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Microbial consortium can enhance plant growth, control leaf miners and parasitic root nematodes in tomato crops grown in Mediterranean greenhouse

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Introduction: Microbial inoculants based on plant growth-promoting microbes offer a promising alternative to chemical inputs, enhancing plant growth, crop yield, and stress resilience without adverse environmental effects.
Methods: A commercial microbial consortium (*Bacillus* spp., *Pseudomonas* spp., *Streptomyces* spp., *Trichoderma* spp., *Glomus* spp.) was evaluated in a cold greenhouse in Sicily (Italy), certified for organic methods. The consortium was applied by fertigation to five tomato cultivars, including one commercial and four Sicilian landraces. The greenhouse was naturally infested with the tomato leaf miner *Phthorimaea absoluta*, which affected plant growth and yield.
Results and discussion: Despite the considerable infestation, plants treated by the above-cited microbial consortium showed enhanced growth and yield compared to the control plants. Furthermore, root galls caused by nematodes (*Meloidogyne* spp.) were observed. Significant differences were observed among the genotype and the treatment. Microbial DNA was extracted from tomato roots and analyzed using amplicon sequencing to characterize the root-associated bacterial, fungal, and nematode communities. Alpha diversity indices were largely unaffected for bacteria. In contrast, the genotype and the soil treatment by the microbial consortium affected the alpha diversity indices for fungi and nematodes. Beta diversity analysis revealed significant differences in microbiota community composition between plants grown in treated and untreated soils for both datasets analyzed. Furthermore, we found several Operational taxonomic units associated with the soil treatment by the microbial consortium utilized.

Finally, the results demonstrated that the microbial consortium utilized alleviated the damage symptoms due to biotic stresses (*P. absoluta* and *Meloidogyne* spp.). Furthermore, the treatment significantly affected the microbial community of the tomato roots depending on the cultivars used.

KEYWORDS

biostimulants, landraces, phytobiome, sustainability, *Trichoderma* spp.

1 Introduction

The growth rate of the world population requires an increase in food production (Gilland, 2002), and taking into account the climate change in progress, the estimated total global food demand is expected to increase by up to 62% by 2050, while the population at risk of hunger is expected to increase by up to 30% (van Dijk et al., 2021). The use of pesticides allowed an improvement in terms of yield and quality of the agricultural products throughout the world (Aktar et al., 2009; Popp et al., 2013). In vegetable crops, for instance, more than 50% of global production would be lost to pests and diseases in the absence of pesticide application (Keulemans et al., 2019; Tudi et al., 2021). However, extensive and unregulated pesticide use has led to profound and potentially irreversible environmental impacts (Pathak et al., 2022; Sarkar et al., 2021; Zhou and Li, 2021).

Agricultural practices can strongly influence the ecological balance of soil, water, and atmosphere, especially when chemical pesticides are overused (Sarkar et al., 2021; Sharma et al., 2019; Shefali et al., 2021). Such inputs pose risks to agricultural products through toxic residues and may also threaten human health (Lammoglia et al., 2017; Tudi et al., 2022; Upadhayay et al., 2020). Nevertheless, not all agricultural practices are detrimental; the adoption of sustainable methods can mitigate these adverse effects while maintaining productivity.

The consumers, due to the negative consequences of the over-application of chemical pesticides, are now concerned about and prefer to consume products produced by certified organic farms (Saleh et al., 2021). The adoption of organic farming might contribute to decreasing the use of farm inputs as chemical pesticides and increase soil carbon sequestration, but it might also exacerbate the use of farm inputs and the emissions through greater food production elsewhere to make up for lower organic yields (Karipidis and Karypidou, 2021; Smith et al., 2019).

In recent years, alternative products based on natural bioactive compounds (Chaudhari et al., 2021; Pacios-Michelena et al., 2021; Picchi et al., 2020) or microorganisms (Elnahal et al., 2022; Lacava et al., 2022; Vishwakarma et al., 2020) have gained greater interest (Anzalone et al., 2022; Ayilara et al., 2023; Toscano et al., 2021). The use of Plant Growth-Promoting Microorganisms (PGPMs) in agricultural crops is considered an environmentally friendly alternative to chemical fertilization in both conventional and organic agriculture (Chouhan et al., 2021; Kumar et al., 2022; Treccarichi et al., 2023; Zhou et al., 2022).

Microbial inoculants are primarily applied to seeds, roots and soil to improve plant growth and development by modulating the plant associated microbiome (Hakim et al., 2021; Paravar et al., 2023; Rizzo et al., 2023, 2022). PGPMs, including bacteria and fungi, contribute to enhancing nutrient availability, regulating phytohormones such as auxins, cytokinins, and gibberellins, and increasing plant tolerance to biotic and abiotic stresses, by also changing the microbiome of the soil, plant roots, and the rhizosphere (Araujo, 2022; Deng et al., 2019; Ghadamgahi et al., 2022; Nicotra et al., 2024). However, a weak point in PGPMs research is the often-inconsistent results (Malgioglio et al., 2022). This may be a consequence of incorrect inoculation methods or may be due to abiotic factors, such as soil characteristics (nutrient or heavy metal content and pH), water availability and temperature (Lopes et al., 2021; Malgioglio et al., 2022). Nevertheless, there are several studies where PGPMs have proven capable of mitigating both abiotic and biotic stress (Christakis et al., 2021; Markakis et al., 2016; Rizzo et al., 2023, 2022). Overall, inoculation of microbial consortia has been reported to give better results than single strain inoculation (Liu et al., 2023).

Tomato (*Solanum lycopersicum* L.) is among the most valuable vegetable crops widely cultivated around the world and it is consumed in both fresh and processed forms (D'Esposito et al., 2023; Padmanabhan et al., 2015). Tomato crops include several landraces, these are especially appreciated for their organoleptic and nutritional traits from the local market but also, they have important genetic traits linked to adaptation to the environment and climate change, as well as resistance to parasites and diseases (Caramante et al., 2023; Argento et al., 2023). Landraces could therefore be an important resource in organic agriculture, but there is a need to verify their adaptability to the protocols and treatments used in organic farming, as their response to the PGPM application.

Among the pests and diseases that can affect tomato cultivation, *Phthorimaea absoluta* Meyrick (=*Tuta absoluta)* (Lepidoptera: Gelechiidae), known as the South American tomato leaf miner, is one of the most destructive and limiting (Silva et al., 2021).

P. absoluta has caused severe economic losses in tomato production across Europe, Africa, Asia, and the Mediterranean region in open field and greenhouse conditions (Acharya et al., 2023). Yield losses can exceed 80% under heavy infestation if not properly managed. *P. absoluta* larvae can destroy tomato canopy by producing mines in leaves, stems and shoots and burrowing into fruits, which significantly affect tomato fruit yield and quality (Campos et al., 2017; Tropea Garzia et al., 2012). Its adaptability and resistance development further exacerbate its economic impact, making it a major threat to global tomato supply chains. Several strategies have been developed to manage *P. absoluta*, including chemical, biological, biotechnical, and agronomic approaches. Chemical control of *P. absoluta* is becoming increasingly ineffective due to the feeding habits of the larvae, the high number of generations per growing cycle, and the emergence of resistance to commonly used insecticides (Desneux et al., 2022; Biondi et al., 2018; Campos et al., 2017; Tropea Garzia et al., 2012). Therefore, there is a growing demand for sustainable approaches to control this invasive pest that includes biological control performed by predators, parasitoids and even microorganisms, in addition to the selection of tolerant varieties (Biondi et al., 2018; Colmenárez et al., 2022; Desneux et al., 2010; D'Esposito et al., 2023). Biotechnical methods, particularly those based on sex pheromones, play an important role in monitoring, early detection, and mass trapping. The synthetic sex pheromone (E3,Z8,Z11)-tetradecatrienyl acetate (TDTA) is especially effective for population monitoring and partial control (Mangrio et al., 2023; Filho et al., 2000; Jabamo et al., 2023; Roda et al., 2015). Agronomic measures, such as crop rotation, the use of tolerant or resistant cultivars, and optimized irrigation, further enhance the effectiveness of integrated pest management.

The entomopathogenic bacterium *Bacillus thuringiensis* is one of the most extensively used and effective biocontrol agents against *P. absoluta* (Alsaedi et al., 2017; Sandeep Kumar et al., 2020). However, in recent years, the interest into other entomopathogenic microbes has grown (Giannoulakis et al., 2023; Ndereyimana et al., 2019; Silva et al., 2020; Urbaneja et al., 2012; Yüksel, 2022).

Among the PGPMs commonly employed, several genera stand out for their different and complementary roles in enhancing plant growth and resilience. *Trichoderma* spp. are well-known biocontrol agents against nematodes and fungal pathogens (Abdelrahman et al., 2016; Ferreira and Musumeci, 2021; Yao et al., 2023). Recent studies have also demonstrated his efficacy also against insect pests, such as *P. absoluta* expanding their biocontrol potential beyond fungi and nematodes (Agbessenou et al., 2022, 2020; Aprile et al., 2022). *Bacillus* spp., and particularly *Bacillus subtilis*, have been shown to promote plant growth through several mechanisms, including improving nutrient availability, modulating plant hormone homeostasis, enhancing plant tolerance to both drought and salt stress, producing antimicrobial compounds, and inducing systemic resistance (Blake et al., 2021; Araujo, 2022; Ghadamgahi et al., 2022; Rizzo et al., 2023). Furthermore, it was demonstrated that a microbial consortium based on *Bacillus* spp. isolated from compost, suppressed reproduction and root invasion of *Meloidogyne javanica* in tomato plants, enhancing the plant growth (Karanastasi et al., 2024). Additionally, several studies have highlighted the strong biocontrol activity of *Pseudomonas* spp. as PGPR, mainly due to their ability to produce different antimicrobial compounds and to induce plant defense responses against pathogens (Deng et al., 2019; Wang et al., 2024; Nicotra et al., 2024).

In addition to promoting plant growth, symbiosis with Arbuscular Mycorrhizal Fungi (AMF), as *Glomus* spp., may also increase plant tolerance or resistance to herbivorous insects. This appears to be related to the plant's secondary metabolism, as plants with AMF show higher biosynthesis of plant health promoting phytochemicals and activity of antioxidant enzymes (Wang et al., 2023; Wu et al., 2021). Although mycorrhiza-induced plant resistance has been studied against several pests, the effects of AMF in the tomato plant and the priming defense against *P. absoluta* are only recently investigated (Shafiei et al., 2024).

Another factor limiting tomato production is the presence of plant parasitic nematodes, recognized as one of the major threats to crops worldwide (Tileubayeva et al., 2021). The most commonly reported plant parasitic nematodes belong to the genera *Meloidogyne* , *Heterodera*, *Pratylenchus* and *Globodera*, and are estimated to cause economic losses of up to USD 100 billion annually (Roopa and Gadag, 2020). Root-knot nematodes (*Meloidogyne* spp.) are among the most widespread and economically damaging plant parasitic nematodes. They invade plant roots and induce the formation of characteristic galls or knots, which impair nutrient and water uptake, resulting in stunted growth and significant yield losses, particularly in tomato (Argento et al., 2019).

