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Streptomyces violaceoruber induces root morphological changes in *Solanum lycopersicum* via early epigenetic and transcriptional reprogramming

Valentina Ricciardi [a], Guglielmo Puccio [a,*], Loredana Abbate [a], Teresa Faddetta [b,c], Margot Lo Pinto [b], Ciro Caldiero [a], Giulia Polito [b], Antonio Palumbo Piccionello [b], Giuseppe Gallo [b,c], Francesco Mercati [a], Vincenzo Cavalieri [b,**]

[a] Institute of Biosciences and Bioresources (IBBR), National Research Council, Palermo, Italy
[b] Department of Biological, Chemical and Pharmaceutical Sciences and Technologies (STeBiCeF), University of Palermo, Palermo, Italy
[c] National Biodiversity Future Center, Palermo, Italy

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ABSTRACT

The increasing demand for sustainable agricultural practices has highlighted the potential of Plant Growth-Promoting Bacteria (PGPB) as eco-friendly tools to enhance crop productivity while minimizing environmental impact. Among PGPBs, members of the *Actinomycetota* phylum (formerly known as actinobacteria), and particularly *Streptomyces violaceoruber*, have emerged as promising candidates due to their ability to produce bioactive metabolites, promote plant growth, and modulate plant physiological responses. In this work, we investigated the effects of *S. violaceoruber* on tomato (*Solanum lycopersicum*) *in vitro* - grown seedlings using an integrated phenotypic, volatilomic, transcriptomic, and epigenetic approach. Seedlings were analyzed at seven (T1) and fifteen days (T2) post-inoculation with *S. violaceoruber*. Phenotypic assessment of inoculated seedlings revealed no significant alterations in shoot length or biomass, while a remarkable increase in seedling root diameter and the formation of aerial roots was observed. Transcriptomic analyses showed substantial transcriptional reprogramming, with a greater number of differentially expressed genes (DEGs) at T1, in particular involved in the regulation of biological processes, metabolic pathways, and responses to external stimuli, such as light. Co-expression network analysis of four root-associated bait genes further confirmed that these pathways are primary targets of *S. violaceoruber* effects. Epigenetic profiling of treated plant roots revealed an increase in global DNA methylation (5-methylcytosine) levels, along with a significant enrichment of histone post-translational modifications associated with permissive chromatin at the bait gene loci. Overall, *S. violaceoruber* inoculation induced notable molecular and developmental changes in tomato seedlings, reinforcing its potential as a sustainable biofertilizer. These findings provide new insights into PGPB–plant interactions and contribute to the development of environmentally-friendly strategies for crop improvement.

1. Introduction

The global demand for food is rapidly increasing. Consequently, issues resulting from intensive agricultural practices, combined with the challenges posed by climate change, demand for the development of environmentally sustainable solutions (Rehman et al., 2022).

Traditional agricultural practices rely heavily on chemical fertilizers and pesticides, that, while effective in boosting yields, contribute to soil depletion, water contamination, and loss of biodiversity (Singh and Singh, 2017; Maaz et al., 2025). To mitigate negative impacts, sustainable alternatives such as biostimulants could be a promising solution. Biostimulants can improve plant growth conditions through different mechanisms (Bhardwaj et al., 2014). Current regulations (Regulation (EU) 2019/1009, https://eur-lex.europa.eu/eli/reg/2019/1009/oj/eng) divide them into two main categories: *i*) non-microbials biostimulants and bioactive substances, and *ii*) microbials biostimulants, including Plant Growth-Promoting Bacteria (PGPB) as well as arbuscular mycorrhizal fungi (AMF) (Du Jardin, 2015; Mauceri et al., 2024).

PGPB have recently emerged as especially promising candidates for

* Corresponding author.
** Corresponding author.
E-mail addresses: guglielmo.puccio@cnr.it (G. Puccio), vincenzo.cavalieri@unipa.it (V. Cavalieri).

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enhancing crop productivity while minimizing the negative impact on the environment. Their beneficial effects are due to the ability to stimulate plant growth, optimizing plant responses to external conditions (Kumar et al., 2022). The known mechanisms include: *i)* production of bioactive metabolites such as phytohormones, antibiotics and antifungals including those released as Volatile Organic Compounds (VOCs); *ii)* enhanced nutrient availability through different metabolic processes, such as nitrogen (N) fixation, phosphorus (P) solubilization, and improved iron (Fe) uptake; *iii*) increased photosynthetic efficiency; *iv*) induction of changes in root architecture; and *v)* improved resistance to both biotic and abiotic stresses (Backer et al., 2018).

Members of the *Actinomycetota* phylum (formerly known as actinobacteria) are usually soil inhabitants with a saprophytic lifestyle. They are usually isolated from soil, rhizosphere and root tissues, where they are among the major components of microbial populations (Lee et al., 2021; Sáhó et al., 2024). The importance of members of this phylum relies on their role in the productivity of agricultural and forest fields. They are able to contribute to the soil systems of those ecosystems by significantly influencing nutrient cycling, improving, as a result, plant health and growth (Barka et al., 2016; Lee et al., 2021). Because of this, and their ability to colonize plants and to act as biocontrol agents, they are considered functional PGPB (Khoso et al., 2024). Within the *Actinomycetota* phylum, *Streptomyces violaceoruber* was characterized for its promising plant growth promoting (PGP) traits found to enclose a rich arsenal of bioactive molecules in the secreted metabolome - including antibiotics and siderophores (Faddetta et al., 2023). *In vivo* assays performed on tomato (*Solanum lycopersicum* L) seeds treated with this actinobacterium revealed improved germination index and growth of the seedlings (Faddetta et al., 2023). Furthermore, *S. violaceoruber* was proven to produce also VOCs likely to possess antimicrobial activity, and the ability to modulate tomato plant volatilome and global DNA methylation (Faddetta et al., 2023).

Tomato is one of the most important horticultural crops worldwide, given its role as both staple food and high-value commercial crop (Fibiani et al., 2022). Its economic significance is accompanied by its importance as a model organism in plant research due to the well-characterized genome, ease of cultivation, and relevance in studies related to plant-microbe interactions, stress responses, and metabolic regulation (Liu et al., 2022; Yuan et al., 2016). Because of the global reliance on tomato production and the increasing challenges posed by climatic changes and related biotic and abiotic stresses, improving its growth and resilience through sustainable approaches is necessary.

The inoculation of PGPB in tomato cultivation practices has shown promising results in this context, with multiple studies reporting significant improvements for plant growth, yield, and stress tolerance (Abbamondi et al., 2016; Zampieri et al., 2023). Nevertheless, further efforts are needed to understand the specific interactions between tomato plants and beneficial bacterial strains, shedding light on the involved molecular mechanisms, to optimize their application under different agricultural conditions (Diwan et al., 2022).

To gain a comprehensive understanding of the PGPB-plant interactions, omics-based approaches can be considered valuable tools. In recent studies, combined transcriptomic, metabolomic, and proteomic results allowed to highlight that *K. rhizophila* inoculation improved tomato plant growth, modulating energy regulators, sugars, and amino acids pathways (Mauceri et al., 2024). Similarly, a multi-omics investigation underlined that the PGPB B13 was able to promote root growth in *Leymus chinensis*, enhancing carbohydrates, energy, and amino acid metabolism (Yuan et al., 2025).

In fact, transcriptomics and epigenetic analyses have significantly advanced the understanding of plant–PGPB interactions in many studies. They allowed to elucidate plant gene expression responses to PGPB inoculation, highlighting the regulation of key pathways involved in nutrient uptake, hormone signaling, and stress responses (Backer et al., 2018). Moreover, they revealed that PGPB are able to induce stable epigenomic reprogramming in host plants, leading to enhanced tolerance to abiotic stress and improved biomass production, even in the absence of the continued presence of the microbial inoculant (Liu et al., 2022). These omics-based insights made it possible to identify molecular markers and regulatory networks associated with beneficial traits, facilitating the rational design and application of microbial consortia tailored to specific crop and environmental contexts. Within this framework, species belonging to the Streptomyces genus emerge as primary candidates for in-depth molecular investigation, given their renowned capacity to modulate plant physiology through complex secondary metabolism. Specifically, *Streptomyces violaceoruber* represents a promising but still under-explored biostimulant, whose interaction with high-value crops requires detailed multi-omics characterization to decode the underlying growth-promoting signals.

The present study focused on the inoculation of the PGPB *S. violaceoruber* into *in vitro* grown tomato seedlings, evaluating its potential to promote plant growth and development as a post-germination treatment. Key molecular changes were highlighted using transcriptomics, epigenetics and volatilomics approaches. The actinobacterial inoculation revealed a considerable impact on root architecture, and on the expression of genes involved in the response to external stimuli, in particular those involved in the photosynthetic machinery, and those underlining hormonal regulation of plants metabolism. Altogether, these findings confirmed the potential of this strain as biofertilizer, bringing new insights into plant-PGPB interactions for the development of sustainable agriculture solutions.

2. Materials and methods

2.1. Bacterial growth conditions

Streptomyces violaceoruber DSM 40783, described and characterized in Faddetta et al. (2023), was used for this study. To prepare the inoculum, 10 μL of a 20% (v/v) glycerol stock containing $(3 \pm 1) \times 10^{10}$ spores mL^{-1} - corresponding to an inoculum size on the order of 10^8 spores - was inoculated into 10 mL of R5A medium (López-García et al., 2018) and incubated at 30 °C for 72 h with shaking at 180 rpm.

