%, 18.9%, 28.9%, and 25.2%, respectively, compared with the control. Again, these higher values were also observed in the 10- to 20-cm soil profile under the 'SS31' treatment compared with those under the control treatment, indicating the positive effects of the PGPR treatment on grape root morphology.

Root vessel anatomy and hydraulic conductivity. The maximum and minimum diameters of fine root vessels were significantly influenced by the soil profile and root diameter, respectively. However, no interaction between these two factors was observed (Table 3). The application of 'SS31' led to a significant increase in the mean maximum diameters (d_{max}) of vessels. Specifically, a 22.6% increase was observed in the root diameters of 0 to 1 mm, and a 13.8% increase was observed in the root diameters of 1 to 2 mm in the 0- to 10-cm soil profile. This trend was also evident in the 10- to 20-cm soil profile (Figs. 2 and 3). Notably, between the two treatments, no significant difference was detected in the mean minimum diameters (d_{min}) of vessels (Fig. 3). The lumen area of vessels was influenced by the treatment, soil profile, root diameter, and their interactions (Table 3). Root vessels treated with 'SS31' exhibited a larger lumen area than those under the control treatment (Fig. 3). Notably, significant increases of 34.1% in the 0- to 1-mm-diameter and 41.3% in the 1- to 2-mm-diameter lumen area of vessels of fine roots treated with 'SS31' were observed within the 0- to 10-cm soil profile. Similarly, the same parameters in the 10- to 20-cm soil profile increased by 23.6% and 29.8%, respectively. In comparison with the control, a significant reduction in vessel density was observed in roots with a diameter of 1 to 2 mm treated with 'SS31'. This reduction was observed in both the 0- to 10-cm and

Fig. 4. Multivariate correlation between the anatomical characteristics of the vessel and specific hydraulic conductivity (K_s). Different colors indicate the roots from the control (CK) and *Streptomyces saraceticus* 31 ('SS31') treatments. Significance levels: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

10- to 20-cm soil profiles, with decreases of 23.1% and 24.6%, respectively.

The 'SS31' treatment, root diameter, soil profile, interaction of the root diameter with treatment, and root diameter significantly explained variations in specific hydraulic conductivity of fine roots (Table 3). In the 0- to 10-cm soil profile, roots with a diameter of 1 to 2 mm exhibited an 85.6% increase in specific hydraulic conductivity under 'SS31' treatment compared with that under the control treatment. Similarly, in the 10- to 20-cm soil profile, there was a 50.7% increase in specific hydraulic conductivity. However, no significant differences were observed in the specific hydraulic conductivity of roots with a diameter of 0 to 1 mm under the 'SS31' treatment and control treatment. The root specific hydraulic conductivity demonstrated a positive correlation with the lumen area of vessels, with a greater upsurge in the roots of grapes treated with 'SS31' than that with the control treatment (Fig. 4). Additionally, more significant negative correlations were observed between root specific hydraulic conductivity and vessel density after 'SS31' application.

Berry weight and quality. The application of 'SS31' treatment had a significant impact on the growth and quality of 'Benifuji' berries (Fig. 5). When compared with the control, the single berry weight of 'Benifuji' under 'SS31' treatment was found to be 4.1% lighter. However, it is noteworthy that 'SS31' treatment significantly increased the TSS content by 10.1% and decreased the total TA by 15.4% compared with those of the control. As a result, the TSS-to-TA ratio of 'Benifuji' berries treated with 'SS31' increased by 30.2%.

Volatile organic compounds. A total of 55 volatile compounds were identified in the berries from both the 'SS31' application and the control groups. Among these, five compounds originated from the amino acid metabolic pathway, 44 originated from the fatty acid metabolic pathway, and six originated from the isoprene metabolic pathway (Fig. 6). Notably, the SS31 treatment significantly increased the total concentrations of VOCs derived from the amino acid and fatty acid metabolic pathways in the berries. However, no significant impact on the VOCs that originated from the isoprene metabolic pathway was observed (Fig. 7A).

The specific analysis of VOCs derived from the fatty acid metabolism pathway revealed a noteworthy pattern, including one acid, 10 alcohols, five aldehydes, 24 esters, and four ketones. The proportions of acids, esters, and aldehydes produced through this pathway increased, whereas the proportions of alcohols and ketones decreased (Fig. 7B). The synthesis of octanoic acid was observed only with the 'SS31' treatment. The application of 'SS31' to 'Benifuji' berries significantly increased the contents of several esters, including ethyl acetate, ethyl-2-methylbutyrate, ethyl propionate, butyric acid ethyl ester, isopentyl acetate, ethyl caproate, and diethyl succinate. Among aldehydes, the 'SS31' treatment led to a general augmentation in leaf aldehyde levels in the berries. Furthermore, compared with the control, there were significant elevations in the levels of trans2-hexen-1-ol, 1-pentanol, and 2-methyl-1-pentanol. The berries from grapes treated with 'SS31' had the highest level of 6-methyl-5-hepten-2-1 (Fig. 6 and Supplemental Table 1).