Even against nematodes, PGPMs are useful as environmentally friendly biocontrol agents (Ali et al., 2023; Migunova and Sasanelli, 2021). Among biocontrol agents, there is a wide range of PGPMs that are effective as nematode antagonists (Bhat et al., 2023). Furthermore, these microbials not only control the parasitic nematodes but also improve plant growth and induce systemic resistance in plants against a variety of biotic stressors (Chouhan et al., 2021; Dixit et al., 2022; Malgioglio et al., 2022). While current research provides strong evidence that microbial consortia enhance plant performance under single stress factors, their potential benefits for organic tomato production facing simultaneous biotic stresses remain poorly understood.

The aim of the present study is to evaluate the effects of a commercial bioinoculant mixture, based on Plant Growth-Promoting Rhizobacteria (PGPR) and Plant Growth-Promoting Fungi (PGPF), on the growth performance and yield of 5 different tomato cultivars, comprising one commercial cultivar and four Sicilian landraces. The effect of the bioinoculant as an inducer of plant resistance to simultaneous natural infestation of tomato leaf miner *P. absoluta* and root-knot nematodes was evaluated. Furthermore, the impact of the microbial consortia on the root microbial community was investigated in relation to the agronomic factors evaluated.

2 Materials and methods

2.1 Microbial consortia composition, plant material and site description

The commercial product Maxy Soil® (Itaka srl, Milan, Italy) consists of a microbial consortium composed of 14 different species of known PGPR and PGPF belonging to the following genera: *Bacillus*, *Pseudomonas*, *Streptomyces*, *Trichoderma*, *Saccharomyces*, *Glomus*, as described in Supplementary Table 1. The selected semi-determined tomato genotypes consisted of 1 commercial cultivar ('UC 82') and 4 Sicilian landraces ('Pizzutello piccolo', 'Riccio', 'Giallo', 'Francavilla'), belonging to the active gene bank of the Department of Agriculture, Food and Environment (Di3A) of the University of Catania (UNICT) (Supplementary Table 2). The experimental trial was conducted in a cold greenhouse located in Comiso, Sicily, Italy (37°00'09.7"N 14° 34'45.4"E) adopting organic farming system. In order to analyze the soil characteristics, about 1 kg of soil samples were taken from 4 different part of the experimental field at 30 cm of depth, and then the samples were mixed together to make a bulk. The soil characteristics were consistent across the field and belonged to the sandy-loamy typology. These soil characteristics are typical of "Vittoria", a specific area in the southeast of Sicily dedicated to tomato crop production. All evaluated soil characteristics are listed in Supplementary Table 3. The temperatures in the greenhouse were recorded through the weather station "Watchdog 2000 series" (Spectrum Technologies Inc., Aurora, IL) (Supplementary Figure 1).

2.2 Experimental setup

The experimental field was designed following a split-plot experimental design. The main plots corresponded to the treatments, with one set receiving the microbial consortium (Maxy Soil; treated) and the other left untreated as the control. Each main plot was divided into 5 subplots, each containing one of the 5 genotypes, and each plot was replicated 3 times in the greenhouse, resulting in a total of 30 subplots with 6 plants in each. The trial was conducted from December 2021 to June 2022. The seeds of each genotype were sown in trays with a commercial peat mix and then transplanted into the experimental field at 2-leaf stage. The microbial consortia Maxy Soil was applied as recommended by the manufacturer by fertigation (5 g/L), with 1 L of solution per square meter, three times: 7 days before the transplanting (using the same concentration as after transplantation), 7 days after the transplanting (DAT), and 30 DAT.

2.3 Plant characterization and yield

Several parameters were recorded to evaluate the effect of the microbial consortia on the plant growth. At 90 DAT, at flowering stage, the number of flowers, the number of truss and the number of set truss (defined as fruit-bearing truss) were recorded. The data were registered for each plant and the mean for each plot was calculated. At 110 DAT, at the end of the flowering stage, the plant height, number of flowers, the number of trusses, and the number of set truss were determined. The data were reported for each plant and the mean for each plot was calculated. The fruit were harvested when completely ripe and the total weight for each plot was recorded. The yield was calculated as g per m^2. At 150 DAT, corresponding to the end of the trial, three plants per elementary plot were randomly collected. For each plant, the following parameters were recorded: nematode damage (0–5 scale), stem length (cm), number of branches, epigeal fresh weight (g), root fresh weight (g), main root length and width (mm).

2.4 Effect on the tomato leaf miner and root-knot nematodes

A population of *P. absoluta* was naturally present in the greenhouse at the beginning of the experiment, with a uniform level of infestation in the treated and control plots. In accordance with the weather conditions, the infestation level showed an increasing trend during the trials, reaching the higher level at the end of the trial; the percentage of damage was calculated at 110 DAT by counting the number of infested leaves per plant using a visual counting method; all leaves with detectable mines of *P. absoluta* were considered as infested. A total of 6 plants per plot were evaluated.

Preliminary analysis of the soil has shown the presence of a uniform population of root-knot nematodes in the experimental plots. Samples were randomly collected from the field, and plot randomization ensured a uniform distribution of nematode infestation across treatments. The nematode damage was assessed based on symptomatology, considering both the severity and incidence of infestation. Root damage was visually assessed and graded according to a severity index based on the root galls, following the scale proposed by Barker (1985) and Seo et al. (2019). The index was assigned on a scale from 0 to 5: 0=0–10%, 1=11–20%, 2=21–50%, 3=51–80%, 4=81–90%, and 5=91–100% root galls. For each replicate, at 150 DAT the percentage of damaged roots was quantified by visual counting of the roots exhibiting nematode galls or necrosis. A total of 3 plants per plot were evaluated.

2.5 Root sampling, DNA extraction and sequencing

The samples for the microbiome profiling were collected at 100 DAT, when the plants have developed many fruits but were still in flowering. From each elementary plot, the roots of three plants were excavated with a small shovel at a depth of 20 cm near to the stem and mixed in a sterile plastic bag to make a bulk. Each bulk is representing a biological replication for a total of 3 replicates for each combination of genotypes and treatment. The roots were shaken to eliminate the soil but not washed in order to maintain the rhizosphere. The sample were then stored at -80 °C and freeze dried before the DNA extraction. The lyophilized roots were grinded with pestle and mortar, then DNA extraction was performed with Power Soil® DNA extraction kit (Qiagen, UK) following manufacture instructions. The microbiome profiling was performed by Eurofins Genomics Italy srl. The 16S rRNA gene region V3-V4 (Bukin et al., 2019) was amplified to analyze the bacterial community using the primers f357F (Turner et al., 1999) (TACGGGAGGCAGCAG) and 800R (Kisand et al., 2002) (CCAGGGTATCTAATCC). The ITS1 (Yang et al., 2018) region was amplified to investigate the fungal community using the primers 1737F-ITS5 (White et al., 1990) (GGAAGTAAAAGTCGTAACAAGG) and 2043-ITS2 (White et al., 1990) (GCTGCGTTCTTCATCGATGC). The raw MiSeq paired-end reads were demultiplexed by the sequencing facility, and bioinformatic analyses were performed by the Genetic Diversity Centre at ETH Zurich (Switzerland). The pairs of high-quality reads were merged after quality control and removal of problematic sequences, and primer sites were trimmed using USEARCH v11.0.667 (Edgar, 2010). The merged reads were further quality filtered using PRINSEQ-lite 0.20.4 (Schmieder and Edwards, 2011). Next, de-replicated amplicons were error-corrected to obtain zero radius OTUs (zOTUs) utilizing UPARSE and UNOISE3, which were then clustered at 97% sequence identity and chimeras were removed (Edgar R, 2016). A count table was generated for the 16S rRNA (bOTU) and ITS (fOTU) dataset by mapping the amplicons to the OTUs. Phylogenetic trees were constructed by Multiple-Sequence Alignment using MUSCLE v3.8.31 (Edgar E.C., 2004). Finally, the taxonomy was assigned using SINTAX v11.0.667 (Edgar RC, 2016) with the databases "SILVA SSU v138" and "UNITE All Eukaryotes (V9)" database for 16S rRNA and ITS sequences (Abarenkov et al., 2010; Quast et al., 2013).

2.6 Statistical analysis of plant phenotypic and microbiota profiling data

The statistical analysis of phenotypic data was performed in R version 4.3.2 (R Core Team, 2023). Data were analyzed by type II analysis of variance (ANOVA) using the car package (Fox and Weisberg, 2019). The normality of the data was verified by graphically visualizing the residuals using the qqPlot() function of the *car* package and using the Shapiro-Wilk normality test (Royston, 1995) (shapiro.test). When necessary, the data was transformed by calculating the square root, data that did not follow a normal distribution after transformation was analyzed by using the Wilcoxon-Mann-Whitney and the Kruskal-Wallis test. For the bOTUs, the OTUs unassigned at phylum level, "Cyanobacteria" and "Mitochondria" were removed, while for the fOTUs all the OTUs belonging to the plant material were filtered. The packages *phyloseq* (McMurdie and Holmes, 2013), *vegan* (Oksanen et al., 2022), *microbiome* (Lahti and Shetty, 2019) and *picante* (Kembel et al., 2010) were used for the microbiome analysis. The graphs were generated by the packages *ggplot2* (Wickham, 2016). The taxa prevalence and the relative abundance were evaluated after filtering out the low abundant OTUs (less than 4 sequences in at least 3 samples). The treatment effect on the relative abundance of different phyla was statistically tested by Wilcoxon-Mann-Whitney and the Kruskal-Wallis test. The alpha diversity was calculated including the low abundant OTUs on rarefied data, the OTUs Richness and the Shannon diversity index were calculated and statistically analyzed by ANOVA as described above. The low abundant OTUs, for the beta diversity, were filtered and the relative abundance was calculated. The beta diversity was analyzed statistically by PERMANOVA (adonis2(), formula "~ Treatment*Genotype") on Bray-Curtis dissimilarities and visualized by Constrained Analysis of Principal Coordinates (CAP), as implemented in the *phyloseq* package. The differential abundance was calculated after filtering the low abundant OTUs and with unrarefied data. The differential abundance analysis was performed using the DESeq() function from the packages *DESeq2* (Love et al., 2014). Differentially abundant OTUs were selected based on their *p-values* that were adjusted for multiple testing using the procedure of Benjamini and Hochberg (1995).

3 Results

3.1 Plant performance and yield

The number of flowers per truss, recorded at 90 DAT, varied significantly in relation to the cultivar (Supplementary Table 4); the minimum value was ascertained for 'Riccio' (4.5) and the maximum value for 'Pizzutello piccolo' (8.1). The total number of flowers per plant recorded at the first measurement also varied significantly based on the genotype with average value varied from 8.9 to 75.8 for 'Riccio' and 'Pizzutello piccolo', respectively (Supplementary Table 4). The number of trusses per plant at 90 DAT was affected by the genotype, varying significantly from the lowest value of 1.7 for 'Riccio' compared to the highest recorded for 'Pizzutello piccolo' (8.8) (Supplementary Table 4). The number of trusses at 110 DAT was affected by the *P. absoluta* infestation, however significant differences due to the treatment and among the cultivars were recorded. Regarding the treatment, a higher number of trusses was recorded for the treated plants (4.0) compared to the control (2.7). These parameters varied also among the genotypes with values varying from 0.8 to 6.1 for 'Riccio' and 'Pizzutello piccolo', respectively (Supplementary Table 4).