2.2. Plant material and treatment

For this experiment, a total of 144 Tomato seedlings (*S. lycopersicum* cv "Red Cherry") were grown *in vitro*. Briefly, tomato seeds were surface sterilized by vigorous shaking in ethanol solution (70%) for 2 min. After that, the seeds were shaken for 6-7 min in NaOCl (4% available chlorine) and rinsed three times in sterile water. For *in vitro* seed culture/seedling growth, Murashige and Skoog (MS) medium agarized with 7 g L^{-1} phytagar (Sigma Chemical Co., St. Louis, Mo, USA), 20 g L^{-1} sugar (Duchefa, Haarlem, The Netherlands) was used. The medium was poured inside 50 mL tubes, where seeds were sown. The tubes were placed in a growth chamber (25 ± 2 °C, 65–75% relative humidity, 16 h of daylight with a light intensity of 3000 lux). Half of the cultivated seedlings (hereafter referred to as V seedlings) were inoculated with 1 mL of a PGPB suspension obtained by a 1:10 dilution in water of *S. violaceoruber* cultures (≈3% *v/v* packed mycelium) performed in R5A growth medium at 30 °C for 72 h (Faddetta et al., 2023); while the others (thereafter referred as Ct seedlings) were treated with 1 mL of distilled water as control condition. For both treatments, three biological replicates for each application (transcriptomics, epigenetics, and volatile organic compound profiles), were collected at 7 (T1) and 15 (T2) days after *S. violaceoruber* inoculation. Fresh material of whole seedlings for each replicate was used for VOCs analysis, while samples for RNA Sequencing were stored at −80 °C. The remaining seedlings were employed to investigate the PGPB effect on plant growth. Seedlings were characterized at each condition and timepoint for shoot length, presence of aerial roots, roots length and diameter. In addition, at T2, fresh and dry weight of Ct and V were assessed. Two-way ANOVA and Tukey test ($p < 0.05$) were performed to assess the significance of results, using R

multcomp package (Hothorn et al., 2008). The applied statistical model evaluated both the main effects of the factors (treatment, time), and the interaction between them (Treatment:Time).

2.3. Volatilome analysis

One-hundred mg of fresh material of whole seedlings for each replicate previously collected were used for VOCs analysis. Solid Phase Micro-Extraction (SPME) coupled to GC/MS was chosen to analyze volatile compounds due to the approach simplicity, based on no solvent use and little sample manipulation (Polito et al., 2022). Due to the kind of plant material studied (young seedlings, with limited surface), and the detection capability, the VOCs profile investigation was carried out only at T2. For each chemical compound, abundance differences between control (C) and treatment (V) conditions were assessed using one way ANOVA applied to raw intensity values. Log2 fold change values were calculated as log2(V/C) using group means. To control for false positives arising from multiple testing, ANOVA p values were adjusted using the Benjamini–Hochberg false discovery rate (FDR), using the R rstatix package (https://CRAN.R-project.org/package=rstatix). Compounds with FDR adjusted p values < 0.05 were considered significant.

2.4. RNA extraction and transcriptomic analysis

For RNA extraction the frozen seedlings, previously stored at – 80 °C, were ground with liquid nitrogen and reduced to a fine powder. Seedlings total RNA was isolated using NucleoSpin Plant RNA extraction kit (Macherey-Nagel, Düren, Germany), and treated with DNAse according to the kit protocol. RNA quantity and integrity were evaluated using Agilent Bioanalyzer RNA nanochip (Agilent, Wilmington, DE). The isolated RNA was used to obtain cDNA libraries, using the TruSeq RNA Sample Preparation Kit v2 (Illumina, San Diego, CA, USA), following the protocol described in Puccio et al. (2022). Quality, quantity, and insert size distribution were assessed with an Agilent Bioanalyzer DNA 1000 chip. After quality control, sequence libraries were pooled in equimolar concentration and sequenced on an Illumina NextSeq500 generating 2×100 nt paired-end (PE) reads.

Quality Control (QC) and trimming of raw reads was performed using FastQC (https://www.bioinformatics.babraham.ac.uk/projects/fastqc/) and trimmomatic with default parameters (http://www.usadellab.org/cms/?page=trimmomatic), respectively. Cleaned reads were used for transcript quantification using Salmon (Patro et al., 2017), with default parameters. Normalization of raw counts was performed with the Size Factor normalization of DESeq2 (Love et al., 2014). Variance Stabilized Transformed (VST) data was used for the Principal Component Analysis (PCA) and to build heatmaps. Differentially Expressed Genes (DEGs) were obtained through pairwise comparisons using DESeq2 applying a False Discovery Rate (FDR) threshold of 0.05 and a Fold Change (FC) defined as $|\log_2 FC| > 1$. UpSet plots of DEGs were generated using TBtools-II (Chen et al., 2023). Heatmaps were generated using Pheatmap R package (10.32614/CRAN.package.pheatmap). Four genes, MeCP11, MTase, RCP, and NPH3/RPT2, were selected as primary co-expression 'baits' based on their established biological relevance in root tissues. Using these genes as anchors, we identified specific gene networks through the co-expression network analysis. This was performed using the Cytoscape module Co-Exp-Net-Viz using the entire dataset (Shannon et al., 2003). Highly correlated genes were selected using 1st and 99th percentiles of the Pearson correlation coefficient as threshold. The network was visualized and analyzed using Cytoscape.

GO enrichment analysis of DEGs and of the most abundant gene clusters in the co-expression network was performed using ShinyGO with an FDR cutoff of 0.05 (Xijin Ge et al., 2020). The results were filtered using REVIGO (Supek et al., 2011), removing redundant terms, and then visualized using TBtools-II.

2.5. Quantification of global DNA methylation

Global DNA methylation levels for each sample investigated, referred to as the total level of 5-methylcytosine (5-meC) content, were quantified using MethylFlash Methylated DNA Quantification kit (Epigentek), as previously described (Faddetta et al., 2023; Mauceri et al., 2024). Briefly, 100 ng of genomic DNA per sample, extracted with NucleoSpin Plant II kit (Macherey-Nagel, Düren, Germany), was bound to an ELISA plate and fluorescently labeled for 5-meC detection using specific antibodies. Each sample was run in duplicate alongside with internal controls provided by the kit, and optical density (OD) was measured at 450 nm, corresponding to the absorbance of 5-meC. A standard curve was generated from the positive controls using linear regression, and the resulting slope was used to quantify the total 5-meC content in each sample. Global DNA methylation was expressed as the percentage ratio of sample OD to the OD of the positive controls, after subtracting the negative control OD values. Statistical significance between Ct and V within each time point was assessed using one-way ANOVA followed by Benjamini–Hochberg false discovery rate correction (FDR).

2.6. Chromatin immunoprecipitation (ChIP) assay

ChIP experiments were performed by adapting previously reported methods (Reina et al., 2023; Saleh et al., 2008). Specifically, three independent biological replicates were used, which were distinct from those processed for RNA-Seq analysis, ensuring the reproducibility of the observed interactions across separate experimental batches. Briefly, seedlings roots were fixed in crosslinking buffer (0.4 M sucrose, 10 mM Tris–HCl pH 8, 1 mM PMSF, 1 mM EDTA and 1% formaldehyde) under vacuum for 10 min at room temperature, followed by quenching of the fix with 125 mM glycine under vacuum for additional 5 min. Cross-linked tissues were washed three times with sterile deionized water, quick-frozen in liquid nitrogen, ground into a fine powder, and resuspended in cold nuclei isolation buffer (0.25 M sucrose, 15 mM PIPES pH 6.8, 5 mM MgCl2, 60 mM KCl, 15 mM NaCl, 1 mM CaCl2, 0.9 % Triton X-100, 1 mM PMSF) supplemented with 1:100 protease inhibitor cocktail (Sigma-Aldrich, Merck Life Science, Milan, Italy). After centrifugation at 11,000 g for 20 min, nuclei were resuspended in cold nuclei lysis buffer (50 mM HEPES pH 7.5, 150 mM NaCl, 1 mM EDTA, 1% SDS, 0.1% sodium deoxycholate and 1% Triton X-100, with 1:100 protease inhibitor cocktail), and chromatin was sonicated using a Sonorex Digitec DT103H high-power ultrasonic bath (Bandelin, Berlin, Germany) to an average fragment size of 150 to 500 bp, as determined by agarose gel electrophoresis.

Aliquots of chromatin were immuno-cleared with salmon sperm DNA/protein A-sepharose and immunoprecipitated overnight at 4 °C either in the absence of antibodies or with the anti-acetyl histone H4, the anti-acetyl H3K9, the anti-trimethyl H3K4, the anti-dimethyl H3K9 antisera purchased from Millipore, Merck Life Science, Milan, Italy (cat# 06-866, 07-352, 07-473, and 07-441, respectively) or the anti-trimethyl H3K36 antiserum purchased from Abcam (cat# ab9050). An equivalent aliquot of chromatin, referred to as input control, was withdrawn and processed in parallel with the immunoprecipitated samples. The immune complexes were washed sequentially, eluted with a buffer consisting of 1% SDS and 0.1 M NaHCO3, treated with 0.2 μg/μL RNase A at 37 °C for 2 h and subsequently digested with 0.2 μg/μL proteinase K in 0.3 M NaCl at 65 °C for 4 h to reverse the cross-links.