Network analysis. The network analysis method was used to investigate the intricate relationships among root morphology, root

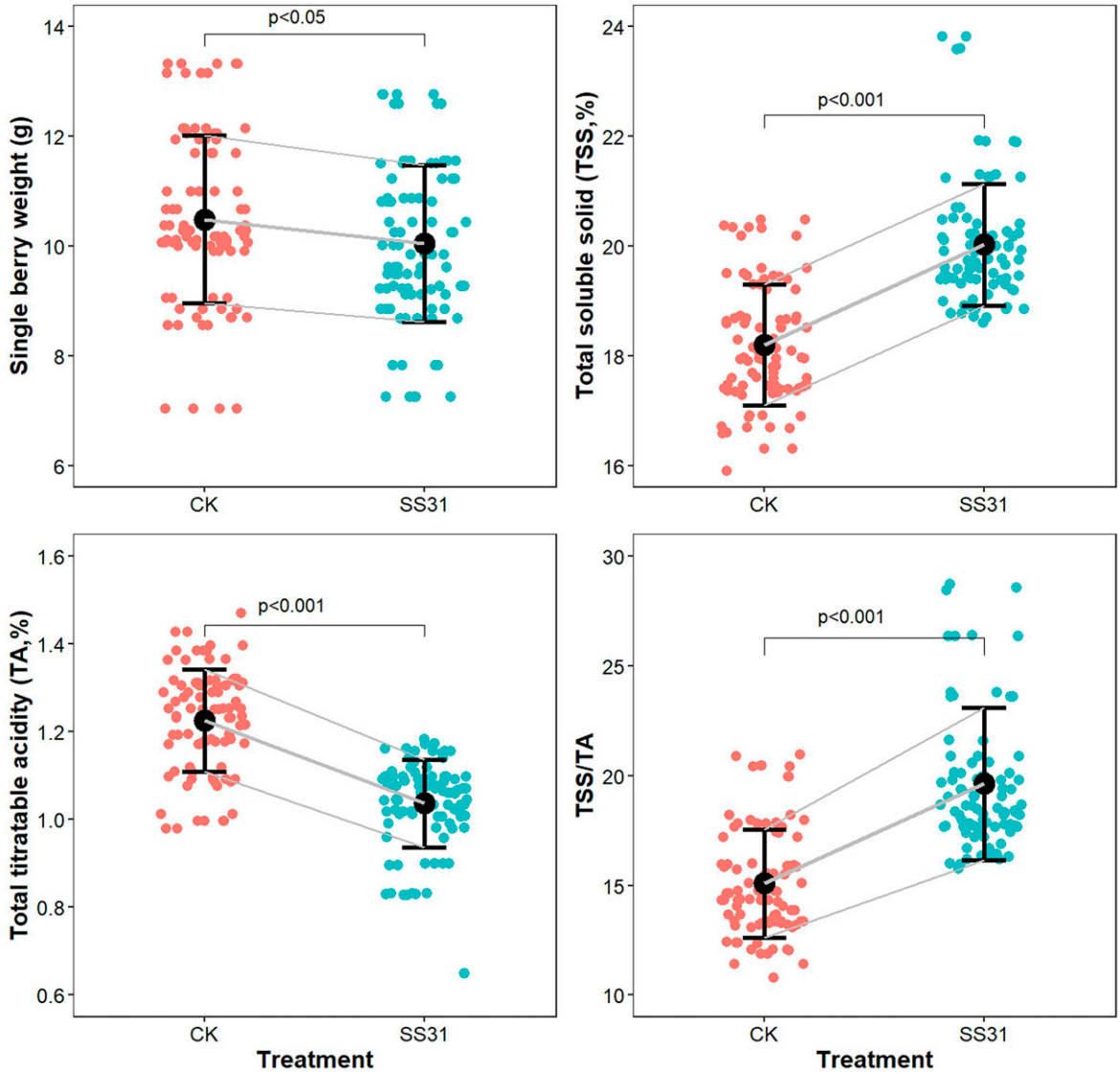

Fig. 5. Effects of the control (CK) and *Streptomyces saraceticus* 31 ('SS31') treatments on berry weight, total soluble solids (TSS), titratable acidity (TA), and TSS/TA ratio of 'Benifuji' grape berries. The *P* value is shown with Student's *t* test between the CK and 'SS31' treatments.

vessel anatomy, hydraulic properties, fruit quality, and volatile organic compounds (Fig. 8). Root morphology emerged as a significant determinant of TSS and TA in berries. Specifically, a strong positive correlation of 0.608 was observed between the fine root volume and TSS in berries, whereas a negative correlation of 0.607 was noted for TA. Furthermore, the vessel lumen area in roots emerged as the primary factor that influenced berry weight, with a robust positive correlation of 0.809. In terms of VOCs in berries, root specific hydraulic conductivity, root vessel lumen area, and fine root length were identified as key variables, with positive correlations exceeding 0.7 and each playing a pivotal role in determining their number and contents.

Discussion

Plant growth-promoting rhizobacteria, including strains of *Pseudomonas fluorescens*, *Pseudomonas putida*, *Bacillus circulans*, *Paenibacillus alvei*, and *Lysinicacillus sphaericus*, are frequently used as alternatives to chemical fertilizers because of their ability to improve soil fertility and plant growth (Itelima et al. 2018). The key objective of this research was to determine whether applying PGPR could improve the root growth and berry quality of the 'Benifuji' grapes. Obviously, the application of *Streptomyces saraceticus* strain 'SS31' confirmed our hypothesis, leading to significant increases in root number, length, volume, and surface area across both soil profiles (Table 2). These findings align with those of a previous study by Liu et al. (2016), who reported that inoculation with phosphate-solubilizing bacteria significantly boosted root dry weight. Walker et al. (2011) also observed that maize seed inoculation with *Azospirillum* strains resulted in increased root biomass. The mechanism behind these positive effects may be the improvement of rhizosphere conditions following microbial application, which promotes root proliferation and expansion. Lu et al. (2020) recently maintained that the enhancement of *Vitis vinifera* growth in response to the introduction of *Pseudomonas putida* Rs198 in the rhizosphere was primarily attributed to the soil's increased invertase and alkaline phosphatase activity triggered by this particular strain. This suggests that specific bacteria can enhance the activation of mineral elements in the soil, thereby enhancing their availability to plants. Moreover, PGPR have been identified as producers of phytohormones, namely IAA, indole-3-pyruvic acid, gibberellins, and polyamines, which have been verified to regulate plant growth (Botha 2011). It has been established that 'SS31' has the ability to produce IAA, which promotes the development of strawberry and oilseed rape (Hua et al. 2019; Nima et al. 2017). Future research should focus on the comprehensive identification of other metabolites produced by 'SS31' that may contribute to its growth-promoting effects.