The percentage of fruit set trusses (defined as fruit-bearing truss) recorded 90 DAT showed significant differences with regards to the treatment (Figure 1A), and the percentage of fruit-bearing trusses was 37.2% for the control and the 87.0% for the treated plants (Supplementary Table 4). Furthermore, a significant effect of the cultivar was recorded, observing the highest value for 'Pizzutello piccolo' (64.5%) and the lowest for 'Riccio' (14.4%) (Supplementary Table 4). During the second measurement (110 DAT), the percentage of set truss ranged from 17.9% to 34.3% for the control and treated plants, respectively (Supplementary Table 4). Regarding the cultivar, the highest value was recorded for 'Francavilla' (50.9%) followed by 'Giallo' (43.3%), 'UC 82'

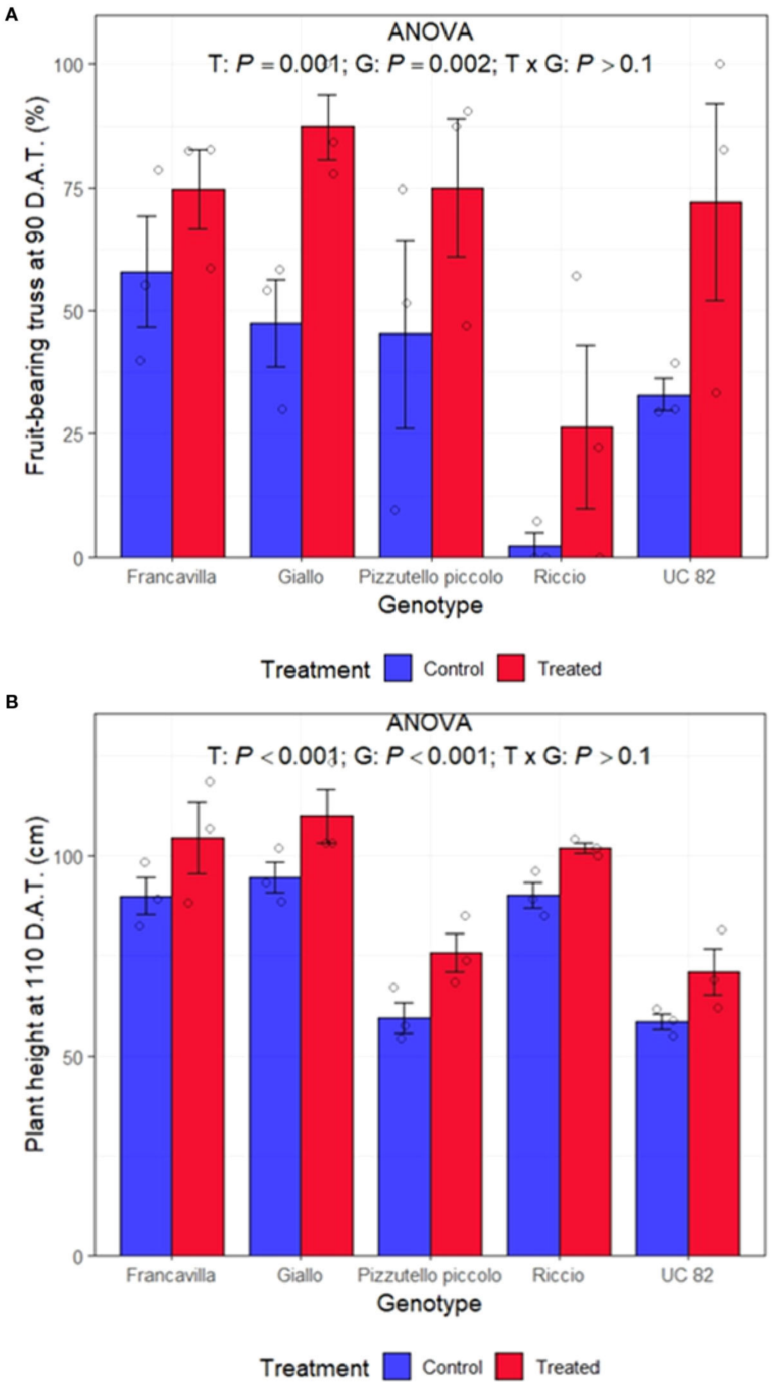

FIGURE 1
Microbial inoculation improves plant vigour across genotypes. **(A)** Number of fruit-bearing trusses 90 DAT and **(B)** plant height 110 DAT of five tomato genotypes treated with the microbial consortium (Treated) and untreated (Control). Bar plots show the mean ± standard error of three replicates, each representing a plot of five plants. The genotypes consist of Sicilian landraces and the tomato cultivar 'UC 82'. The data were analysed by ANOVA: T = Treatment; G = Genotype.

(16.0%), 'Pizzutello piccolo' (15.9%) and 'Riccio' (4.2%) (Supplementary Table 4).

The plant height recorded at 110 DAT was significantly affected by the microbial consortia application (78.6 cm for the control and 92.7 cm for the plant grown in the inoculated soil) (Figure 1B). Furthermore, a significant effect of the genotype was observed for the plant height which varied from 64.7 to 102.3 cm for 'UC 82' and 'Giallo', respectively. Several plant characteristics were also evaluated at the end of the experimental trial (150 DAT), such as the number of branches that varied significantly in relation to the microbial consortium treatment (from 23.2 to 30.3 for the control and the treated plant, respectively) (Supplementary Table 1). The root fresh weight varied significantly only among the cultivar (from 16.5 to 106.9 g for 'Pizzutello piccolo' and 'UC 82', respectively) while the root length varied significantly both according to the soil treatment with the microbial consortium (24.9 cm and 33.2 cm for the control and for the plants grown in the inoculated soil, respectively) and the cultivar (from 22.8 to 36.7 cm for 'Pizzutello piccolo' and 'Riccio', respectively) (Supplementary Table 4). For the root width, a significant interaction (treatment x genotype) was observed, where the benefits of the treatment were most pronounced for 'Pizzutello piccolo' (Supplementary Table 4).

Treated plants were significantly more productive (1292 g m^{-2}) than the control (504 g m^{-2}) (Figure 2A). In addition, a significant

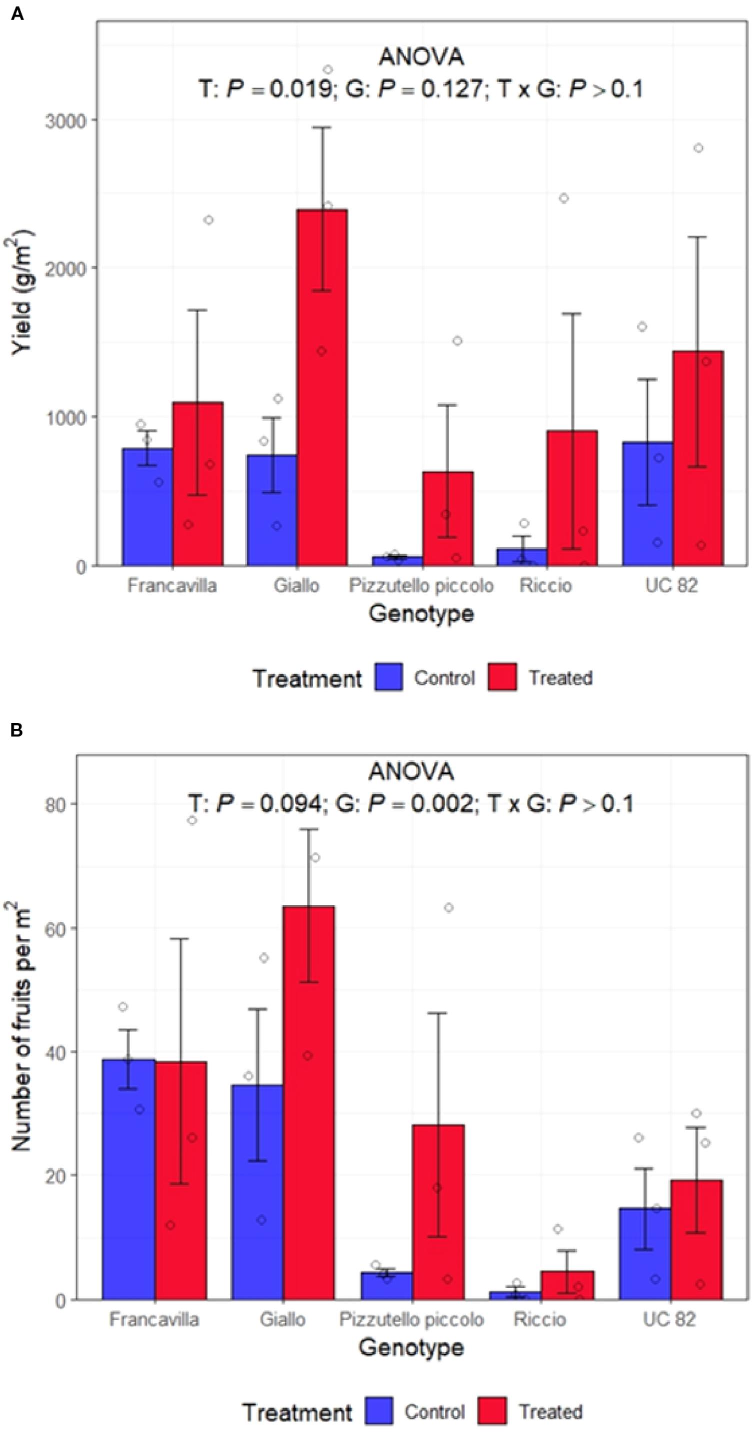

FIGURE 2
A fair production was obtained under the biotic stresses, inoculated plants showed significantly higher production compared to the control plant. **(A)** Yield of harvested fruits expressed as g per m2. **(B)** Number of fruits per m2. Bar plots show the mean ± standard error of three replicates, each representing a plot of five plants. The genotypes consist of Sicilian landraces and the tomato cultivar 'UC 82'. The data were analysed by ANOVA: T = Treatment; G = Genotype.

difference of production among the cultivars was observed with 'Giallo' (1568 g m^{-2}) being the most productive followed by 'UC 82' (1134 g m^{-2}), 'Francavilla' (940 g m^{-2}), 'Riccio' (506 g m^{-2}) and 'Pizzutello piccolo' (344 g m^{-2}) (Figure 2A). Regarding the number of fruits per m^2, although the difference was not significant *(p-value* = 0.094), a higher number of fruits was observed in the inoculated plants (30.8) compared to the control (18.7) (Figure 2B). The number of fruits per m^2 varied significantly also among the cultivars: 2.8 for 'Riccio', 16.2 for 'Pizzutello piccolo', 17 for 'UC 82', 28.6 for 'Francavilla' and 49.1 for 'Giallo' (Figure 2).