DNA from chromatin samples was then extracted with phenol/chloroform, precipitated with ethanol and dissolved in 50 μL of nuclease-free water. DNA samples were quantified by readings in a Qubit Fluorometer (Invitrogen, Life Technologies Italia, ThermoFisher Scientific, Monza, Italy) using the Quant-iT dsDNA HS assay kit (Invitrogen, Life Technologies Italia, ThermoFisher Scientific, Monza, Italy).

Finally, to evaluate whether the centrality of the selected bait genes was linked to specific epigenetic modifications, the same four loci

(MeCP11, MTase, RCP, and NPH3/RPT2) were further analyzed via Chromatin Immunoprecipitation (ChIP) assay. The enrichment of gene promoter sequences in 100 pg aliquots of ChIPed DNA and input controls was examined by qPCR, as described above, using the oligonucleotide primers indicated in Table S1. Ct values obtained for each IP sample were normalized to Ct values of the Input, and the percent of Input values were calculated separately for each of the three replicates of an IP sample using the $2^{-\Delta\Delta Ct}$ method (Livak and Schmittgen, 2001).

3. Results

3.1. Morphological changes and VOC profiles modification induced by *S. violaceoruber* treatment in tomato plants

To assess the PGP effects of *S. violaceoruber*, a total of 48 tomato seedlings - with 24 seedlings assigned to the control group (Ct) and 24 to the inoculated group (V) - were evaluated by collecting phenotypical measurements at seven (T1) and fifteen days (T2) after treatment (Fig. 1A; Table S2). Overall, the comparison between V and Ct seedlings did not highlight significant differences concerning the analyzed shoot parameters. At T1, V seedlings showed a lower shoot length (7.20 cm ± 1.81) compared to control plants (9.48 cm ± 1.86), although the difference was not statistically significant. By T2, shoot length was comparable between treatments, with no noticeable variation observed (Fig. 1, Table S2).

By contrast, root-related parameters showed significant differences between V and Ct seedlings (Fig. 1, Table S2). The roots of treated plants revealed increased diameters, considering both the minimum (T1-Ct = 0.22 cm ± 0.00; T1-V = 0.28 cm ± 0.03) and the maximum (T1-Ct = 0.25 cm ± 0.00; T1-V = 0.55 cm ± 0.07) values at T1, and only the maximum diameter at T2 (T2-Ct = 0.35 cm ± 0.00; T2-V = 0.64 cm ± 0.14). On the contrary, root length was significantly higher in Ct compared to V plants. Moreover, samples treated with *S. violaceoruber* were able to develop aerial roots at both time points (T1-V = 4.75 ± 5.89; T2-V = 12.70 ± 2.79), a developmental feature that was completely absent in Ct seedlings (Table S2). Finally, the differences in fresh and dry weight at T2 between conditions (Ct *vs.* V) for each tissue were not significant (Fig. S1).

The VOCs analysis allowed to the detection of 15 distinct metabolites both in control (Ct) and treated tomato seedlings (V) at T2 (Table S3). The major identified compounds included the following structurally distinct classes: monoterpenes (alfa-pinene, beta-pinene, menthadiene, terpinolene, alfa-phellandrene, menthatriene and gamma-terpinene), aromatic monoterpenes (o-Cymene, p-Cymene), sesquiterpenes (aristolene, beta-cadinene, beta-guaiene, NIST26182, caryophyllene) and methylfuran. Interestingly, the *S. violaceoruber* treatment induced a change in the amount of produced VOCs in the tomato profile. Indeed, except for gamma-terpinene, terpenes levels were significantly lower in the V treated samples compared to control seedlings (Fig. 2; Table S4). By contrast, recorded levels of 3-methylfuran, alpha- and beta-pinene were significantly higher in inoculated samples than non-inoculated ones.

3.2. Differentially expressed genes and enriched GO terms associated to *S. violaceoruber* treatment

The effect of *S. violaceoruber* inoculation on tomato seedlings transcriptome was investigated at T1 and T2, identifying the Differentially Expressed Genes (DEGs) among conditions and time points (Table S5; Table S6). The hierarchical clustering of the Variance Stabilized Transformed (VST) data for the most variable genes highlighted four main clusters, with a clear split and different profiling between Ct and V (Fig. 3A). Consistently, the PCA analysis identified the major source of variation between the inoculated (T1-V; T2-V) and not-inoculated samples (T1-Ct, T2-Ct), while a minor distinction was highlighted between corresponding samples at different time points. PC1 and PC2 explained 74% and 8% of the total variance (Fig. 3B).

The pairwise comparisons for each time point between V and Ct seedlings revealed 1.096 down-regulated DEGs and 806 up-regulated DEGs shared between T1 and T2 samples, with the highest number of DEGs at T1 for both up-regulated (915) and down-regulated (879) genes. At T2, the number of DEGs was drastically reduced, with 490 and 475 up-regulated and down-regulated DEGs, respectively (Fig. 3C).

To shed light on the PGPB treatment effects on tomato, molecular processes impacted by *S. violaceoruber* inoculation were investigated by performing a GO enrichment analyses for the main three GO categories

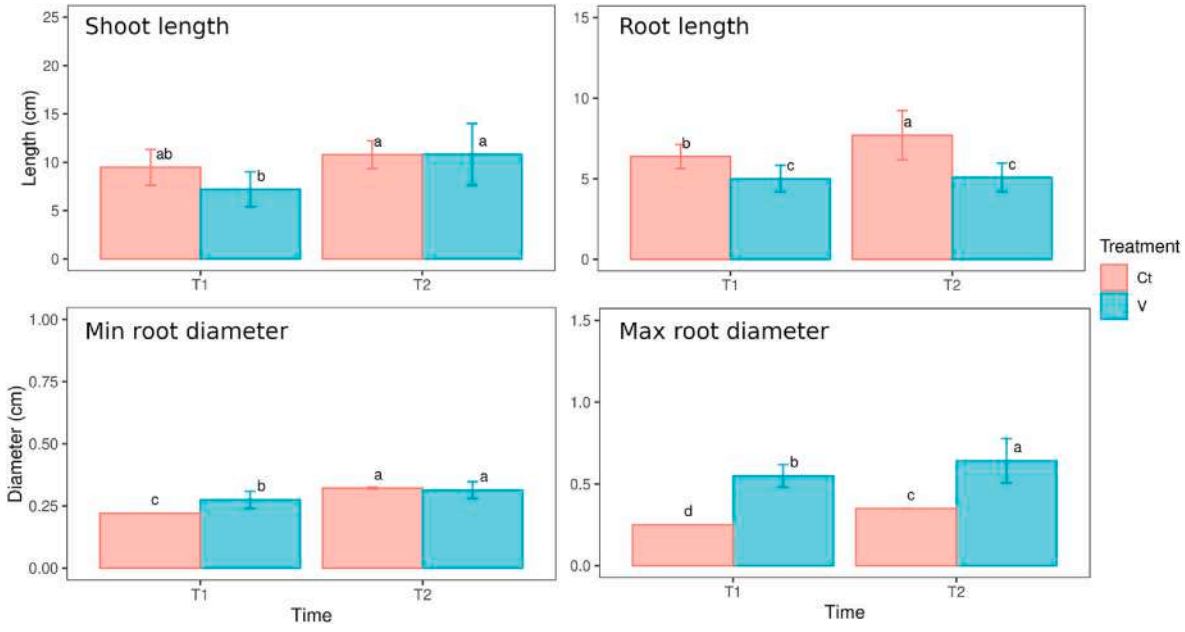

Fig. 1. Phenotypic data collected on control seedlings (Ct) and seedlings inoculated with *S. violaceoruber* (V) at each sampling point (24 seedlings for each condition). **A)** Barplots showing shoot length, root length, minimum root diameter and maximum root diameter collected data. Letters represent statistical significance according to Tukey-test.