The vessels within the root xylem serve as the primary conducting tissue and are a promising indicator of water and nutrient transportation efficiency. Practical adjustments to soil conditions can influence how these root vessels

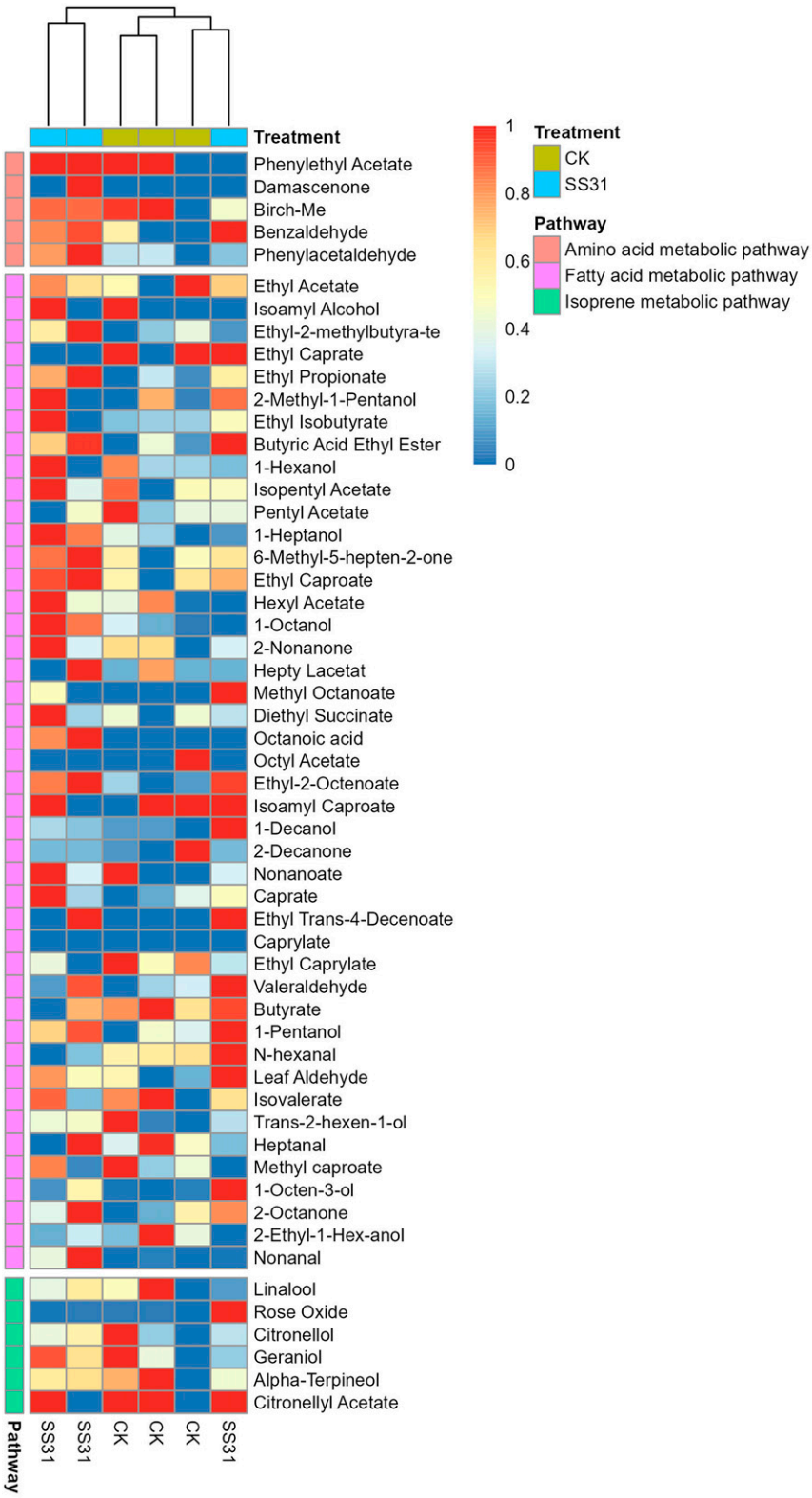

Fig. 6. Heatmap showing the differences in the volatile organic compounds of 'Benifuji' grape berries under the control (CK) and *Streptomyces saraceticus* 31 ('SS31') treatments. Data were standardized using the range method and clustered based on the Euclidean distance.

develop structurally (Wang et al. 2018). In this study, the 'SS31' treatment increased the maximum vessel diameter, with no significant effect on the minimum vessel diameter. However, it significantly increased the lumen area and decreased density, particularly in roots with a diameter of 1 to 2 mm. Rajaei et al. (2013) reported that the roots of *V. vinifera* cv. Yaghooti-Syah Shiraz exhibited a larger mean vessel diameter and fewer vessel numbers under irrigation. Theoretical models proposed that wider and fewer vessels are more efficient at transporting water than multiple narrower vessels (Zanne et al. 2010). However, wider vessels are more prone to cavitation and embolism during drought conditions. High hydraulic conductivity in plant organs generally indicates adaptation to long-term growth in favorable habitats (Wang et al. 2016). In this study, an improvement in root hydraulic conductivity was observed, which was driven by an expansion of the vessel lumen area, particularly under the 'SS31' treatment (Figs. 2 and 3). Marulanda et al. (2010) reported that plants inoculated with a *Bacillus megaterium* strain exhibited elevated root hydraulic conductance under both unstressed and salt-stressed conditions. This suggested that the beneficial effects of PGPR on plants may be linked to their ability to minimize hydraulic resistance and enhance water use efficiency in the roots.