3.2 Effect on the tomato leaf miner and root-knot nematodes

Due to *P. absoluta* infestation, several trusses were lost between the first and the second measurement (90–110 DAT; Supplementary Table 4), as a result of the biotic stress on the plants caused by the feeding activity of *P. absoluta* larvae. A significant effect of the microbial treatment was observed between the first and the second measurement with a lower percentage of lost trusses in treated plots with the microbial consortium (22.6%) compared to the control plots (50.8%) (Supplementary Table 4). Significant differences in *P. absoluta* damage among cultivars and treatments were also observed. Plants treated with the microbial consortium showed, on average, less damage (34.3%) than the control (55.9%) (Figure 3A). Among the cultivars, the lowest number of infested leaves per plant was observed for 'Giallo' (29.1%) followed by 'UC 82' (37.9%), 'Francavilla' (41.7%), 'Riccio' (51.5%) and 'Pizzutello Piccolo' (65.0%) (Figure 3A). A Spearman's correlation analysis was performed to analyze the correlations among the variables described. The correlogram (Supplementary Figure 2A) showed that *P. absoluta* damage is negatively correlated with the yield and related parameter, as the percentage of fruited trusses (2^{nd} measurement). Furthermore, the correlogram also showed a negative correlation between the *P. absoluta* damage and the parameters related to the plant growth, as the plant height and the fruit weight (Supplementary Figure 2A).

Assessment of root damage by nematodes at the end of the trial showed a marginally statistically significant effect of the microbial treatment (*p-value* = 0.06), with values of 3.5 and 4.6 for the treated and not treated plots, respectively (Figure 3B). Significant differences in root damage among the cultivars were observed. The lowest values were recorded for 'Pizzutello Piccolo' (2.5) followed by 'Francavilla' (4.0), 'Riccio' (4.0), 'UC 82' (4.8) and 'Giallo' (5.0) (Figure 3B). The nematode root damage was found to be negatively correlated with the root width and positively correlated with the root weight, however no significant correlation between nematode root damage and plant performance or productivity was determined (Supplementary Figure 2A).

Principal Component Analysis (PCA) was performed to investigate the entire variation among the experimental factors studied. The PC1 represent 34.2% of the variation, while the PC2 represents 22.4% (Supplementary Figure 2B). The figure showed a clustering trend of the samples by cultivar and treatment, since control and treated plants clearly separated within each cultivar. With regards to the parameters evaluated, samples associated with higher yield and traits related to production and plant growth tend to cluster in the upper part of the graph (Supplementary Figure 2C). In contrast, the samples with the highest damages of *P. absoluta* and nematodes were located in the lower part of the graph (Supplementary Figure 2C).

3.3 Root DNA sequencing results and microbiome taxonomic overview

DNA was extracted from the roots at flowering stage and the V3-V4 region of the 16S ribosomal RNA and of the fungal ITS1 region were sequenced to investigate the effect of the microbial consortia treatment on the root microbiome. The 16S rRNA sequencing resulted in 1'600'513 reads which passed the quality and length filtering. We obtained 1'244'021 sequences with an average number of 41'467 reads per sample, varying from 30'330 to 63'409 reads, after removing reads associated with chloroplast and mitochondria. Sequencing of the ITS1 region resulted in 1'244'182 reads which passed the quality and length filtering. It was known that primers designed to amplify the ITS region, could also amplify DNA of plants and other eukaryotes. However, the proportion of reads provided by the sequencing platform that were assigned to plants and nematodes was surprisingly high; more than 50% of reads were assigned to plants.

Considering that the forward primer (ITS5) was reported for nematode profiling (Kuzmin et al., 2007; Langford and Janovy, 2013; Tkach et al., 2014), and that the OTUs associated with nematodes belong to two well-known plant pathogenic genera, *Meloidogyne* and *Pratylenchus*, we decided to analyze all sequences belonging to Fungi and Nematodes together. The dataset of fungi and nematodes consisted of 466'599 reads, with an average number of 15'553 per sample, varying from 4'456 to 27'875. The high-quality reads were clustered in OTUs at >97% sequence identity, resulting in 1'190 bacterial OTUs (bOTUs) and 356 fungi and nematode OTUs (fOTUs).

In the bacterial population, the phylum Actinobacteriota showed the highest relative abundance (38.9%) followed by Proteobacteriota (27.4%), Firmicutes (24.0%), Bacteroidota (5.2%), and Myxomicoccota (1.5%). The remaining 13 phyla showed a relative abundance lower than 1%. In the fungi and nematode dataset, 69.6% of the reads were assigned to nematode OTUs and the remaining 30.4% to fungal OTUs. Within the fungal community, the phylum Ascomycota showed the highest relative abundance (39.7%), followed by Basidiomycota (13.2%), Mucoromycota (3.6%), Mortierellomycota (3.44%), the remaining 40.0% belonged to the Fungi Kingdom but remained unassigned at phylum level.

For both datasets, OTUs from low abundant phyla were mostly also found to be less prevalent across samples (Supplementary Figure 3). Visual inspection and statistics analysis of the relative abundance of different phyla among the samples revealed that bacteria from the phyla Bacteroidota (*p-value*=0.007) and Proteobacteria (*p-value*=0.006) were more abundant in roots of

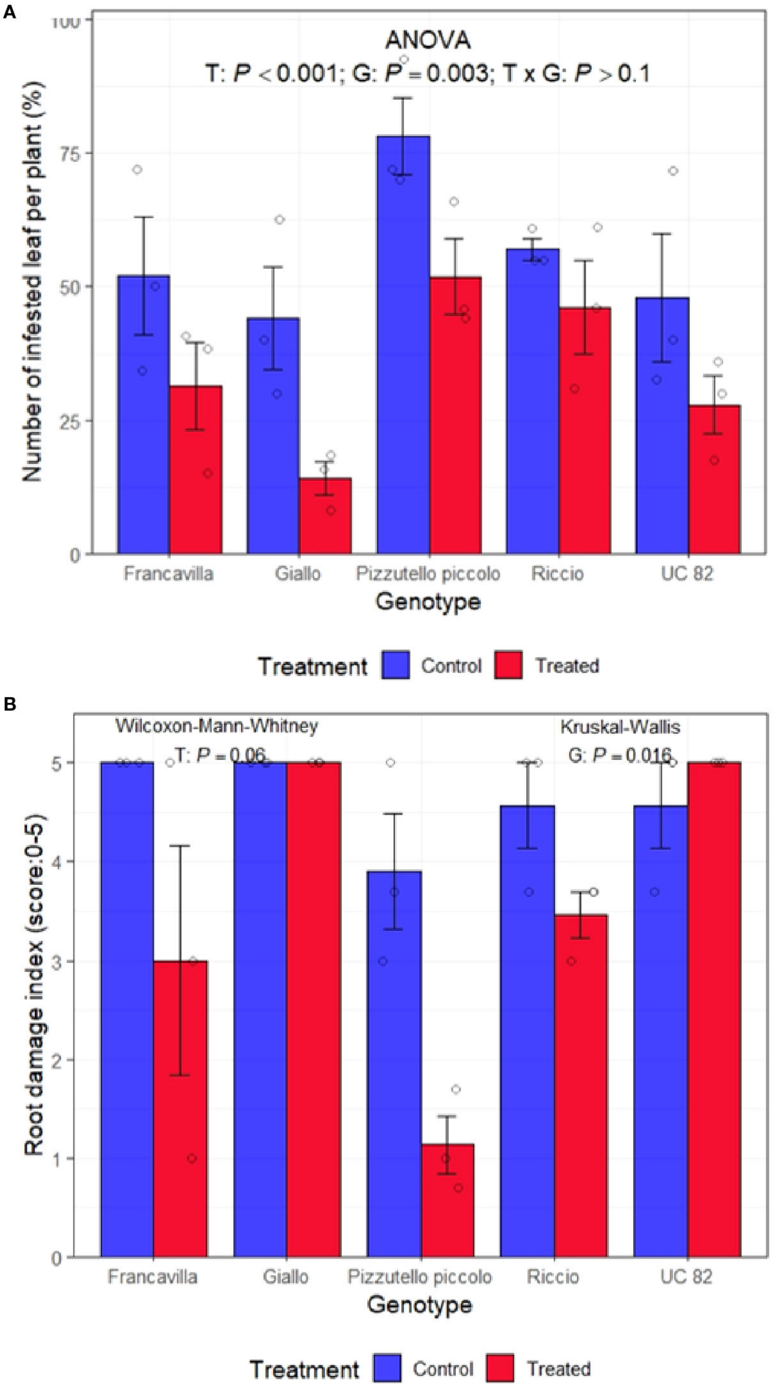

FIGURE 3
Microbial inoculation and tomato genotype affect resistance to pests. **(A)** infested leaf per plant (%) by P. absoluta and **(B)** damage severity index by nematodes. Bar plots show the mean ± standard error of three replicates, each representing a plot of five plants. The genotypes consist of Sicilian landraces and the tomato cultivar 'UC 82'. The root damage was ranked from 0 to 5 scale (0; 0–10%, 1; 11–20%, 21–50%, 3; 51–80%, 4; 81–90%, and 5; 91–100%). The infested leaf per plant was analysed by ANOVA while the Root damage index was analysed through "Wilcoxon-Mann-Whitney" and "Kruskal-Wallis" test: T = Treatment; G = Genotype.

the control plants, while Actinobacteriota (*p-value*=0.06) and Firmicutes (*p-value*=0.02) were more abundant in the roots of treated plants (Supplementary Figure 4A). For the dataset of fungi and nematodes, we found that in terms of relative abundance, relative to fungi, there were more nematodes (*p-value*=0.03) in the control plants than in inoculated plants (Supplementary Figure 4B). Further, in the inoculated plants, the Ascomycota were more abundant (*p-value*=0.06) (Supplementary Figure 4B).