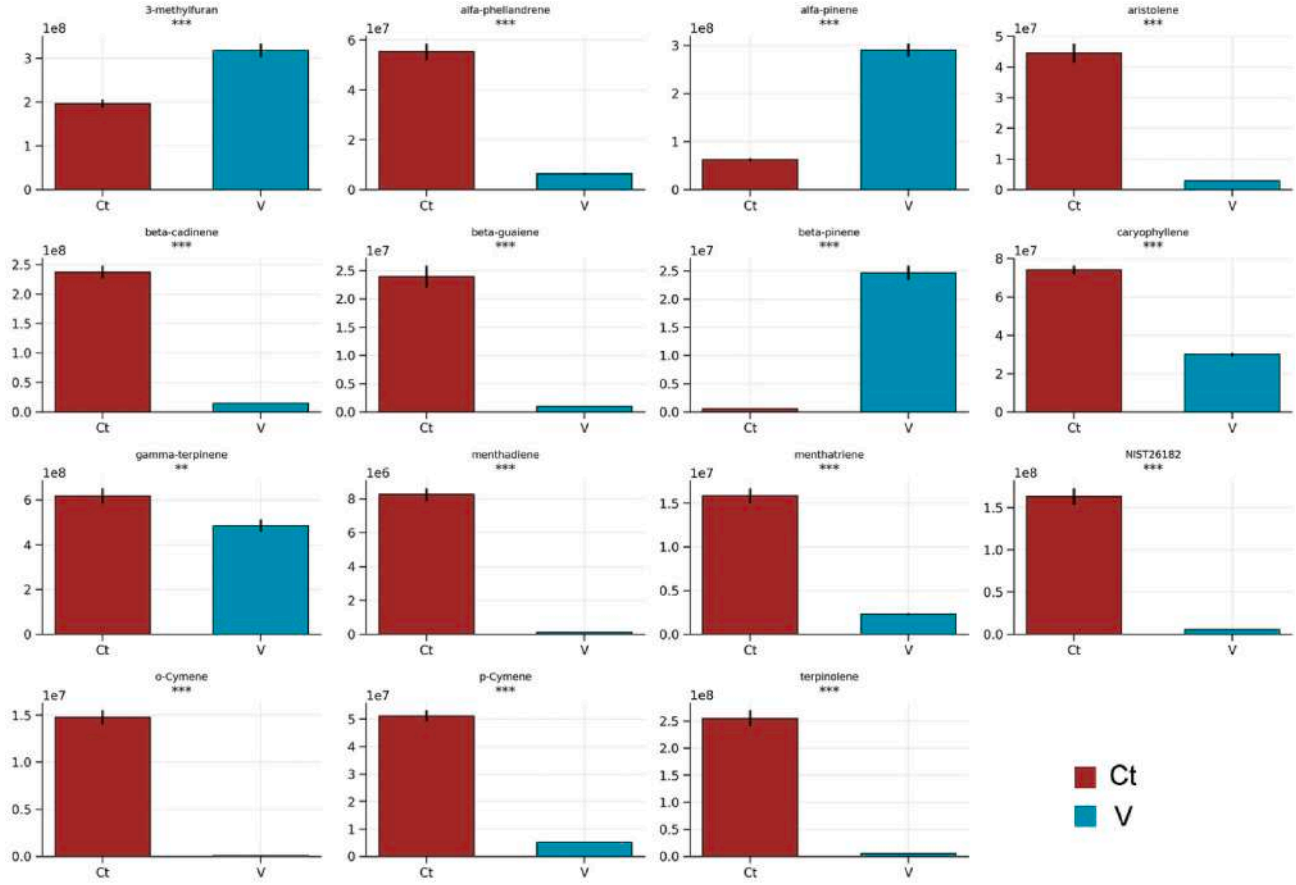

Fig. 2. Differences between control (Ct) and *S. violaceoruber* inoculated samples (V) for each compound (Table S3; Table S4) belonging to the VOCs profiles recorded 15 days after treatment (T2). Bars represent mean values ± SD calculated from three independent biological replicates. Differences between C (darkred) vs. V (cyan) were assessed for each compound using one-way ANOVA followed by Benjamini–Hochberg false discovery rate correction (FDR): *p < 0.05; **p < 0.01; ***p < 0.001 (Table S4).

(Biological Process, BP; Molecular Function, MF; Cellular Component, CC) (Fig. 4; Table S7). According to the analysis, the up-regulated genes isolated in seedlings after seven days (T1) from *S. violaceoruber* inoculation (V) were mainly involved in two BP macro-categories: *i*) Regulation of biological processes, including the regulation of cellular processes such as those involved in primary and secondary metabolism biosynthetic pathways; *ii*) Response to external stimuli, in particular light and other abiotic stimuli. On the other hand, down-regulated genes were primarily associated with general cellular processes, along with more specific pathways, including a) transmembrane transport; b) stress and defense-related responses (including response to chemicals, regulation of jasmonate pathways); c) cell communication (among which Signaling and Signal transduction); and d) other biological mechanisms (e.g. protein phosphorylation, lipidic metabolic processes, cell wall organization and biogenesis) (Fig. 4; Table S7).

At T2, in V seedlings the same responses were found to be conserved for both categories of DEGs. Nonetheless, the highlighted BP revealed more specific and specialized pathways, belonging to the previously identified biological processes. Specifically, the most relevant BP identified for up-regulated genes were photosynthesis related processes, and biosynthetic processes concerning small molecules; while for down-regulated genes transcriptional regulation and regulation of biosynthetic pathways were highlighted (Fig. 4; Table S7).

3.3. Co-expression analysis and histone variations of key genes associated to PGPB inoculation

Four bait genes were selected based on their distinct expression profiles in response to *S. violaceoruber* treatment in tomato roots, as revealed by our integrated multi-disciplinary analysis (Solyc06g068140 – *MeCP11* - Methyl-CpG-binding domain-containing protein; Solyc02g084950 - *MTase* - SAM dependent carboxyl methyltransferase; Solyc07g043130 – *NPH3/RPT2* - NPTH3/RPT2 Root phototropism protein 2; Solyc02g078930 - *RCP* - Root cap protein). These genes represent key molecular players potentially involved in root-specific regulatory or defense responses triggered by the treatment (Table S5; Table S6). Using these four bait genes, a co-expression network was constructed, revealing a total of 2085 genes that were highly correlated with them (Fig. 5; Table S8). Three out of four bait genes (*MeCP11, MTase and NPH3/RPT2*) formed an interconnected sub-network, with 7 main clusters formed based on the shared connections. These were involved in many key biological processes, highlighted by the GO enrichment analysis (Fig. 5). In particular, the most significantly enriched processes were linked to biological regulation of cellular processes in response to stimuli, coupled with the subsequent modifications in biosynthetic pathways (Fig. 5B; Fig. S1). In V seedlings, all the bait genes were strongly up-regulated at T1 ($\log_2$FC ≥ 2), while at T2 three genes maintained a slightly decreased up-regulation ($\log_2$FC ~ 1.5) and Solyc02g084950 was not expressed (Table S5; Table S6). The Methyl-CpG-binding domain-containing protein was found to be correlated to the expression of 1244 genes divided into four distinct clusters, including several transcriptional factors (such as AP2/ERF transcription factors - Solyc06g082590, or Ethylene insensitive 3 transcription factor - Solyc06g073720) and genes like Light-harvesting chlorophyll *a*/b-binding (LHCB) proteins (Solyc09g014520, Solyc12g011450). The SAM dependent carboxyl methyltransferase gene expression was found

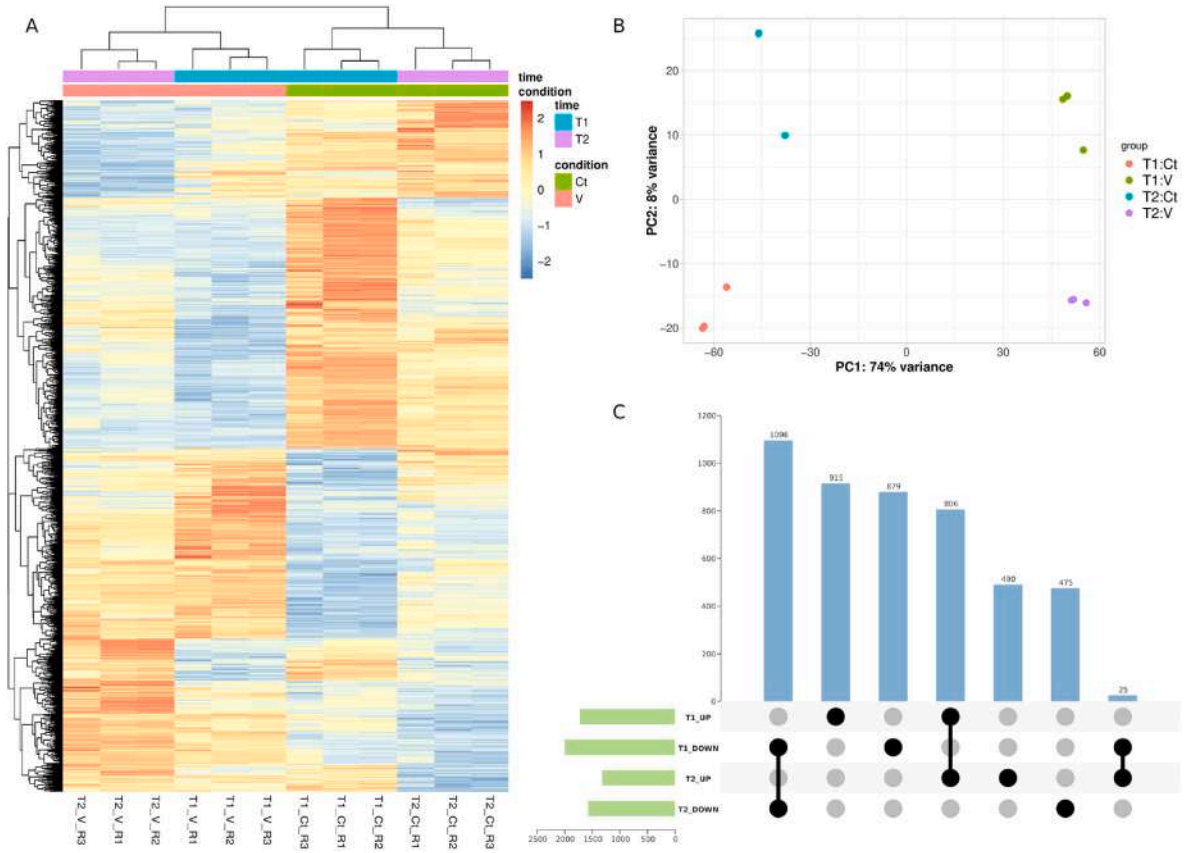

Fig. 3. Differential expression analysis of the RNA-Seq data. **A)** Heatmap showing the Variance Stabilized Transformed (VST) for differentially expressed genes. Samples metadata were shown using a color scheme. Hierarchical clustering was performed on both rows and columns. **B)** Principal Component Analysis (PCA) based on the VST data. **C)** UpSet plot of the Differentially Expressed Genes (DEGs) at both time-points (for each V *vs* Ct comparison). Three biological replicates for each treatment and time were analyzed.