In various crop production systems, the utilization of PGPR induces beneficial outcomes and has the capacity to enhance yield (Ibrahim et al. 2005; Mosa et al. 2016). According to Esitken et al. (2003), *Pseudomonas*, *Rhizobium*, and *Klebsiella* species of bacteria can effectively stimulate plant growth, boost yield, and enhance crop quality of apple and apricot. Wu et al. (2021) previously found that the application of 'SS31' led to increased biomass yields of water spinach across three growing seasons, as compared with that during the first season. In our study, a slight reduction in the weight of a single berry was observed under the 'SS31' treatment as compared with that under the control treatment, indicating a limited impact of 'SS31' on crop yield during the initial year of fertilization. Additionally, it was observed that 'Benifuji' berries treated with 'SS31' exhibited an increase in soluble solids and a decrease in TA compared with those under the control treatment, indicating the effectiveness of 'SS31' to enhance grape berry quality (Fig. 5). The improvement in berry quality has been found to exhibit a strong positive correlation with fine root morphologies (Fig. 8). This correlation may be attributed to the fact that the application of 'SS31' not only significantly elevated the levels of available phosphorus, K, and nitrate N in the soil but also enhanced root morphology indices, thereby improving the efficiency of mineral nutrient absorption and translocation. In a study conducted by Chen et al. (2022b), it was observed that treatment with the *Bacillus velezensis* strain GUMT319 led to increased sugar/acid ratios and vitamin C contents in grapes compared with those of the control group.

During fruit ripening, VOCs emerge as crucial metabolites that significantly impact grape quality, thereby defining the organoleptic value of the horticulture commodity (Alem et al. 2019). In this study, applying 'SS31' resulted in a significant change in the concentrations of volatile compounds found in 'Benifuji' berries, particularly those that originate from the fatty acid metabolic pathway (Fig. 7). In fruits, this metabolic pathway is primarily responsible for the synthesis of straight-chain aliphatic alcohols, aldehydes, ketones, and esters (Ma et al. 2021). When 'SS31' was applied, the concentrations of ethyl-2-methylbutyra-te, ethyl propionate,

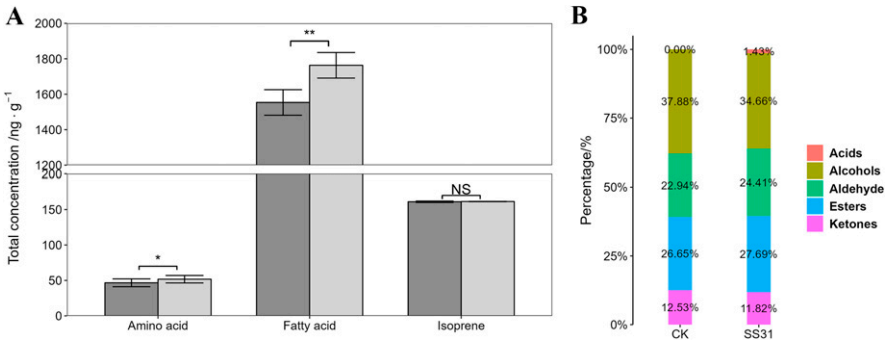

Fig. 7. Concentrations (**A**) and percentages (**B**) of different types of volatile compounds in 'Benifuji' berries determined under the control (CK) and *Streptomyces saraceticus* 31 ('SS31') treatments. Significance level with Student's *t* test: $*P < 0.05$.

butyric acid ethyl ester, and ethyl caproate within 'Benifuji' grape berries were significantly higher than those of the control. These esters are characteristically abundant in the strawberry-like aroma of grapes. These findings aligned with the observations of Chinachanta et al. (2021), who reported similar enhancements in the aroma of Thai jasmine rice through the application of *Sinomonas* sp. strain ORF15-23. The plant–microorganism interaction plays a pivotal role in dictating the emission of plant volatiles (Miransari 2010; Velasquez et al. 2020). Specifically, rhizosphere microorganisms enhance plants' resilience to biotic and abiotic stressors through the regulation of gene expression involved in plant immune responses, including the ethylene-mediated response (Gupta et al. 2019; Schuman and Baldwin 2018). During this process, the upregulated expression of genes related to fatty acid metabolism, such as the *LOX* gene family, is considered to be the reason for the increased VOC concentrations. However, VOC emission is greatly influenced by environmental factors such as light intensity, atmospheric CO_2 concentration, temperature, relative humidity, and nutrient status (Dudareva et al. 2013; Velasquez et al. 2020; Yuan et al. 2018). The signaling mechanisms that regulate fluctuations in VOCs in response to PGPR are intricate and complex; therefore, further investigations are warranted.