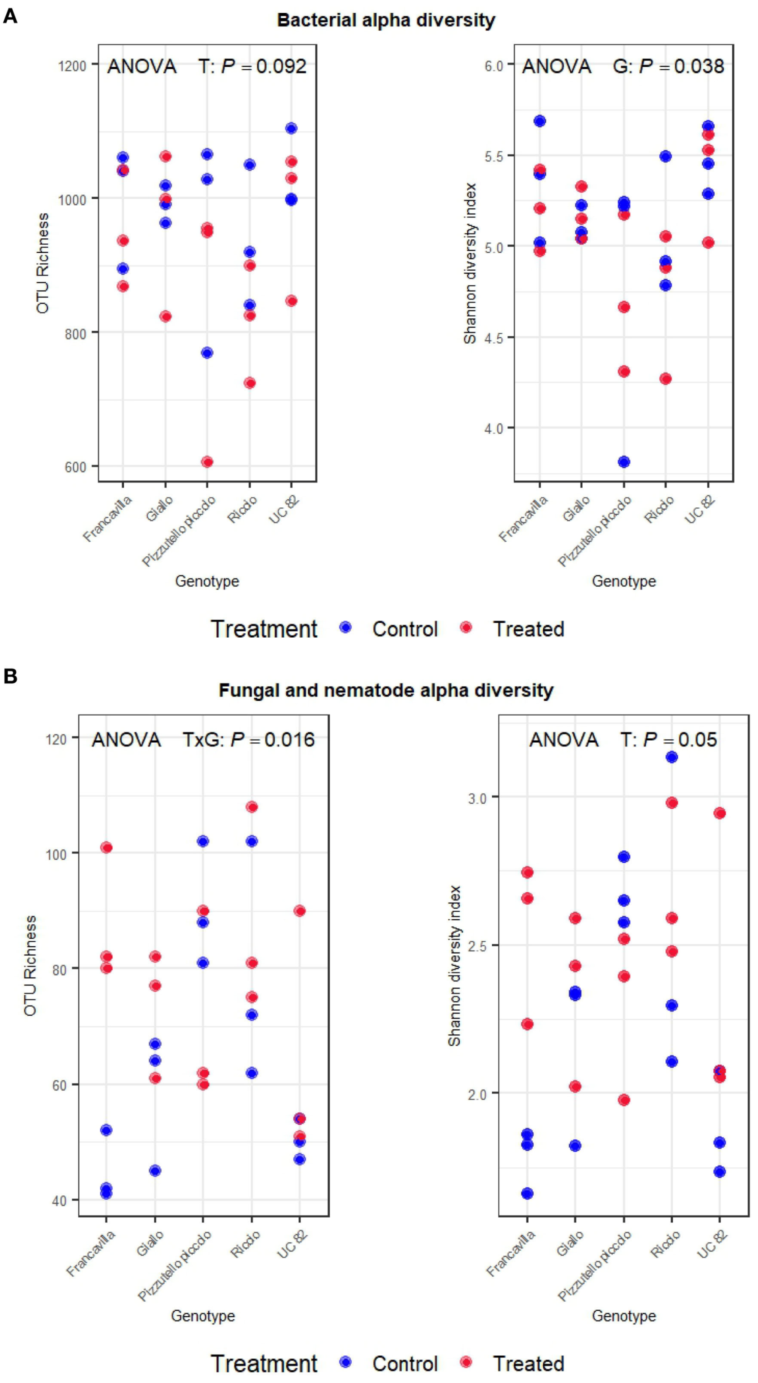

FIGURE 4
Microbial application and plant genotype affect the root alpha diversity of fungi and nematodes. **(A)** OTUs richness and Shannon diversity index are shown for bacteria **(B)** and fungi plus nematodes.

3.3.1 Alpha diversity of fungi and nematode

The alpha diversity was evaluated by analyzing OTU richness and Shannon diversity index. Bacterial alpha diversity did not differ significantly depending on the inoculation (Figure 4A). However, analysis of variance (ANOVA) revealed significant differences among the genotypes for the Shannon index (*p-value*=0.038). For the fungi and nematode dataset, overall alpha diversity was significantly increased by the inoculation treatment (Figure 4B). This was more apparent for the OTU richness (*p-value*=0.018) than the Shannon index (*p-value*=0.05). Alpha diversity also differed among genotype (OTU richness, *p-value*=0.020; Shannon index, *p-value*=0.07). Further, ANOVA revealed a significant interaction between the inoculation treatment and plant genotype (OTU richness, *p-value*=0.016; Shannon index, *p-value*=0.063). For example, while the treatment markedly increased alpha diversity in ‘Francavilla’, it led to a reduction in ‘Pizzutello Piccolo’. Overall, the results indicate that fungal and nematode alpha diversity were affected by the microbial consortium, plant genotype and their interaction, while bacterial alpha diversity was mostly unaffected by the treatment and only marginally by the plant genotypes.

3.3.2 Root microbial community composition

The beta diversity was evaluated by Permutational Multivariate Analysis of Variance (PERMANOVA) followed by a Constrained Analysis of Principal Coordinates (CAP) for visualization. For bacterial beta diversity, PERMANOVA showed significant effects of the treatment (*p-value*=0.003), explaining 11.8% of the variation found in bacterial community composition. Accordingly, the CAP showed a differentiation between the two treatment groups (Figure 5A). For the fungi and nematode dataset, the PERMANOVA indicated a significant effect of the microbial application (*p-value*=0.023), explaining 11.7% of the variation

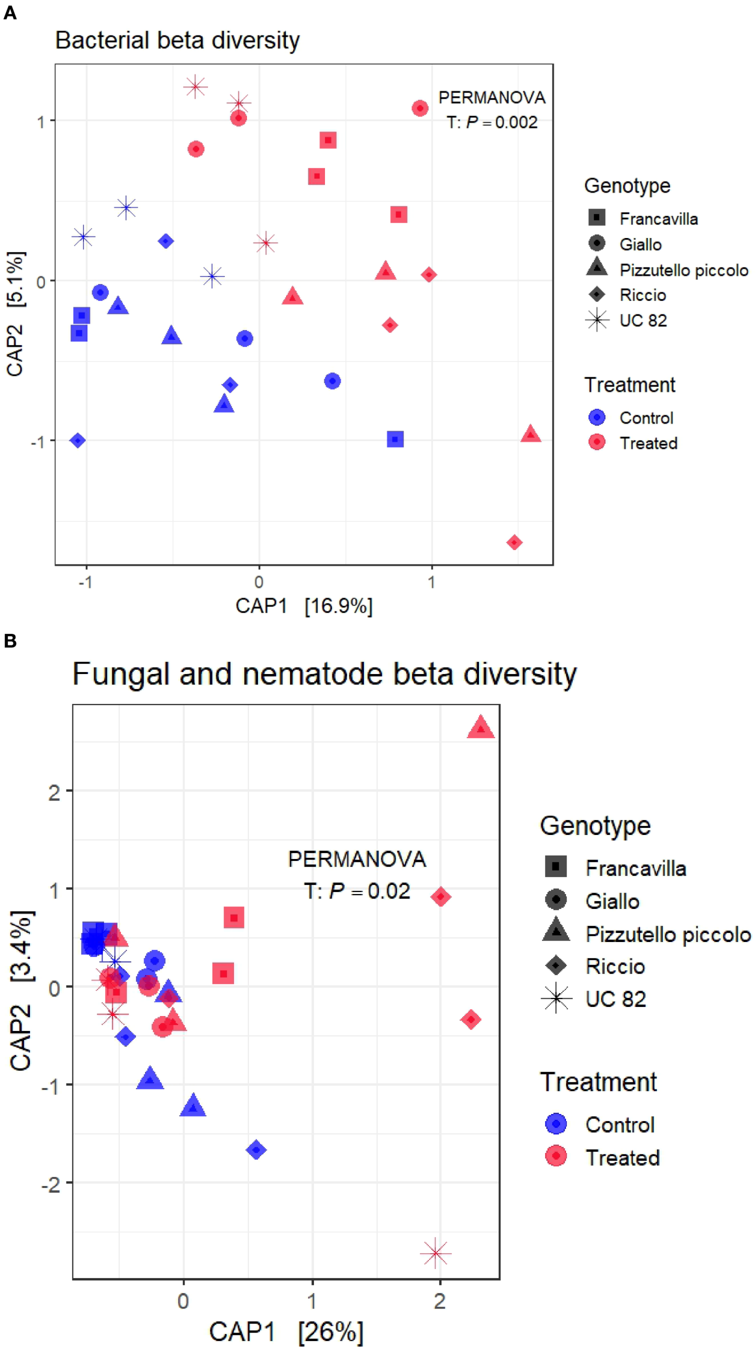

FIGURE 5
The Constrained Analysis of Principal Coordinates (CAP) on Bray-Curtis distances of community profiles shows different distribution among inoculated and control plants. **(A)** CAP visualizing the bacterial beta diversity. **(B)** CAP visualizing the Fungal and nematode beta diversity. Model for CAP '~ Treatment * Genotype'.

found in community composition. The CAP visualization exhibited that other factors affect the ordination more strongly compared to the treatment (Figure 5B).

3.3.3 Relative abundance of specific OTUs

We performed a differential abundance analysis using DESeq2 to determine whether individual OTUs were associated with the microbial treatment. For the bacteria, a total of 40 bOTUs were found to be differentially abundant (*p-value*<0.001) between treated and control plants (Figure 6A). The identified OTUs are taxonomically diverse and belong to the phyla Actinobacteriota, Bacteroidota, Bdellovibrionota, Firmicutes and Proteobacteria. For fungi and nematodes, a total of 16 fOTUs (*p-value*<0.001) were found to be differentially abundant between treated and control plants (Figure 6B). The identified OTUs were fungi that are unassigned at phylum level, followed by Ascomycota and the fOTU23 belonging to Mortierellomycota.

Interestingly, no nematode OTU was found to be differentially abundant with the given significance threshold. However, when the significance threshold was related to *p-value*<0.05, two nematode OTUs belonging to the genus of *Pratylenchus* were found to be abundant in the control plants compared to treated ones.

4 Discussion

4.1 Plant characterization and crop performance

Although chemical pesticides improve yields and protect crops from pests and diseases, their negative impact on the environment and human health has convinced many farmers to use alternative eco-friendly products as microbial inoculants based on PGPMs (Nicolopoulou-Stamati et al., 2016; Anzalone et al., 2021; Batista and Singh, 2021).