correlated to four different clusters, for a total of 773 genes, sharing two clusters of co-expression with the Methyl-CpG-binding domain-containing protein gene. These clusters included a variety of transporters, such as ABC-transporters (Solyc09g064440), K+ transporters (Solyc04g025880), Nucleotide/sugars transporters (Solyc05g051590), and different cytochromes-coding genes (Solyc04g078360). Moreover, several genes involved in lipid metabolism were detected (Fatty acid desaturases - Solyc07g005510, Plant lipase like genes - Solyc06g064970, Dihydrolipoyl dehydrogenase gene - Solyc12g099100). The NPTH3/RPT2 gene expression was also found correlated to four clusters of expression, two of which in common with the two previously described genes, for a total of 1020 significantly co-expressed genes detected. Finally, the Root cap protein gene expression was found correlated to a single cluster composed of 92 genes, not shared with the other three bait genes (Fig. 5, Table S8). In this cluster, several cytochromes genes were also found (Solyc06g051750), together with Expansines genes (Solyc06g076220) and enzymes involved in primary metabolism, such as glutathione transferases (Solyc09g074850).

3.4. *S. violaceoruber* treatment induce epigenetic modifications in the chromatin of tomato roots

To uncover the epigenetic changes associated to *S. violaceoruber* treatment, global DNA methylation evaluation of tomato seedlings at T1 and T2 was performed. *S. violaceoruber* treatment elicited significant hypermethylation in shoots at T2 and roots at both sampling times (Fig. 6A). In particular, in roots the average 5-meC percentages were increased of about 35% and 98% at T1 and T2, respectively, following *S. violaceoruber* treatment. In shoot tissue, methylation levels did not differ between Ct and V at T1 and showed only a marginal negative change (log2FC = −0.10) (Table S9). In contrast, a significant increase in DNA methylation was observed at T2, corresponding to a positive log2 fold-change (log2FC = +0.25) (Table S9). Root tissue displayed a markedly stronger and earlier response. Indeed, DNA methylation was significantly increased in V compared to Ct already at T1 (FDR-BH = 5.60×10^{-7}; log2FC = +0.46). This effect was further amplified at T2, reaching nearly a two-fold increase over controls (log2FC = +0.97; FDR-BH = 6.80×10^{-14}) (Fig. 6A; Table S9). Together, these results indicate a tissue-specific and time-dependent epigenetic response to *S. violaceoruber*, with roots exhibiting an earlier and more pronounced increase in DNA methylation compared to shoots (Fig. 6A).

Next, the gene-specific epigenetic profiles of four selected genes, namely *MeCP11*, *MTase*, *RCP* and *NPTH3/RPT2*, involved in biological processes occurring in root tissue, was carried out. Investigated genes showed a common trend, which was upregulated following exposure to *S. violaceoruber*. In particular, chromatin immunoprecipitation assay confirmed that, in roots of treated seedlings at T2, the promoter of the aforementioned genes was significantly enriched ($p < 0.05$) in histone post-translational modifications associated with permissive chromatin (Table S10). Such modifications included trimethylation of histone H3K4 and H3K36, and acetylation of histone H3K9 and H4, in the absence of the heterochromatic mark dimethylated H3K9 (Fig. 6B). This type of epigenetic signature typically foreshadows high propensity for gene expression (Cavalieri, 2020), thus justifying the observed increase in mRNA abundance for the selected genes in tomato V seedlings.

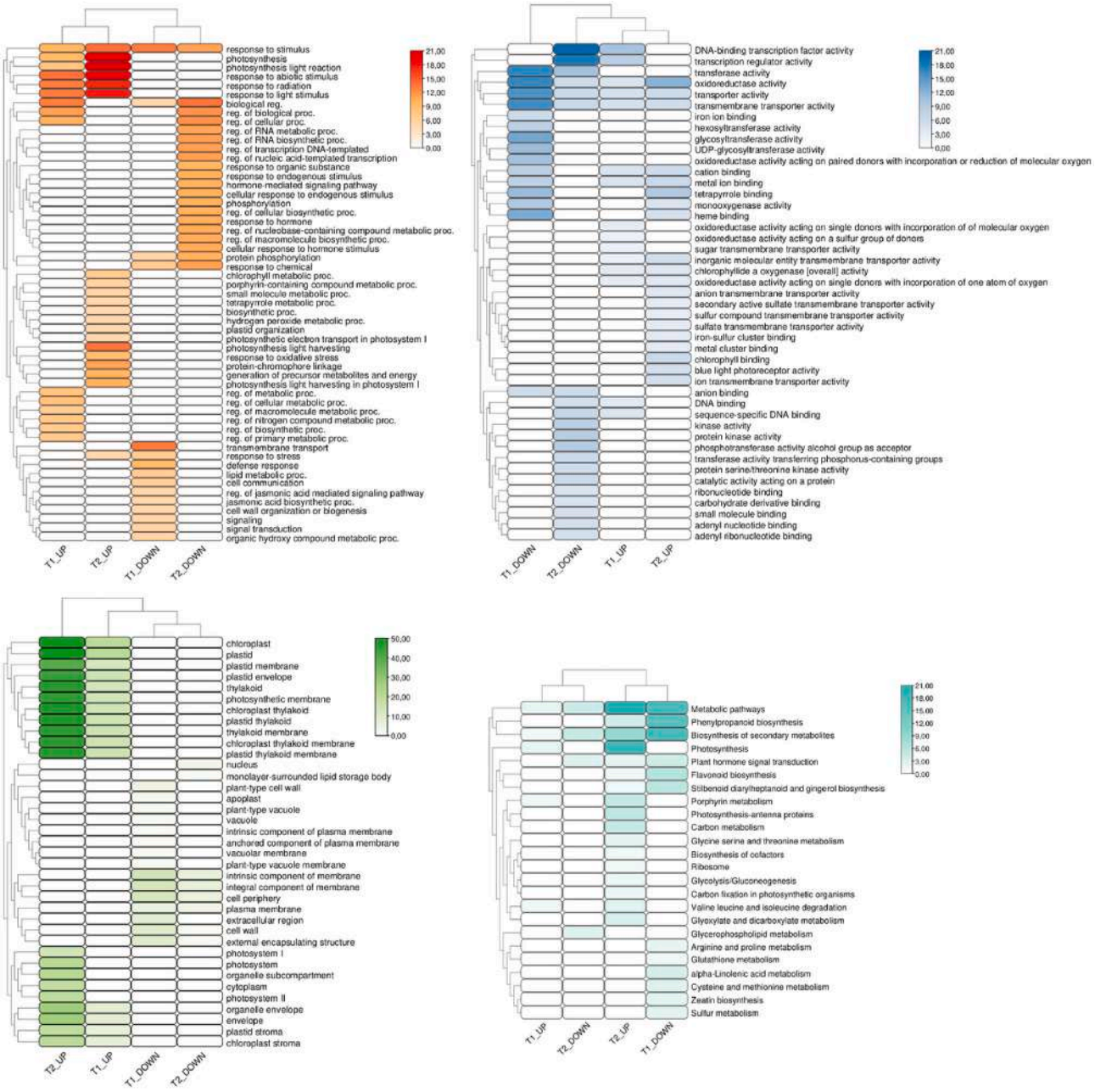

Fig. 4. Gene Ontology (GO) enrichment analysis. Heatmap of the False Discovery Rate (FDR) for each significantly enriched GO term for both up- and down-regulated genes in the samples inoculated with *S. violaceoruber,* at T1 and T2. The four GO categories were highlighted using a color scheme (red: BP, blue: MF, green: CC, light blue: KEGG).

4. Discussion

To be able to feed the growing world population, while reducing the human impact on the environment, agriculture needs to develop new sustainable and efficient solutions. A possible tool that could help to reach the forementioned aim would be the exploitation of PGPB. Because of their characteristics, PGPB can act as biostimulators of metabolic processes, boosting plant agronomical performances (Zuluaga et al., 2021). However, a lot is yet to be discovered about their many mechanisms of action (Rodríguez-Vázquez and Mesa-Marín, 2023).

In this study, the effect of the inoculation of the PGPB *S. violaceoruber* into *in vitro* grown tomato seedlings was investigated through molecular and multi-omics approaches, including volatilomics, transcriptomics, and epigenetic investigations. The results helped to shed light on the peculiar activities of PGPB, revealing the mechanisms linked to the effects on plant development and functioning.