Conclusion

In summary, the results of this comprehensive study demonstrated that the application of *Streptomyces saraceticus* strain 'SS31' had numerous beneficial effects on soil physicochemical properties. By elevating the available phosphorus, K, and nitrate N levels as well as the organic matter content, 'SS31' enhanced soil fertility. Furthermore, it reduced pH levels and improved soil phosphatase and invertase activity, which are vital for nutrient cycling and plant growth. The application of 'SS31' also stimulated the growth of 'Benifuji' grape fine roots, thus increasing their number, length, surface area, and volume. A detailed investigation of fine roots ≤2 mm in diameter revealed that 'SS31' performed significantly better than the control in terms of root vessel lumen area and specific hydraulic conductivity. This was achieved by increasing the maximum diameter and reducing the vessel density of fine roots. Notably, the beneficial effects of 'SS31' were more pronounced in roots with a diameter of 1 to 2 mm. Moreover, the TSS of the berry grew by 10.1%, and the total TA decreased by 15.4% following 'SS31' fertilization; however, the berry weight of 'Benifuji' grapes treated with 'SS31' was lower than that of the control. Additionally, the application of 'SS31' substantially elevated the formation of volatile compounds in the berries, especially those derived from the fatty acid metabolic pathway. A network analysis revealed that root morphology played a pivotal role in enhancing fruit quality, whereas a notable positive correlation existed between the root vessel anatomy and VOCs within fruits. These findings offered a fresh insight into how root morphology and water conductivity may be related to the stimulation of plant growth and fruit quality when the plant growth-promoting rhizobacterium is used. Despite the preliminary findings of this study, the limited sample size and experimental duration posed constraints on the generalizability of the hypothesis. Future research is imperative to further explore this hypothesis among diverse microorganisms, thereby expanding the understanding of the underlying mechanisms and potential applications.

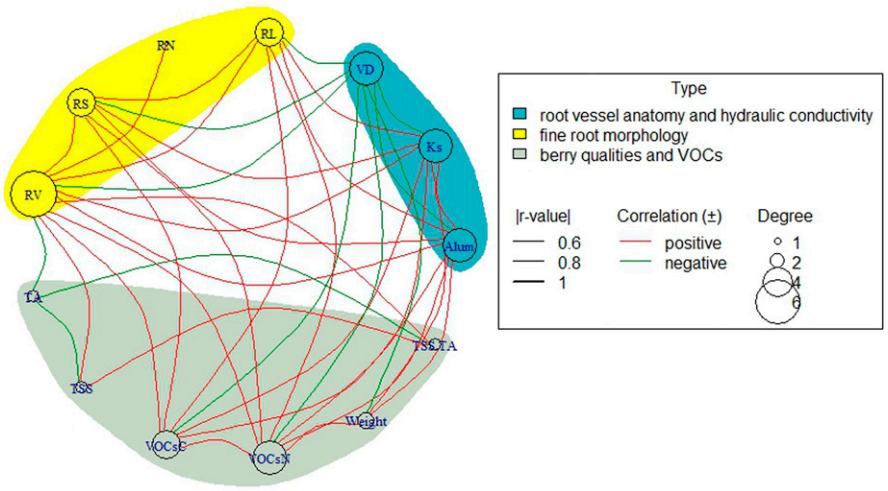

Fig. 8. Network analyses of berry qualities and volatile compounds with fine root characteristics in 'Benifuji' grapes. A_{lum} = root vessel lumen area; K_s = root hydraulic conductivity; RL = root length; RN = root number; RS = root surface area; RV = root volume; TA = berry titratable acidity; TSS = berry total soluble solids; weight = single berry weight; TSS.TA = ratio of total soluble solids to titratable acidity; VD = root vessel density; VOCsC = the total content of volatile organic compounds; VOCsN = the number of volatile organic compounds.

References Cited

Alem H, Rigou P, Schneider R, Ojeda H, Torregrosa L. 2019. Impact of agronomic practices on grape aroma composition: A review. J Sci Food Agr. 99(3):975–985. https://doi.org/10.1002/jsfa.9327.

Alsina MM, Smart DR, Bauerle T, de Herralde F, Biel C, Stockert C, Negron C, Save R. 2011. Seasonal changes of whole root conductance by a drought-tolerant grape root system. J Expt Bot. 62(1):99–109. https://doi.org/10.1093/jxb/erq247.

Anderson JM, Ingram JSI. 1993.Tropical soil biology and fertility: A handbook of methods. Oxford University Press, Oxford UK.

Aslantas R, Cakmakci R, Sahin F. 2007. Effect of plant growth promoting rhizobacteria on young apple tree growth and fruit yield under orchard conditions. Scientia Hortic. 111(4):371–377. https://doi.org/10.1016/j.scienta.2006.12.016.

Botha A. 2011. The importance and ecology of yeasts in soil. Soil Biol Biochem. 43(1):1–8. https://doi.org/10.1016/j.soilbio. 2010.10.001.

Chen TC, Xu T, Shen LY, Zhang TY, Wang LR, Chen ZH, Wu YY, Yang J. 2022a. Effects of girdling and foliar fertilization with K on physicochemical parameters phe-nolic and volatile composition in 'Hanxiangmi' table grape. Horticulturae. 8(5):388. https://doi.org/10.3390/horticulturae8050388.

Chen XR, Yang F, Bai CW, Shi QR, Hu S, Tang XY, Peng LJ, Ding HX. 2022b. *Bacillus velezensis* strain GUMT319 reshapes soil microbiome biodiversity and increases grape yields. Biology. 11(10):1486. https://doi.org/10.3390/biology11101486.