During the trial, a range of agronomic characteristics related to the plant growth and production were evaluated (Branca and Ruggeri, 2003). Furthermore, since the greenhouse was naturally infested by *P. absoluta*, we had the opportunity to evaluate the effect of the microbial consortium and the performance of the 5 tomato cultivars under biotic stress. Overall, a greater growth rate of the inoculated plants was observed compared to the control, furthermore also the genotypes showed different growth and response to the treatment. This can be seen in particular from the greater percentage of set trusses recorded before infestation by *P. absoluta* and from the greater height of the inoculated plants (Figure 1). Furthermore, despite the plants were affected by *P. absoluta* infestation, also the yield was higher in the inoculated plants than the control (Figure 3). It is well reported in literature that PGPMs facilitate the growth and development of plants by producing various phytohormones such as cytokinins, abscisic acid, gibberellins, auxins and ethylene (Mohanty et al., 2021; Mondal et al., 2020). Another interesting observation is that the treated plants appear to be less damaged by *P. absoluta* compared to the control (Figure 2). There is also ample evidence that PGPMs induce the resistance to biotic stress (Bhat et al., 2022), in addition, among the several PGPR and PGPF strains utilized as biocontrol agents and resistance inductors, one of the most effective and utilized is *Trichoderma* spp (Dutta et al., 2023). *Trichoderma* spp. is well known as fungal biocontrol agents against plant pathogens and nematodes, but recently also their activity against *P. absoluta* was shown by *T. asperellum* (Agbessenou et al., 2022, 2020; Urbaneja et al., 2012), which is present in the microbial consortia applied together with *T. harzianum* and *T. atroviridae* (Supplementary Table 1). However, since the treatment was applied by fertigation to the roots rather than a direct effect on *P. absoluta*, our hypothesis is that the growth promoting effect of the microbial consortium helped the plants to react by producing more biomass and by enhancing the systemic defenses which contrast the feeding activity of *P. absoluta*. Similar results have already been obtained and reported in the literature where plants inoculated with PGPM showed less damage by to *P. absoluta* and

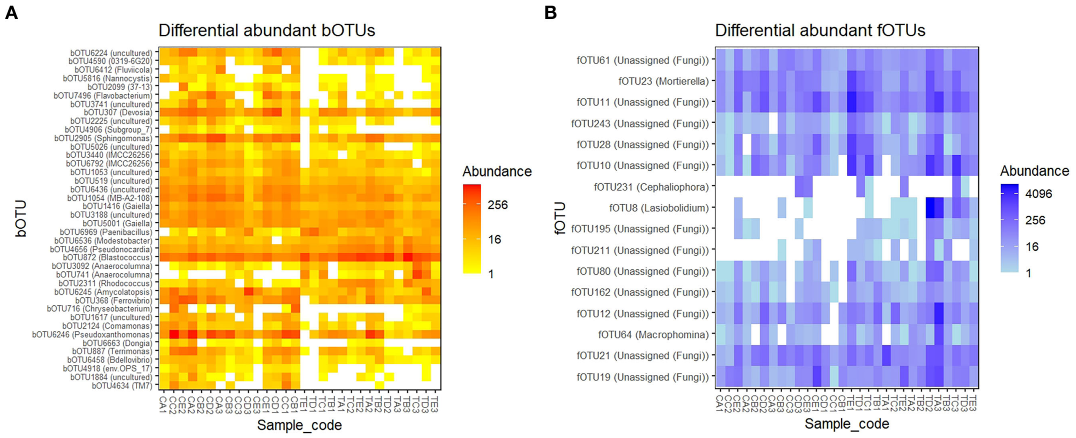

FIGURE 6

Significant differential abundance (*p*-value < 0.001) calculated by DESq2 were observed for several bacterial OTUs (bOTU) and several fungal OTUs due to the treatment. **(A)** Differentially abundant bacterial OTUs and **(B)** differentially abundant fungal OTUs (fOTU). The intensity of the colour represents the absolute abundance of each OTUs in each sample replicated three times. The individual rows represent individual OTU, on y-axis are indicated the OTU identity and the Phylum. On x-axis are represented the samples by a code: the first letter represents the treatment (T = Treated, C= Control); the second letter represents the genotype (A = 'UC 82', B = 'Giallo', C = 'Francavilla', D = 'Riccio', E = 'Pizzutello piccolo').

nematodes (Molinari and Leonetti, 2023). The microbial treatment reduced the RKN root damage scores, close to significance (*p-value* = 0.06), suggesting a potential biocontrol efficacy. This observation aligns with recent findings that PGPR and *Bacillus* spp. can suppress *Meloidogyne* spp. through different mechanisms and the induction of systemic resistance (Vasantha-Srinivasan et al., 2025; Aioub et al., 2022; Mhatre et al., 2019). Here we found marginal effects on root width and weight. This is consistent with previous studies that showing that microbial amendments can modulate the plant root architecture (Grover et al., 2021; Sharafzadeh, 2012). Notably, the root damage showed significant differences in relation to the cultivar, with 'Pizzutello Piccolo' exhibiting the lowest score, supporting evidence that the genetic traits strongly influence RKN impact and responsiveness to biocontrol strategies. The lack of a clear correlation between root damage and productivity shows how complex it is to turn root scores into useful agronomic data. This may be due to the plant's ability to grow or adapt when biocontrol helps reduce stress (Vinothini et al., 2024; Banora, 2023; Bavaresco et al., 2020). Further experiments are needed to disentangle direct and indirect resistance-mediated effects of the microbial application on plant performance and productivity.

4.2 Microbiome taxonomic overview

Microbial inoculants could modify the soil microbial community (Jiang et al., 2023; Mawarda et al., 2020) and the microbiome of plant roots (Akyol et al., 2019; Berg et al., 2021). The microbiome profiling was performed to investigate the effect of the microbial treatment evaluated on the plant root microbiome. Analysis of the bacterial community revealed significant differences between the treated and control plants, mainly involving phyla such as Actinobacteria, Bacteroidota, Firmicutes and Proteobacteria. The Actinobacteria represents one of the largest taxonomic units among the domain Bacteria (Ludwig et al., 2012), present various and different lifestyles including plant pathogens (Ventura et al., 2007; Wanner, 2006). However, this phylum has been widely reported as promising bioinoculant, as it is known to be involved in nutrient cycling, soil quality and crop productivity as well as plant health (Boubekri et al., 2022; Boukhatem et al., 2022; Kaari et al., 2023). This is in line with our observation that it was more abundant in the roots of treated plants relative to the control (Supplementary Figure 4A). The Firmicutes are also an important phylum that includes several genera involved in agriculturally important processes such as phosphorus solubilization and biocontrol (Hashmi et al., 2020; Lee et al., 2021). In addition, Lee et al. (2021) reported that the relative abundance of Gram-positive Actinobacteria and Firmicutes was lower in diseased, *Ralstonia solanacearum* infested rhizosphere soils compared to healthy ones, at constant *R. solanacearum* abundance. Artificial suppression of these Gram-positive taxa in healthy soils significantly increased bacterial wilt incidence, indicating that disruption of these protective bacterial phyla promotes disease (Lee et al., 2021). This finding is compatible with our results since the relative abundance of Actinobacteria and Firmicutes was found to be higher in treated plants than the control.

Regarding the data obtained from the ITS amplification, some limitations should be considered. The primers adopted were specifically designed to amplify the fungal ITS region (Dodd et al., 2000; Hariharan and Prasannath, 2021; Procopio et al., 2020; Toju et al., 2012; White et al., 1990). Although some plant DNA amplification is expected for ITS (Aslam et al., 2017; Bellemain et al., 2010; Saar et al., 2001), we did not expect a considerable amplification of nematode DNA. However, considering the specificity of the primers and the forward primer (ITS5) has been reported in the literature for nematodes classification (Langford and Janovy, 2013; Tkach et al., 2014), combined with evidence of considerable nematode damage on the roots, we decided to include the nematode reads together with the fungal reads in our dataset. The analysis identified OTUs belonging to *Pratylenchus* spp. and *Meloidogyne* spp., both of them are well known as plant parasitic nematodes. Noteworthy, significant differences were observed in alpha and beta diversity, with a tendency for nematode OTUs to be less abundant in the treated plants, while fungi OTUs (mostly belonging to Ascomycota) tended to be more abundant in the roots of treated plots compared to the control. The Ascomycota is a huge phylum that includes PGPFs such as mycorrhizal fungi and biocontrol agents such as the famous *Trichoderma* spp. but also plant pathogens (Benítez et al., 2004; Egidi et al., 2019; Heitman, 2011; Poveda, 2021). fOTU23, which was more abundant in the treated plants (Figure 6), was identified at the genus level as belonging to the genera *Mortierella*. *M. alpina* has been reported to alleviate diseases caused by *Fusarium oxysporum* in *Panax ginseng* and to increase the nitrogen and phosphorus availability to plants (Wang et al., 2022). Moreover, *M. globalpina* was reported to be pathogenic for *Meloidogyne* spp. nematodes (DiLegge et al., 2019). Sequencing did not reach the genus level for all the differentially abundant OTUs, but since the applied microbial consortia include PGPFs belonging to Ascomycota such as *Trichoderma* spp., which are known as biocontrol agents of plant-parasitic nematodes (TariqJaveed et al., 2021). It is therefore plausible that the fungal community of the inoculated plants colonized the roots at the expense of nematodes.

Further experiments are needed to validate these results and confirm the effectiveness of the microbial consortium applied under the biotic stresses due to the root-knot nematodes and *P. absoluta*, in replicated trials on different field sites. However, this study shows that beneficial microbial inoculants can increase tomato resilience to biotic stresses, making them a promising tool for eco-sustainable pest control and for reducing chemical inputs in agriculture.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/Supplementary Material.

Author contributions

GR: Data curation, Formal analysis, Investigation, Software, Writing – original draft. LC: Investigation, Writing – review & editing. DA: Investigation, Writing – review & editing. VC: Supervision, Writing – review & editing. GS: Writing – review & editing. VG: Data curation, Software, Supervision, Writing – review

& editing. MM: Funding acquisition, Supervision, Writing – review & editing. FB: Funding acquisition, Methodology, Supervision, Visualization, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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References

Abarenkov, K., Nilsson, R. H., Larsson, K. H., Alexander, I. J., Eberhardt, U., Erland, S., et al. (2010). The UNITE database for molecular identification of fungi - recent updates and future perspectives. *New Phytol.* 186 (2), 281-285. doi: 10.1111/j.1469-8137.2009.03160.x

Abdelrahman, M., Abdel-Motaal, F., El-Sayed, M., Jogaiah, S., Shigyo, M., Ito, S.i., et al. (2016). Dissection of *Trichoderma longibrachiatum*-induced defense in onion (*Allium cepa* L.) against *Fusarium oxysporum* f. sp. *cepa* by target metabolite profiling. *Plant Sci.* 246, 128-138. doi: 10.1016/j.plantsci.2016.02.008

Acharya, R., Barman, A. K., Sharma, S. R., Kafle, L., Kim, S. M., and Lee, K. Y. (2023). Biology, distribution, and management of invasive South American tomato leafminer, *Tuta absoluta* (Meyrick) (*Lepidoptera; Gelechiidae*), in Asia. *Arch. Insect Biochem. Physiol.* 114 (4), e22056. doi: 10.1002/arch.22056

Agbessenou, A., Akutse, K. S., Yusuf, A. A., Ekesi, S., Subramanian, S., and Khamis, F. M. (2020). Endophytic fungi protect tomato and nightshade plants against *Tuta absoluta* (*Lepidoptera: Gelechiidae*) through a hidden friendship and cryptic battle. *Sci. Rep.* 10, 22195. doi: 10.1038/s41598-020-78898-8

Agbessenou, A., Akutse, K. S., Yusuf, A. A., and Khamis, F. M. (2022). The Endophyte Trichoderma asperellum M2RT4 Induces the Systemic Release of Methyl Salicylate and (Z)-jasmone in Tomato Plant Affecting Host Location and Herbivory of *Tuta absoluta*. *Front. Plant Sci.* 13, 860309. doi: 10.3389/fpls.2022.860309

Aioub, A. A. A., Elesawy, A. E., and Ammar, E. E. (2022). Plant growth promoting rhizobacteria (PGPR) and their role in plant-parasitic nematodes control: a fresh look at an old issue. *J. Plant Dis. Prot* 129, 1305–1321. doi: 10.1007/s41348-022-00642-3

Aktar, W., Sengupta, D., and Chowdhury, A. (2009). Impact of pesticides use in agriculture: Their benefits and hazards. *Interdiscip Toxicol.* 2, 1. doi: 10.2478/v10102-009-0001-7