4.1. Transcriptomics analyses highlighted numerous biological processes affected by S. violaceoruber inoculation

Tomato seedlings inoculated with *S. violaceoruber* showed noticeable changes both at phenotypical and molecular level, suggesting the evident ability of this strain to act as a PGPB. Bacteria characterized by PGP traits can enhance plant growth in different ways. Primarily, an improvement of mineral nutrients availability can be determined, for example through siderophore production and phosphate solubilization, and/or by plant development stimulation caused by phytohormones, antimicrobials compounds, and VOCs emission. Moreover, because of these features they are also able to increase plant tolerance to biotic and abiotic stress (Zuluaga et al., 2021). From the molecular point of view,

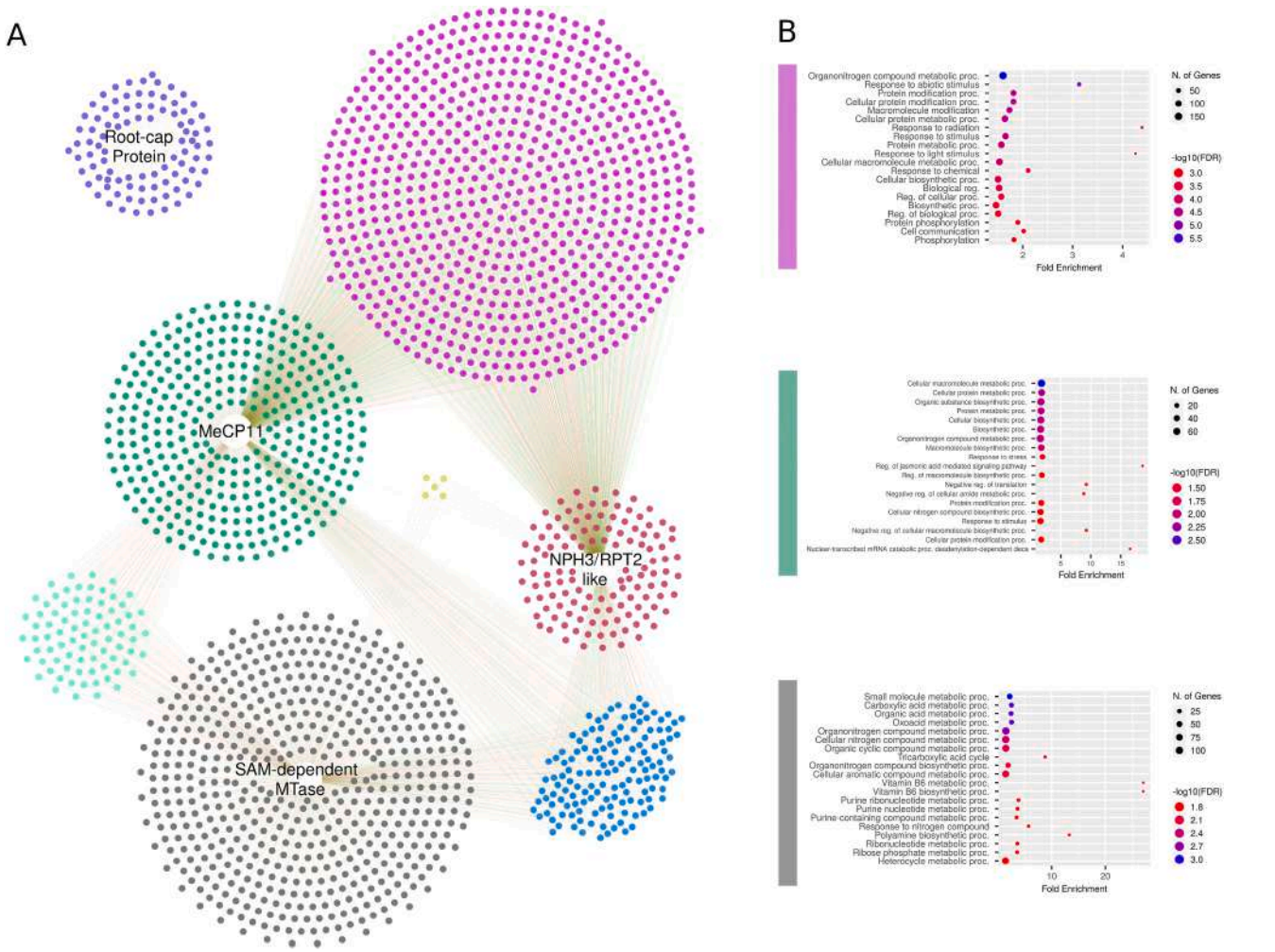

Fig. 5. Co-expression network analysis based on four bait genes (Solyc06g068140 – *MeCP11*; Solyc02g084950 - *SAM dependent MTase*; Solyc07g043130 – *NPTH3/RPT2 like*; Solyc02g078930 - *Root cap protein*). **A** Co-expression was evaluated using bait genes and with the 1st and 99th percentile as thresholds for the Pearson-correlation score. Annotations for bait genes are shown. Positive and negative correlations were highlighted using green and red edges respectively. **B** Go enrichment analysis (BP) of the three most abundant co-expression clusters.

plant responses to PGPB originated from the elicitation of a dynamic and temporal response. The first step is usually defined by the up-regulation of defense-responsive transcriptional factors, followed by a down-regulation of those genes, and then a final up-regulation providing a long-term stress tolerance (Kaleh et al., 2024). In this study, a response coherent with the above transcriptional dynamics was observed in seedlings treated with *S. violaceoruber*. From the transcriptomics point of view, a significant number of DEGs were detected in the V *vs.* Ct seedlings comparison, mainly at T1. At that timepoint, the GO enrichment analyses highlighted relevant changes in the expression of genes related to the regulation of biological processes, particularly those involved in the response to external factors. In accordance with the previously described model (Kaleh et al., 2024), this seems to confirm *S. violaceoruber* ability to generate the plant coordinated genetic response characteristic of PGPB, resulting in the enhancement of plant growth and adaptation to external conditions. At T1, V seedlings showed a significant up-regulation of genes involved in primary and secondary metabolism biosynthetic pathways, coupled with the up-regulation of genes related to the response to light and abiotic stimuli. Among these genes, different Light-harvesting chlorophyll *a*/b-binding (LHCB) proteins were characterized by significant changes in their fold change values ($\log_2FC \geq 2$) in treated seedlings. These class of genes code for apoproteins of the light-harvesting complex of photosystem II. Previous studies on *Arabidopsis thaliana* showed that their down-regulation induced abscisic acid (ABA)-insensitive phenotypes in seed germination and post-germination growth, demonstrating the positive role of LHCB proteins in developmental processes in response to ABA (Liu et al., 2013). To further corroborate these evidences, an essential role of ABA in the full expression of some LHCB proteins was demonstrated, highlighting a correlation between high levels of ABA and the enhanced LHCB genes expression in plant (Liu et al., 2013). In agreement, in our study, the co-expression network of one of the bait genes selected for the co-expression analyses, a methyl-CpG-binding domain-containing (MBD) protein (Solyc068140), was found to enclose genes involved in the ABA signaling pathway. In the same co-expression network, genes involved in primary metabolism macromolecules biosynthesis and transport, like those involved in carbohydrates and nitrogenous bases biosynthesis (GDP-4-keto-6-deoxymannose-3,5-epimerase-4-reductase - Solyc07g006070, Purine Nucleoside Phosphorylase - Solyc11g007730), or lipid metabolic pathways (Fatty acid desaturase - Solyc07g005510, Glycerol-3-phosphate acyltransferase - Solyc07g056320 - Solyc08g082340, Lipoxygenase - Solyc08g014000), were highly represented. Therefore, this result could point to a possible ABA central role in orchestrating plant responses to *S. violaceoruber*, where the PGPB-induced enhanced response to light is exploited from the seedling to boost its core metabolism, improving growth conditions. Afterall, ABA is a known systemic coordinator of light response, able to optimize core metabolic and developmental processes, such as ROS detoxification