Chinachanta K, Shutsrirung A, Herrmann L, Lesueur D, Pathom-Aree W. 2021. Enhancement of the aroma compound 2-acetyl-1-pyrroline in Thai Jasmine rice (*Oryza sativa*) by rhizobacteria

under salt stress. Biology. 10(10):1065. https://doi.org/10.3390/biology10101065.
Coombe BG. 2010. Growth stages of the grapevine: Adoption of a system for identifying grapevine growth stages. Aust J Grape Wine Res. 1(2):104–110. https://doi.org/10.1111/j.1755-0238.1995.tb00086.x.
Duan BB, Li L, Chen GQ, Su-Zhou C, Li YS, Merkeryan H, Liu W, Liu X. 2021a. 1-aminocyclopropane-1-carboxylate deaminase-producing plant growth-promoting rhizobacteria improve drought stress tolerance in grapevine (*Vitis vinifera* L.). Front Plant Sci. 12:706990. https://doi.org/10.3389/fpls.2021.706990.
Duan WK, Peng LY, Zhang H, Han L, Li YQ. 2021b. Microbial biofertilizers increase fruit aroma content of *Fragaria×ananassa* by improving photosynthetic efficiency. Alexandria Eng J. 60(6):5323–5330. https://doi.org/10.1016/j.aej.2021.04.014.
Dudareva N, Klempien A, Muhlemann JK, Kaplan I. 2013. Biosynthesis, function and metabolic engineering of plant volatile organic compounds. New Phytol. 198(1):16–32. https://doi.org/10.1111/nph.12145.
El-Serafy RS, El-Sheshtawy AA. 2020. Effect of nitrogen fixing bacteria and moringa leaf extract on fruit yield estragole content and total phenols of organic fennel. Scientia Hortic. 265:1–10. https://doi.org/10.1016/j.scienta.2020.109209.
Esitken A, Karlidag H, Ercisli S, Turan M, Sahin F. 2003. The effect of spraying a growth promoting bacterium on the yield growth and nutrient element composition of leaves of apricot (*Prunus armeniaca* L. cv. Hacihaliloglu). Aust J Agric Res. 54(4):377–380. https://doi.org/10.1071/ar02098.
Frankeberger WT, Johanson JB. 1983. Method of measuring invertase activity in soils. Plant Soil. 74(3):301–311.
Gebauer R, Volarik D. 2013. Root hydraulic conductivity and vessel structure modification with increasing soil depth of two oak species: *Quercus pubescens* and *Quercus robur*. Trees. 27(3):523–531. https://doi.org/10.1007/s00468-012-0805-5.
Gosewinkel U, Broadbent FE. 2008. Conductimetric determination of soil urease activity. Commun Soil Sci Plant Anal. 15(11):1377–1389. https://doi.org/10.1080/00103628409367564.
Gu JC, Xu Y, Dong XY, Wang HF, Wang ZQ. 2014. Root diameter variations explained by anatomy and phylogeny of 50 tropical and temperate tree species. Tree Physiol. 34(4):415–425. https://doi.org/10.1093/treephys/tpu019.
Guan S, Zhang D, Zhang Z. 1986. Soil enzymes and research methods. Agriculture Press, Beijing, China.
Gupta VVSR, Bramley RGV, Greenfield P, Yu J, Herderich MJ. 2019. Vineyard soil microbiome composition related to rotundone concentration in Australian cool climate 'Peppery' shiraz grapes. Front Microbiol. 10:1–19. https://doi.org/10.3389/fmicb.2019.01607.
Hacke HU, Spicer R, Schreiber SG, Plavcová L. 2016. An ecophysiological and developmental perspective on variation in vessel diameter. Plant Cell Environ. 40(6):831–845. https://doi.org/10.1111/pce.12777.
Hafeez FY, Yasmin S, Ariani D, Mehboobur R, Zafar Y, Malik KA. 2006. Plant growth-promoting bacteria as biofertilizer. Agron Sustain Dev. 26(2):143–150. https://doi.org/10.1051/agro:2006007.
Hua MY, Song LF, Cui SJ, Tong YN, Kong WD, Yang XL. 2019. Effects of combined application of *Streptomyces saraceticus* and compound fertilizer on yield and quality of strawberry. J Hebei Agric Univ. 4(2):81–84. https://doi.org/10.13320/j.cnki.jauh.2019.0037.
Ibrahim HK, Abd ELGS, Khalil AA. 2005. Effect of soil application of different treatments on growth fruiting parameters fruit properties and leaf nutrient content of "Canino" apricot trees. J Agric Sci Mansoura Univ. 30:1617–1629. https://doi.org/10.21608/jpp.2005.237195.
Itelima JU, Bang WJ, Onyimba IA, Sila MD, Egbere OJ. 2018. Bio-fertilizers as key player in enhancing soil fertility and crop productivity: A review. Direct Res J Agric Food Sci. 6:73–83. https://doi.org/10.26765/DRJAFS.2018.4815.
Jia N, Yin YG, Li MM, Han B, Sun Y, Liu CJ, Tian KQ, Liu SY, Wang YJ, Guo ZJ. 2023. Berry thinning affects the fruit quality composition of two table grape cultivars under linkage greenhouse conditions. HortScience. 58(1):134–140. https://doi.org/10.21273/hortsci16952-22.
Jimenez-Gomez A, Garcia-Estevez I, Garcia-Fraile P, Teresa Escribano-Bailon M, Rivas R. 2020. Increase in phenolic compounds of *Coriandrum sativum* L. after the application of a *Bacillus halotolerans* biofertilizer. J Sci Food Agr. 100(6):2742–2749. https://doi.org/10.1002/jsfa.10306.
Kafi SA, Arabhosseini S, Karimi E, Koobaz P, Mohammadi A, Sadeghi A. 2021. *Pseudomonas putida* P3-57 induces cucumber (*Cucumis sativus* L.) defense responses and improves fruit quality characteristics under commercial greenhouse conditions. Scientia Hortic. 280(1):109942. https://doi.org/10.1016/j.scienta.2021.109942.