Akyol, T. Y., Niwa, R., Hirakawa, H., Maruyama, H., Sato, T., Suzuki, T., et al. (2019). Impact of introduction of arbuscular mycorrhizal fungi on the root microbial community in agricultural fields. *Microbes Environ.* 34, 23-32. doi: 10.1264/jsme2.ME18109

Ali, W. M., Abdel-Mageed, M. A., Hegazy, M. G. A., Abou-Shlell, M. K., Sultan, S. M. E., Salama, E. A. A., et al. (2023). Biocontrol agent of root-knot nematode *Meloidogyne javanica* and root-rot fungi, Fusarium solani in okra morphological, anatomical characteristics and productivity under greenhouse conditions. *Sci. Rep.* 13, 11103. doi: 10.1038/s41598-023-37837-z

Alsaedi, G., Ashouri, A., and Talaei-Hassanloui, R. (2017). Evaluation of *Bacillus thuringiensis* to Control *Tuta absoluta* (Meyrick) (*Lepidoptera: Gelechiidae*) under Laboratory Conditions. *Agric. Sci.* 08 (7), 591-599. doi: 10.4236/as.2017.87045

Anzalone, A., Di Guardo, M., Bella, P., Ghadamgahi, F., Dimaria, G., Zago, R., et al. (2021). Bioprospecting of beneficial bacteria traits associated with tomato root in greenhouse environment reveals that sampling sites impact more than the root compartment. *Front. Plant Sci.* 12, 637582. doi: 10.3389/fpls.2021.637582

Anzalone, A., Mosca, A., Dimaria, G., Nicotra, D., Tessitori, M., Privitera, G. F., et al. (2022). Soil and soilless tomato cultivation promote different microbial communities that provide new models for future crop interventions. *Int. J. Mol. Sci.* 23 (15), 8820. doi: 10.3390/ijms23158820

Aprile, A. M., Coppola, M., Turrà, D., Vitale, S., Cascone, P., Diretto, G., et al. (2022). Combination of the Systemin peptide with the beneficial fungus *Trichoderma afroharzianum* T22 improves plant defense responses against pests and diseases. *J. Plant Interact.* 17 (1), 569-579. doi: 10.1080/17429145.2022.2072528

Araujo, R. (2022). Advances in soil engineering: sustainable strategies for rhizosphere and bulk soil microbiome enrichment. *Front. Bioscience - Landmark.* 27 (6), 195. doi: 10.31083/j.fbl2706195

Argento, S., Melilli, M. G., and Branca, F. (2019). Enhancing Greenhouse Tomato-Crop Productivity by Using *Brassica macrocarpa* Guss. Leaves for controlling root-knot nematodes. *Agronomy* 9 (12), 820. doi: 10.3390/agronomy9120820

Argento, S., Treccarichi, S., Arena, D., Rizzo, G. F., and Branca, F. (2023). Exploitation of a grafting technique for improving the water use efficiency of eggplant (*Solanum melongena* L.) grown in a cold greenhouse in mediterranean climatic conditions. *Agronomy* 13 (11), 2705. doi: 10.3390/agronomy13112705

Aslam, S., Tahir, A., Aslam, M. F., Alam, M. W., Shedayi, A. A., and Sadia, S. (2017). Recent advances in molecular techniques for the identification of phytopathogenic fungi – a mini review. *J. Plant Interact.* 12 (1), 439-504. doi: 10.1080/17429145.2017.1397205

Ayilara, M. S., Adeleke, B. S., Akinola, S. A., Fayose, C. A., Adeyemi, U. T., Gbadegesin, L. A., et al. (2023). Biopesticides as a promising alternative to synthetic pesticides: A case for microbial pesticides, phytopesticides, and nanobiopesticides. *Front. Microbiol.* 14, 1040901. doi: 10.3389/fmicb.2023.1040901

Banora, M. Y. (2023). "Impacting of root-knot nematodes on tomato: current status and potential horizons for its managing," in *Tomato Cultivation and Consumption-Innovation and Sustainability* (IntechOpen). doi: 10.5772/intechopen.112868

Barker, K. R. (1985). "An advanced treatise on *Meloidogyne*. Volume II: Methodology," in *Biology and Control I* (Department of Plant Pathology North Carolina State University).

Batista, B. D., and Singh, B. K. (2021). Realities and hopes in the application of microbial tools in agriculture. *Microb. Biotechnol.* 14 (4), 1258-1268. doi: 10.1111/1751-7915.13866

Bavaresco, L. G., Guaberto, L. M., and Araujo, F. F. (2020). Interaction of Bacillus subtilis with resistant and susceptible tomato (*Solanum lycopersicum* L.) in the control of *Meloidogyne incognita*. *Arch. Phytopathol. Plant Prot.* 54 (7-8), 359–374. doi: 10.1080/03235408.2020.1833279

Bellemain, E., Carlsen, T., Brochmann, C., Coissac, E., Taberlet, P., and Kauserud, H. (2010). ITS as an environmental DNA barcode for fungi: An in silico approach reveals potential PCR biases. *BMC Microbiol.* 10 (1), 189. doi: 10.1186/1471-2180-10-189

Benítez, T., Rincón, A. M., Limón, M. C., and Codón, A. C. (2004). Biocontrol mechanisms of Trichoderma strains. *Int. Microbiol.* 7, 249–260.

Benjamini, Y., and Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J. R. Stat. society: Ser. B (Methodological)* 57 (1), 289–300. doi: 10.1111/j.2517-6161.1995.tb02031.x

Berg, G., Kusstatscher, P., Abdelfattah, A., Cernava, T., and Smalla, K. (2021). Microbiome modulation—Toward a better understanding of plant microbiome response to microbial inoculants. *Front. Microbiol.* 12, 650610. doi: 10.3389/fmicb.2021.650610

Bhat, A. A., Shakeel, A., Waqar, S., Handoo, Z. A., and Khan, A. A. (2023). Microbes vs. Nematodes: Insights into Biocontrol through Antagonistic Organisms to Control Root-Knot Nematodes. *Plants.* 12 (3), 451. doi: 10.3390/plants12030451

Bhat, B. A., Tariq, L., Nissar, S., Islam, S. T., Islam, S. U., Mangral, Z., et al. (2022). The role of plant-associated rhizobacteria in plant growth, biocontrol and abiotic stress management. *J. Appl. Microbiol.* 133 (5), 2717-2741. doi: 10.1111/jam.15796

Biondi, A., Guedes, R. N. C., Wan, F. H., and Desneux, N. (2018). Ecology, worldwide spread, and management of the invasive south American tomato pinworm, *Tuta absoluta*: past, present, and future. *Annu. Rev. Entomol.* 63 (1), 239-258. doi: 10.1146/annurev-ento-031616-034933

Blake, C., Christensen, M. N., and Kovács, Á.T. (2021). Molecular aspects of plant growth promotion and protection by *Bacillus subtilis*. *Mol. Plant-Microbe Interact.* 34 (1), 15-25. doi: 10.1094/MPMI-08-20-0225-CR

Boubekri, K., Soumare, A., Mardad, I., Lyamlouli, K., Ouhdouch, Y., Hafidi, M., et al. (2022). Multifunctional role of Actinobacteria in agricultural production sustainability: A review. *Microbiol. Res.* 261, 127059. doi: 10.1016/j.micres.2022.127059

Boukhatem, Z. F., Merabet, C., and Tsaki, H. (2022). Plant growth promoting actinobacteria, the most promising candidates as bioinoculants? *Front. Agron.* 4, 849911. doi: 10.3389/fagro.2022.849911

Branca, F., and Ruggeri, A. (2003). Response of some Italian tomato landraces to protected cultivation. *Acta Hortic.* 614, 711-717. doi: 10.17660/ActaHortic.2003.614.106

Bukin, Y. S., Galachyants, Y. P., Morozov, I. V., Bukin, S. V., Zakharenko, A. S., and Zemskaya, T. I. (2019). The effect of 16s rRNA region choice on bacterial community metabarcoding results. *Sci. Data* 6 6 (1), 1-14. doi: 10.1038/sdata.2019.7

Campos, M. R., Biondi, A., Adiga, A., Guedes, R. N. C., and Desneux, N. (2017). From the Western Palaearctic region to beyond: *Tuta absoluta* 10 years after invading Europe. *J. Pest Sci.* 90 (3), 787-796. doi: 10.1007/s10340-017-0867-7

Caramante, M., Rouphael, Y., and Corrado, G. (2023). Genetic diversity among and within tomato (*Solanum lycopersicum* L.) landraces grown in Southern Italy. *Genet. Resour Crop Evol* 71 (1), 157-166. doi: 10.1007/s10722-023-01613-9

Chaudhari, A. K., Singh, V. K., Kedia, A., Das, S., and Dubey, N. K. (2021). Essential oils and their bioactive compounds as eco-friendly novel green pesticides for management of storage insect pests: prospects and retrospects. *Environ. Sci. pollut. Res.* 28 (15), 18918-18940. doi: 10.1007/s11356-021-12841-w

Chouhan, G. K., Jaiswal, D. K., Gaurav, A. K., Mukherjee, A., and Verma, J. P. (2021). "PGPM as a potential bioinoculant for enhancing crop productivity under sustainable agriculture," in *Biofertilizers* Woodhead Publishing, vol. 1, 221-237. Advances in Bio-Inoculants. doi: 10.1016/B978-0-12-821667-5.00009-9

Christakis, C. A., Daskalogiannis, G., Chatzaki, A., Markakis, E. A., Mermigka, G., Sagia, A., et al. (2021). Endophytic bacterial isolates from halophytes demonstrate phytopathogen biocontrol and plant growth promotion under high salinity. *Front. Microbiol.* 12, 681567. doi: 10.3389/fmicb.2021.681567

Colmenárez, Y. C., Vásquez, C., De Freitas Bueno, A., Cantor, F., Hidalgo, E., Corniani, N., et al. (2022). Sustainable management of the invasive *Tuta absoluta* (*Lepidoptera: Gelechiidae*): an overview of case studies from Latin American countries participating in plantwise. *J. Integr. Pest Manag.* 13 (1), 15. doi: 10.1093/jipm/pmac012

D'Esposito, D., Guadagno, A., Amoroso, C. G., Cascone, P., Cencetti, G., Michelozzi, M., et al. (2023). Genomic and metabolic profiling of two tomato contrasting cultivars for tolerance to *Tuta absoluta*. *Planta* 257 (3), 47. doi: 10.1007/s00425-023-04073-8

Deng, S., Wipf, H. M. L., Pierroz, G., Raab, T. K., Khanna, R., and Coleman-Derr, D. (2019). A plant growth-promoting microbial soil amendment dynamically alters the strawberry root bacterial microbiome. *Sci. Rep.* 9 (1), 17677. doi: 10.1038/s41598-019-53623-2

Desneux, N., Han, P., Mansour, R., Arnó, J., Brévault, T., Campos, M. R., et al. (2022). Integrated pest management of *Tuta absoluta*: practical implementations across different world regions. *J. Pest Sci.* 95, 17–39. doi: 10.1007/s10340-021-01442-8