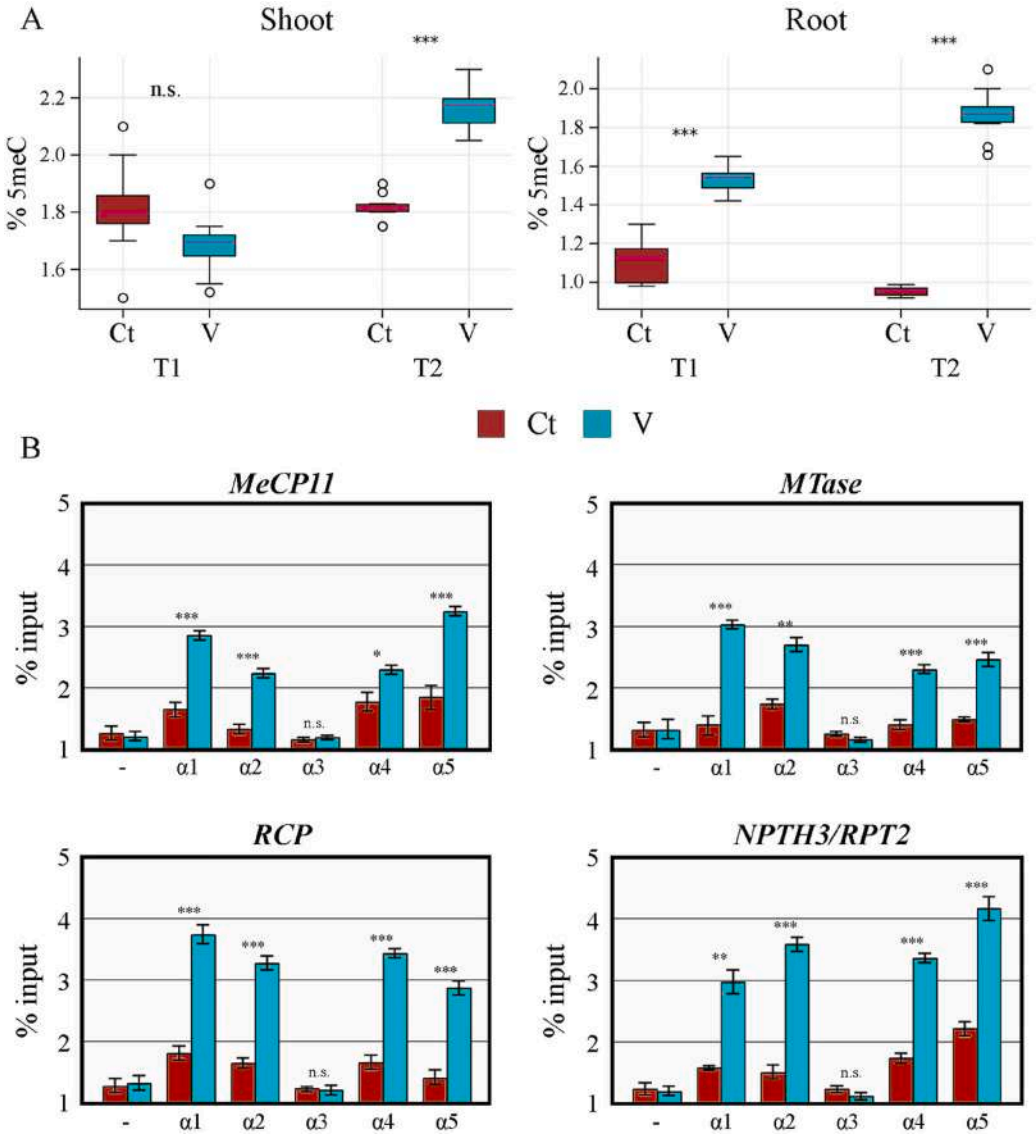

Fig. 6. Epigenetic changes in tomato root chromatin provoked by *S. violaceoruber* exposure. **A)** Global 5-meC level by ELISA-based assays of inoculated (V) and non-inoculated (Ct) samples evaluated at T1 and T2, in both shoot (left panel) and root tissue (right panel). Boxplots show the median, interquartile range, and data dispersion. Ct samples are shown in brown and V samples in cyan. Statistical significance between Ct and V within each time point was assessed using one way ANOVA followed by Benjamini–Hochberg false discovery rate correction (*** FDR <0.001). (Table S9). **B)** ChIP-qPCR analysis of the *MeCP11, MTase, RCP,* and *NPTH3/RPT2* promoter occupancy by H3K4me3 (α 1), H3K36me3 (α 2), H3K9me2 (α 3), H3K9ac (α 4), and H4ac (α 5). -: no antiserum (negative control). ChIP assays were performed on chromatin extracted from roots of control and *S. violaceoruber*-treated tomato seedlings at T2. Purified chromatin was precipitated with the indicated antisera or incubated without adding antibodies, followed by qPCR amplification of the indicated promoter fragments. Data were normalized according to the percentile of input method. Error bars are standard errors for the qPCR replicates. The significance between condition (Ct and V) for each gene was evaluated by Tukey-test (n.s. not significant; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$) (Table S10).

regulation and root elongation promotion (Gil et al., 2018). A previous study on *A. thaliana* revealed that the volatiles produced by the PGPB *Bacillus subtilis* GB03 were able to increase chlorophyll content and photosynthetic efficiency in the plants. The effect was absent in ABA-deficient mutants, highlighting ABA essential role for PGPB-enhanced light-driven metabolism (Zhang et al., 2008). An indirect effect of the enhanced activation of the light responsive apparatus following PGPB inoculation could also affect biotic stress responses. Photosynthesis-related modifications can determine changes in soluble sugar levels, sugar types and their distribution (Su et al., 2024). Soluble sugars can act as secondary messengers under stressed conditions, and thus carbohydrate metabolism modifications induced by PGPB may also play a key role in improving plant resistance through indirect mechanisms (Su et al., 2024).

Interestingly, after *S. violaceoruber* inoculation, many plant genes involved in the response to biotic stresses and linked hormonal signaling pathways were found to be down-regulated. Based on their level of down-regulation ($log_2FC < -2$) some of the genes included in this GO category, such as genes coding for 12-Oxophytodienoate reductases, were particularly interesting in the jasmonate pathway. Indeed, they code for an enzyme involved in the biosynthesis of jasmonate starting from oxylipins, and their expression can be induced by several external stimuli, among which UV-light is one of the most important (Schaller et al., 2000). Once again, *S. violaceoruber* effect on plant seems to be strongly related to pathways involved in a modified perception of external signals and, in particular, to light. The peculiar expression pattern is not atypical in PGPB-plant interactions. The modulation of plants JA pathways is part of a broader plant–microbe interaction, where plant-produced JA is able to shape root-associated microbial communities, by developing a mechanism that often involve

JA-mediated suppression of defense during early colonization (Pascale et al., 2020). The following JA-mediated crosstalk fine-tuning maintains then a predominant role in modulating beneficial microbial interactions, through the alteration of plant root exudate profiles. Consequently, the generated changes in bacterial community composition are able to reinforce the profitable plant-microbe interaction (Carvalhais et al., 2015).

The down-regulation of defense-related genes may also suggest an interaction causing the plant to decrease its active defenses because of a counterbalancing protective effect exercised by *S. violaceoruber,* likely to be due to its arsenal of bioactive metabolites (Faddetta et al., 2023). This evidence paralleled the VOC profiles recorded. PGPB treatments often induce a physiological trade-off between growth and defense. Typically, PGPBs enhance plant growth by improving nutrient uptake and overall metabolic efficiency, which leads the plant to allocate a larger share of energy and carbon resources toward growth-related processes (respiration, photosynthesis, biomass accumulation). At the same time, some PGPB can act as biostimulants that prime defense responses and enhance plant health, creating favorable conditions for the production of volatile monoterpenes such as α- and β-pinene. However, when the environment is perceived as non-threatening—or when PGPB mitigate stress—plants may downregulate costly defense pathways, including terpene biosynthesis, enabling them to conserve energy for growth. This shift in resource allocation can result in a lower accumulation of certain defensive compounds (Figueroa-Macías et al., 2021; He et al., 2022; Maciel-Rodríguez et al., 2025). As previously displayed (Faddetta et al., 2023), the *S. violaceoruber* treatment significantly reduced the production of several compounds belonging to terpenes, a class of metabolites known for its antibacterial and antifungal activities (Leyva-López et al., 2017). This reduction can be related to the complexity of PGPB-plant interactions that can lead to the regulation of plant terpene production likely due to the bioactive compounds produced by the bacterial strains (Faddetta et al., 2023). As a consequence, metabolic resources appear to be destinated to other metabolic pathways requiring an increased metabolic supply. Therefore, besides its role as biostimulant, these findings also suggest a potential role of *S. violaceoruber* as plant biocontrol agent. The increased accumulation of specific VOCs such as α- and β-pinene and 3-methylfuran in inoculated seedlings at T2 may also be functionally linked to the root architectural changes observed at earlier stages. Monoterpenes like α- and β-pinene have been reported to act as signaling molecules influencing root development and auxin-related pathways, potentially contributing to the increased root diameter and aerial root formation. Moreover, VOC-mediated signaling may reflect a sustained plant–microbe interaction that reinforces developmental reprogramming beyond the initial transcriptional response. Together, these observations suggest that volatilomic changes at T2 are not merely a consequence of metabolic shifts but may actively participate in shaping root architecture.

Interestingly the metabolic hubs upregulated by the PGPB-treatment were found at both timepoints considered in this study. In addition, specific pathways and sub-categories were highlighted in T2-V seedlings. In particular, a general up-regulation of genes involved in the photosynthesis related processes and the biosynthesis of small molecules was observed. The up-regulation of genes related to the photosynthetic machinery, combined with the detected differential regulation of hormonal pathways, point toward an effect of *S. violaceoruber* on photosynthetic efficiency. In fact, the improvement of photosynthetic efficiency is usually an effect by which PGPB are able to improve plant growth conditions. Usually, it is the result of a lowered accumulation of ethylene due to ACC-deaminase production, a common ability of PGPB. Through this mechanism, the bacteria are able to reduce the environmental stress levels impacting plants, even though the specifics of it are still to be defined (Duarte et al., 2024). In agreement with this, several genes part of the ethylene signaling pathway were either strongly down-regulated ($log_2FC < -4$) or not-expressed in V seedlings. Among them, interesting changes in the expression were detected for an Ethylene insensitive 3 gene (Solyc01g006650), and some Ethylene-responsive transcription factors ABR1, such as Solyc04g012050. Ethylene insensitive 3 is a key transcription factor in ethylene signaling, associated with plant senescence. When expressed, the gene functions as a repressor of miR164 transcription, accelerating age-dependent leaf senescence (Li et al., 2013). Since the gene is down-regulated (V-T1 $log_2FC < -2.8$) or not expressed (T2-V) in seedlings treated with *S. violaceoruber*, this could indicate a decrease of leaf senescence among the PGPB protective effects. On the other hand, Ethylene-responsive transcription factors ABR1 are repressors of ABA hormone during seed germination and ABA stress-induced gene expression (Pandey et al., 2005). In V seedlings, the ABR1 gene (Solyc04g012050) was strongly down-regulated at T1 ($log_2FC = -4.5$) and T2 ($log_2FC = -7$). This expression pattern, combined with previously described LHCB genes information, supports the hypothesis of a central role of ABA in the coordination of plant responses to *S. violaceoruber*, determining plants optimized adaptation to external conditions.