Karakurt H, Kotan R, Dadasoglu F, Aslantas R, Sahin F. 2011. Effects of plant growth promoting rhizobacteria on fruit set pomological and chemical characteristics color values and vegetative growth of sour cherry (*Prunus cerasus* cv. Kutahya). Turk J Biol. 35(3):283–291. https://doi.org/10.3906/biy-0908-35.
Kirfel K, Leuschner C, Hertel D, Schuldt B. 2017. Influence of root diameter and soil depth on the xylem anatomy of fine- to medium-sized roots of mature beech trees in the top- and subsoil. Front Plant Sci. 8:1194. https://doi.org/10.3389/fpls.2017.01194.
Lacroux F, Tregoat O, Van Leeuwen C, Pons A, Tominaga T, Lavigne-Cruege V, Dubourdieu D. 2008. Effect of foliar nitrogen and sulphur application on aromatic expression of *Vitis vinifera* L. cv. Sauvignon blanc. J Int Sci Vigne Vin. 42(3):125–132. https://doi.org/10.20870/oeno-one.2008.42.3.816.
Liu M, Liu X, Cheng BS, Ma XL, Lyu XT, Zhao XF, Ju YL, Min Z, Fang YL. 2016. Selection and evaluation of phosphate-solubilizing bacteria from grapevine rhizospheres for use as biofertilizers. Span J Agric Res. 14(4):E1106. https://doi.org/10.5424/sjar/2016144-9714.
Lu HD, Wu ZS, Wang WF, Xu XL, Liu XC. 2020. Rs-198 liquid biofertilizers affect microbial community diversity and enzyme activities and promote *Vitis vinifera* L. growth. BioMed Res Int. 8321462. https://doi.org/10.1155/2020/8321462.
Ma ZH, Yang SJ, Mao J, Li WF, Li W, Zuo CW, Chu MY, Zhao X, Zhou Q, Chen BH. 2021. Effects of shading on the synthesis of volatile organic compounds in 'Marselan' Grape Berries (*Vitis vinifera* L.). J Plant Growth Regul. 40(2):679–693. https://doi.org/10.1007/s00344-020-10123-2.
Marulanda A, Azcon R, Chaumont F, Ruiz-Lozano JM, Aroca R. 2010. Regulation of plasma membrane aquaporins by inoculation with a *Bacillus megaterium* strain in maize (*Zea mays* L.) plants under unstressed and salt-stressed conditions. Planta. 232(2):533–543. https://doi.org/10.1007/s00425-010-1196-8.
Miransari M. 2010. Contribution of arbuscular mycorrhizal symbiosis to plant growth under different types of soil stress. Plant Biol. 12(4):563–569. https://doi.org/10.1111/j.1438-8677.2009.00308.x.
Mitter B, Brader G, Afzal M, Compant S, Naveed M, Trognitz F, Sessitsch A. 2013. Advances in elucidating beneficial interactions between plants soil and bacteria. Adv Agron. 121:381–445. https://doi.org/10.1016/B978-0-12-407685-3.00007-4.
Mosa WFAE-G, Paszt LS, Frac M, Trzcinski P, Przybyl M, Treder W, Klamkowski K. 2016. The influence of biofertilization on the growth yield and fruit quality of cv. Topaz apple trees. Hortic Sci. 43(3):105–111. https://doi.org/10.17221/154/2015-HORTSCI.
Naveed M, Qureshi MA, Zahir ZA, Hussain MB, Sessitsch A, Mitter B. 2015. L- tryptophan-dependent biosynthesis of indole-3-acetic acid (IAA) improves plant growth and colonization of maize by *Burkholderia phytofirmans* PsJN. Ann Microbiol. 65(3):1381–1389. https://doi.org/10.1007/s13213-014-0976-y.
Nima ZX, Gao X, Liu GY, Bianba ZM, Zhang HG. 2017. A study on application of introduced *Streptomyces saraceticus* in agricultural area of Tibet. Tibet J Agric Sci. 39(2):7–12. https://doi.org/10.3969/j.issn.1005-2925.2017.02.003.
Paul K, Viviana H, Ingo B, Christoph L. 2012. Hydraulic properties and embolism in small-diameter roots of five temperate broad-leaved tree species with contrasting drought tolerance. Ann For Sci. 69(6):693–703. https://doi.org/10.1007/s13595-012-0189-0.
Phogat V, Skewes MA, Cox JW, Sanderson G, Alam J, Simunek J. 2014. Seasonal simulation of water salinity and nitrate dynamics under drip irrigated mandarin (*Citrus reticulata*) and assessing management options for drainage and nitrate leaching. J Hydrol. 513:504–516. https://doi.org/10.1016/j.jhydrol.2014.04.008.
Rajaei H, Yazdanpanah P, Dadbin M, Haghighi AAK, Sepaskhah AR, Eslamzadeh T. 2013. Comparison of root anatomy and xylem vessel structure in rain-fed and supplementary irrigated 'Yaghooti-Syah Shiraz' grapevine (*Vitis vinifera* L.). Hortic Environ Biotechnol. 54(4):297–302. https://doi.org/10.1007/s13580-013-0079-x.
Ramirez-Carino HF, Morales I, Guadarrama-Mendoza PC, Gonzalez-Terreros E, Martinez-Gutierrez GA, Dunlap CA, Valadez-Blanco R. 2023. Biofertilizing effect of putative plant growth promoting rhizobacteria in vitro and in tomatillo seedlings (*Physalis ixocarpa* Brot.). Scientia Hortic. 308:111567. https://doi.org/10.1016/j.scienta.2022.111567.
Ruggiero C, Di Lorenzo R, Angelino G, Scaglione G, Gambino C, Di Vaio C. 2012. Root hydraulic conductivity in three self-rooted and grafted table grape cultivars. J Int Sci Vigne Vin. 46(3):177–183. https://doi.org/10.20870/oeno-one.2012.46.3.1519.
Sasaki T, Ando S, Miyazawa T, Yamauchi D, Enomoto T. 2020. Characterisation of 'Ruby Roman' table grapes (*Vitis labruscana* Bailey) by sensory evaluation and analysis of aroma and taste compounds. Food Sci Technol Res. 26(3):423–434. https://doi.org/10.3136/fstr.26.423.
Schuman MC, Baldwin IT. 2018. Field studies reveal functions of chemical mediators in plant

interactions. Chem Soc Rev. 47(14):5338–5353. https://doi.org/10.1039/c7cs00749c.

Spaepen S, Dobbelaere S, Croonenborghs A, Vanderleyden J. 2008. Effects of *Azospirillum brasilense* indole-3-acetic acid production on inoculated wheat plants. Plant Soil. 312(1–2): 15–23. https://doi.org/10.1007/s11104-008-9560-1.

Stamford NP, Andrade IP, da Silva S Jr, Lira MA Jr, de Rosalia e Silva Santos CE, Santiago de Freitas AD, Van Straaten P. 2011. Nutrient uptake by grape in a Brazilian soil affected by rock biofertilizer. J Soil Sci Plant Nutr. 11(4):79–88. https://doi.org/10.4067/s0718-95162011000400006.

Su H, Tian SF, Shang JY, Wang D, Huang JQ, Wang CX. 2020. Effects of 'SS31' microbial fertilizer on soil microbial metabolism and leaf fluorescence characteristics of Muscat Hamburg grape. J Jilin Agric Univ. 45:285–297. https://doi.org/10.13327/j.jjlau.2020.5723.

Sun QY, Zhao Y, Zhu SS, Du F, Mao RZ, Liu LJ, Zhu YF, Li S, Sun M, Tian B. 2022. Rain-shelter cultivation affects the accumulation of volatiles in 'Shuijing' grape berries during development. HortScience. 57(8):877–888. https://doi.org/10.21273/hortsci16567-22.

Tarin MWK, Fan LL, Shen L, Lai JL, Tayyab M, Sarfraz R, Chen LY, Ye J, He TY, Rong JD, Chen LG. 2020. Effects of different biochars amendments on physiochemical properties of soil and root morphological attributes of *Fokenia hodginsii* (Fujian cypress). Appl Ecol Environ Sci Res. 17(5):11107–11120. https://doi.org/10.15666/aeer/1705_1110711120.

Tyree MT, Ewers FW. 1991. The hydraulic architecture of trees and other woody plants. New Phytol. 119(3):345–360. https://doi.org/10.1111/j.1469-8137.1991.tb00035.x.

Tyree MT, Zimmermann MH. 2002. Xylem structure and the ascent of sap (2nd ed). Springer-Verlag, Berlin, Germany.

Velasquez A, Valenzuela M, Carvajal M, Fiaschi G, Avio L, Giovannetti M, D'Onofrio C, Seeger M. 2020. The arbuscular mycorrhizal fungus *Funneliformis mosseae* induces changes and increases the concentration of volatile organic compounds in *Vitis vinifera* cv. Sangiovese leaf tissue. Plant Physiol Biochem. 155: 437–443. https://doi.org/10.1016/j.plaphy.2020.06.048.

Walker V, Bertrand C, Bellvert F, Moenne-Loccoz Y, Bally R, Comte G. 2011. Host plant secondary metabolite profiling shows a complex strain-dependent response of maize to plant growth-promoting rhizobacteria of the genus *Azospirillum.* New Phytol. 189(2):494–506. https://doi.org/10.1111/j.1469-8137.2010.03484.x.

Wang WN, Wang Y, Hoch G, Wang ZQ, Gu JC. 2018. Linkage of root morphology to anatomy with increasing nitrogen availability in six temperate tree species. Plant Soil. 425(1-2): 189–200. https://doi.org/10.1007/s11104-018-3563-3.

Wang Y, Dong XY, Wang HF, Wang ZQ, Gu JC. 2016. Root tip morphology anatomy chemistry and potential hydraulic conductivity vary with soil depth in three temperate hardwood species. Tree Physiol. 36(1):99–108. https://doi.org/10.1093/treephys/tpv094.

Wu PH, Tsay TT, Chen PC. 2021. Evaluation of *Streptomyces saraciticas* as soil amendments for controlling soil-borne plant pathogens. Plant Pathol J. 37(6):596–606. https://doi.org/10.5423/ppj.oa.08.2021.0131.

Yuan F, Schreiner RP, Qian MC. 2018. Soil nitrogen phosphorus and potassium alter beta-Damascenone and other volatiles in Pinot noir Berries. Am J Enol Viticult. 69(2):157–166. https://doi.org/10.5344/ajev.2017.17071.

Zadworny M, Comas LH, Eissenstat DM. 2018. Linking fine root morphology hydraulic functioning and shade tolerance of trees. Ann Bot. 122(2):239–250. https://doi.org/10.1093/aob/mcy054.

Zanne AE, Westoby M, Falster DS, Ackerly DD, Loarie SR, Arnold SEJ, Coomes DA. 2010. Angiosperm wood structure: Global patterns in vessel anatomy and their relation to wood density and potential conductivity. Am J Bot. 97(2):207–215. https://doi.org/10.3732/ajb.0900178.

Zhang CY, Wang XJ, Ji H, Niu JX. 2014. Research of bio-bacterial manure application in red jujube in southern Xinjiang. Xinjian Agric Sci. 51(9):1644–1651. https://doi.org/10.6048/j.issn.1001-4330.2014.09.012.