4.2. S. violaceoruber led to changes in root architecture of tomato seedlings reflected by epigenetic landscape modification

Plant growth enhancement derived from PGPB interaction involves different mechanisms that are yet to be fully determined. The induced changes can be caused by the release of key hormones involved in plant development, such as indoleacetic acid (IAA), or by the reduction of growth-limiting hormones, like ethylene (Khoso et al., 2024). Furthermore, another determinant could be the altered mineral nutrition, consequence of the ionic transport system direct stimulation, and/or the increase in mineral availability. Whichever the mechanisms involved, the ultimate impact of PGPB is a quantitative change in root and/or shoot growth (Khoso et al., 2024; Larcher et al., 2003). In our study, the most impactful morphological modifications induced by PGPB treatment were observed at root level. Compared to Ct seedlings, the PGPB-treated seedlings (V) showed an increased root diameter, both in terms of maximum and minimum diameter, and were able to develop aerial roots. On the contrary, the control showed significantly higher root length compared to treated plants. The effect of reducing primary root length with an increase in root diameter and lateral branching is a typical result of inoculation with PGPB strains that produce a high amount of auxins, such as IAA (Mangmang et al., 2015; Han et al., 2023). Plants can develop aerial roots as adaptive responses to environmental cues and microbial interactions (Steffens and Rasmussen, 2016). When influenced by PGPB, these roots can confer multiple functional benefits linked to hormonal signaling, water uptake, and stress mitigation (Vacheron et al., 2013). The root development reprogramming is induced by a shift in hormonal balance due to the presence of the microorganism. Among these changes, increased IAA production and decreased ethylene levels are able to boost the root system plasticity, resulting in the improvement of water and nutrient uptake (Vacheron et al., 2013). Moreover, aerial roots are often able to produce mucilage, that can prevent plants internal dehydration and support the selection of a microbial community able to support the plant metabolic requirements under environmentally challenging conditions.

Based on the detected traits, two genes involved in transcriptional regulation through methylation and two genes involved in root architecture and development were selected as bait for a co-expression analysis. The results showed significant differential regulation of the four selected genes, and co-expressed clusters showing the most abundant GO terms coherent with metabolic changes highlighted at whole plant level. The Methyl-CpG-binding domain-containing protein (MeCP11/MBD; Solyc06g068140) was found to be involved in the regulation of multiple cellular processes centered on cell homeostasis through regulation of redox and protein pathways. In particular, in the network analysis MBD encoding gene was linked to the regulation of nitrogen compound based metabolic paths, such as those related to protein and secondary metabolites biosynthesis, and phosphate

transport. Previous studies revealed that MDB proteins can be considered essential players in the response to multiple abiotic stresses, such as combined water and salt stress, as well as cold and heat stress, through their ability of regulating different metabolic pathways (Ravi et al., 2025; Wang et al., 2023; Yang et al., 2023). Their proven role in the responses to environmental stresses suggest a role in orchestrating plant responses to *S. violaceoruber* inoculation, leading to the improvement of seedlings growth conditions. Consistently, *A. thaliana mdb* mutants exhibited an altered root morphology linked to variations in the phosphate starvation genes, suggesting a role of MDB genes as regulators of phosphate starvation response suppression (Ravi et al., 2025). Therefore, the relevant changes in the expression of MeCP11/MBD encoding gene in V seedlings could also indicate a contribution of *S. violaceoruber* to the enhancement of nutritional metabolism efficiency, by stimulating the modification of seedlings roots architecture, improving their adaptability to external conditions. The expression and co-expression network analysis of the other bait gene selected, a SAM dependent carboxyl methyltransferase (MTase - Solyc02g084950), is consistent and supports the previous results. The co-expression network analysis highlighted its involvement in the regulation of carriers and solutes transporters. Moreover, the effects of its differential expression on hormonal cross-talks and cell wall biosynthesis and organization were emphasized. Previous studies demonstrated the role and involvement of this class of genes in the response against different stresses, by exercising a role both at transcriptional level and in the transformation of metabolites during their biosynthesis (Lashley et al., 2023; Wang et al., 2019), once again posing them as important players in the coordination of plants responses to PGPB applications and consequent effects.

Finally, the other two bait genes selected in our study, a *Root phototropism protein 2-like* gene (NPTH3/RPT2 - Solyc07g043130) and a gene coding for a *Root cap protein* gene (RCP - Solyc02g078930), were strongly linked to the most relevant phenotypic features observed on tomato seedlings after *S. violaceoruber* inoculation. Indeed, the co-expression analyses of these genes revealed their involvement in plant developmental processes in response to light and radiation stimuli, and in the biosynthetic pathways of secondary metabolism concerning responses to biotic and abiotic factors. Sustaining our findings, a fundamental role of NPH3 gene in the establishment of lateral auxin gradients, required for the differential growth response underlying phototropism, was previously revealed both in *A. thaliana* e *Vicia faba* (Christie et al., 2018). In V seedlings, the stable overexpression across timepoints of this gene agreed to the observed effect of *S. violaceoruber* on boosting roots architecture in response to abiotic stimuli, putatively allowing the seedling to exploit growth conditions more efficiently. Corroborating this hypothesis, Root cap protein gene (Solyc02g078930) expression was found to be correlated to that of genes involved in similar processes to the ones above described. Some interesting genes were, for example, an ABA-responsive MYB transcription factor - Solyc05g053150, several Expansins genes - Solyc06g076220, and an Homeobox protein gene involved in cation efflux- Solyc09g074690.

DNA methylation has been identified as a key regulator of processes such as bolting and secondary metabolite synthesis, involved in both root lignification and architecture (Yuan et al., 2025). Based on this, the histone variations induced by *S. violaceoruber* treatment at the four selected bait genes was investigated. Interestingly, in addition to a significant increased level of global methylation, mainly in roots, the four selected genes showed specific histones post-translational modifications. As reported in other plant species, modifications in H3K4me3 could play a functional role in the expression of genes involved in developmental processes and stress responses (Seni et al., 2023). In this work, the correspondence between the differential expression profiles of the four selected bait genes and their epigenetic landscape modifications seems to confirm the hypothesis. Furthermore, H3K36me3 deposition was proved to be involved in the gene activation driving light and sucrose responses (Yu et al., 2025), processes that in this study were found to be affected by changes in gene expression following seedlings treatment with *S. violaceoruber*. Supporting even more the pivotal role of these modifications in participating to the changes induced by *S. violaceoruber* on tomato plant, stress-responsive genes were also reported to be fine-tuned by bivalent H3K4me3–H3K9ac modifications, allowing plants to adapt to environmental changes, such as those related to the transcriptional regulation under drought stress (Nguyen et al., 2022). Moreover, the stress memory process is known to be affected by increasing salicylic acid concentrations, which alter H3/H4 acetylation and H3K4 methylation at genes related to stress (Ramakrishnan et al., 2022). In this experiment, this hormonal pathway was detected as significantly affected by *S. violaceoruber* treatment, suggesting the ability of the PGBP to reprogram the plant transcriptional machinery through epigenetic modifications, improving its resilience.

In conclusion, this study provides evidences revealing the PGPB *S. violaceoruber* affecting tomato seedling development through a complex and multilayered mechanism. Using a multi-omics approach, the study was able to demonstrate the ability of *S. violaceoruber* to influence tomato key biological processes, by modulating transcriptomic and epigenetic landscapes associated to ABA and ethylene pathways, photosynthetic efficiency, and root architecture, increasing its environmental adaptability and resilience.

These findings deepen the understanding of plant-microbe interaction and highlight the potential role of *S. violaceoruber* as a biostimulant and biocontrol agent, to be employed in agriculture management strategies aimed at reducing environmental impact while ensuring crop productivity. To further resolve these findings, future studies incorporating organ-separated or single-cell transcriptomics will be indispensable to validate tissue-specific conclusions and to provide a higher-resolution map of the localized molecular responses triggered by *S. violaceoruber*.

CRediT authorship contribution statement

Valentina Ricciardi: Writing – review & editing, Writing – original draft, Formal analysis. **Guglielmo Puccio:** Writing – review & editing, Writing – original draft, Investigation, Data curation. **Loredana Abbate:** Writing – review & editing, Formal analysis. **Teresa Faddetta:** Writing – review & editing, Formal analysis. **Margot Lo Pinto:** Writing – review & editing, Formal analysis. **Ciro Caldiero:** Writing – review & editing, Formal analysis. **Giulia Polito:** Writing – review & editing, Formal analysis. **Antonio Palumbo Piccionello:** Writing – review & editing, Formal analysis. **Giuseppe Gallo:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Francesco Mercati:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Vincenzo Cavalieri:** Writing – review & editing, Data curation, Conceptualization.

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This manuscript reflects only the authors' views and opinions, neither the European Union nor European Commission can be considered responsible for them.

Declaration of competing interest

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

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.plaphy.2026.111428.

Data availability

All sequenced data produced were deposited in the Sequence Read Archive (SRA) of NCBI (National Center for Biotechnology Information) with the identifier: PRJNA1257063.

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