Desneux, N., Wajnberg, E., Wyckhuys, K. A. G., Burgio, G., Arpaia, S., Narváez-Vasquez, C. A., et al. (2010). Biological invasion of European tomato crops by *Tuta absoluta*: Ecology, geographic expansion and prospects for biological control. *J. Pest Sci.* 83 (3), 197-215. doi: 10.1007/s10340-010-0321-6

DiLegge, M. J., Manter, D. K., and Vivanco, J. M. (2019). A novel approach to determine generalist nematophagous microbes reveals Mortierella globalpina as a new biocontrol agent against Meloidogyne spp. nematodes. *Sci. Rep.* 9 (1), 7521. doi: 10.1038/s41598-019-44010-y

Dixit, R., Kamat, S., Srivastava, A., and Kumari, M. (2022). "Molecular basis of plant-PGPM interactions during amelioration of biotic stress," in *Microbial Biocontrol: Food Security and Post Harvest Management*, vol. 2. Cham: Springer International Publishing, p. 129-165. doi: 10.1007/978-3-030-87289-2_5

Dodd, S. L., Crowhurst, R. N., Rodrigo, A. G., Samuels, G. J., Hill, R. A., and Stewart, A. (2000). Examination of Trichoderma phylogenies derived from ribosomal DNA sequence data. *Mycol Res.* 104 (1), 23-34. doi: 10.1017/S0953756299001100

Dutta, P., Mahanta, M., Singh, S. B., Thakuria, D., Deb, L., Kumari, A., et al. (2023). Molecular interaction between plants and Trichoderma species against soil-borne plant pathogens. *Front. Plant Sci.* 14, 1145715. doi: 10.3389/fpls.2023.1145715

Edgar, R. C. (2004). MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Res.* 32 (5), -1797. doi: 10.1093/nar/gkh340

Edgar, R. C. (2010). Search and clustering orders of magnitude faster than BLAST. *Bioinformatics* 26 (19), 2460-2461. doi: 10.1093/bioinformatics/btq461

Edgar, R. (2016). SINTAX: a simple non-Bayesian taxonomy classifier for 16S and ITS sequences. *bioRxiv* 2016, 074161. doi: 10.1101/074161

Edgar, R. C. (2016). UNOISE2: improved error-correction for Illumina 16S and ITS amplicon sequencing. *bioRxiv* 2016, 081257. doi: 10.1101/081257

Egidi, E., Delgado-Baquerizo, M., Plett, J. M., Wang, J., Eldridge, D. J., Bardgett, R. D., et al. (2019). A few Ascomycota taxa dominate soil fungal communities worldwide. *Nat. Commun.* 10 (1), 2369. doi: 10.1038/s41467-019-10373-z

Elnahal, A. S. M., El-Saadony, M. T., Saad, A. M., Desoky, E. S. M., El-Tahan, A. M., Rady, M. M., et al. (2022). The use of microbial inoculants for biological control, plant growth promotion, and sustainable agriculture: A review. *Eur. J. Plant Pathol.* 162 (4), 759-792. doi: 10.1007/s10658-021-02393-7

Ferreira, F. V., and Musumeci, M. A. (2021). Trichoderma as biological control agent: scope and prospects to improve efficacy. *World J. Microbiol. Biotechnol.* 37 (5), 90. doi: 10.1007/s11274-021-03058-7

Filho, M. M., Vilela, E. F., Attygalle, A. B., Meinwald, J., Svatoš, A., and Jham, G. N. (2000). Field trapping of tomato moth, *Tuta absoluta* with pheromone traps. *J. Chem. Ecol.* 26 (4), 875-881. doi: 10.1023/A:1005452023847

Fox, J., and Weisberg, S. (2019). *An {R} Companion to Applied Regression. 3rd ed.* (Thousand Oaks CA: Sage).

Ghadamgahi, F., Tarighi, S., Taheri, P., Saripella, G. V., Anzalone, A., Kalyandurg, P. B., et al. (2022). Plant Growth-Promoting Activity of Pseudomonas aeruginosa FG106 and Its Ability to Act as a Biocontrol Agent against Potato, Tomato and Taro Pathogens. *Biol. (Basel)* 11 (1), 140. doi: 10.3390/biology11010140

Giannoulakis, E., Mantzoukas, S., Lagogiannis, I., Dervisoglou, S., and Perdikis, D. (2023). Efficacy of endophytic wild strains of entomopathogenic fungi against the tomato leafminer *Tuta absoluta* Meyrick (*Lepidoptera: Gelechiidae*) in tomato plants. *Egypt J. Biol. Pest Control* 33 (1), 9. doi: 10.1186/s41938-023-00663-6

Gilland, B. (2002). World population and food supply can food production keep pace with population growth in the next half-century? *Food Policy* 27 (1), 47-63. doi: 10.1016/S0306-9192(02)00002-7

Grover, M., Bodhankar, S., Sharma, A., Sharma, P., Singh, J., and Nain, L. (2021). PGPR mediated alterations in root traits: way toward sustainable crop production. *Front. Sustain. Food Syst.* 4, 618230. doi: 10.3389/fsufs.2020.618230

Hakim, S., Naqqash, T., Nawaz, M. S., Laraib, I., Siddique, M. J., Zia, R., et al. (2021). Rhizosphere engineering with plant growth-promoting microorganisms for agriculture and ecological sustainability. *Front. Sustain Food Syst.* 5, 617157. doi: 10.3389/fsufs.2021.617157

Hariharan, G., and Prasannath, K. (2021). Recent advances in molecular diagnostics of fungal plant pathogens: A mini review. *Front. Cell Infect. Microbiol.* doi: 10.3389/fcimb.2020.600234

Hashmi, I., Bindschedler, S., and Junier, P. (2020). "Chapter 18 - firmicutes," in *Beneficial Microbes in Agro-Ecology.* 2020, 363-396. doi: 10.1016/B978-0-12-823414-3.00018-6

Heitman, J. (2011). Microbial pathogens in the fungal kingdom. *Fungal Biol. Rev.* doi: 10.1016/j.fbr.2011.01.003

Jabamo, T., Ayalew, G., Goftishu, M., and Wakgari, M. (2023). Integrated effect of insecticide and sex pheromone on the tomato leafminer, *Tuta absoluta* (*Lepidoptera: Gelechiidae*). *Crop Prot.* 171, 106285. doi: 10.1016/j.cropro.2023.106285

Jiang, M., Delgado-Baquerizo, M., Yuan, M. M., Ding, J., Yergeau, E., Zhou, J., et al. (2023). Home-based microbial solution to boost crop growth in low-fertility soil. *New Phytol.* 239 (2), 752-765. doi: 10.1111/nph.18943

Kaari, M., Manikkam, R., Annamalai, K. K., and Joseph, J. (2023). Actinobacteria as a source of biofertilizer/biocontrol agents for bio-organic agriculture. *J. Appl. Microbiol.* 134 (2), lxac047. doi: 10.1093/jambio/lxac047

Karanastasi, E., Kotsantonis, V., and Pantelides, I. S. (2024). Compost-Derived Bacterial Communities Offer Promise as Biocontrol Agents against Meloidogyne javanica and Promote Plant Growth in Tomato. *Agriculture* 14 (6), 891. doi: 10.3390/agriculture14060891

Karipidis, P., and Karypidou, S. (2021). Factors that impact farmers' organic conversion decisions. *Sustainability (Switzerland).* (9), 4715. doi: 10.3390/su13094715

Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., et al. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26 (11), 1463-1464. doi: 10.1093/bioinformatics/btq166

Keulemans, W., Bylemans, D., and De Coninck, B. (2019). *Farming without plant protection products: Can we grow without using herbicides, fungicides and insecticides*? (Strasbourg, France: European Parliament.).

Kisand, V., Cuadros, R., and Wikner, J. (2002). Phylogeny of culturable estuarine bacteria catabolizing riverine organic matter in the northern Baltic Sea. *Appl. Environ. Microbiol.* 68 (1), 379-388. doi: 10.1128/AEM.68.1.379-388.2002

Kumar, S., Sindhu, S. S., and Kumar, R. (2022). Biofertilizers: An ecofriendly technology for nutrient recycling and environmental sustainability. *Curr. Res. Microb. Sci*. 3, 100094. doi: 10.1016/j.crmicr.2021.100094

Kuzmin, Y., Tkach, V. V., and Brooks, D. R. (2007). Two new species of Rhabdias (Nematoda: *Rhabdiasidae*) from the marine toad, *Bufo marinus* (L.) (Lissamphibia: Anura: *Bufonidae*), in Central America. *J. Parasitol.* 93 (1), 159-165. doi: 10.1645/GE-858R.1

Lacava, P. T., Bogas, A. C., Cruz, F., and de, P. N. (2022). Plant growth promotion and biocontrol by endophytic and rhizospheric microorganisms from the tropics: A review and perspectives. *Front. Sustain Food Syst*. 6, 796113. doi: 10.3389/fsufs.2022.796113

Lahti, L., and Shetty, S. A. (2019). *microbiome R package*. Available online at: http://microbiome.github.io.Bioconductor (Accessed September 1, 2023).

Lammoglia, S. K., Kennedy, M. C., Barriuso, E., Alletto, L., Justes, E., Munier-Jolain, N., et al. (2017). Assessing human health risks from pesticide use in conventional and innovative cropping systems with the BROWSE model. *Environ. Int.* 105, 66-78. doi: 10.1016/j.envint.2017.04.012

Langford, G. J., and Janovy, J. (2013). Host specificity of north american rhabdias spp. (nematoda: *Rhabdiasidae*): Combining field data and experimental infections with a molecular phylogeny. *J. Parasitol.* 99 (2), 277-286. doi: 10.1645/GE-3217.1

Lee, S. M., Kong, H. G., Song, G. C., and Ryu, C. M. (2021). Disruption of Firmicutes and Actinobacteria abundance in tomato rhizosphere causes the incidence of bacterial wilt disease. *ISME J.* 15 (1), 330-347. doi: 10.1038/s41396-020-00785-x

Liu, X., Mei, S., and Salles, J. F. (2023). Inoculated microbial consortia perform better than single strains in living soil: A meta-analysis. *Appl. Soil Ecol.* 190, 2023.03.17.533112. doi: 10.1016/j.apsoil.2023.105011

Lopes, M. J., dos, S., Dias-Filho, M. B., and Gurgel, E. S. C. (2021). Successful plant growth-promoting microbes: inoculation methods and abiotic factors. *Front. Sustain Food Syst*. 5, 606454. doi: 10.3389/fsufs.2021.606454

Love, M. I., Huber, W., and Anders, S. (2014). Moderated estimation of fold change and dispersion for RNA-seq data with DESeq2. *Genome Biol.* 15, 550. doi: 10.1186/s13059-014-0550-8

Ludwig, W., Euzéby, J., Schumann, P., Busse, H.-J., Trujillo, M. E., Kämpfer, P., et al. (2012). "Road map of the phylum Actinobacteria," in *Bergey's Manual® of Systematic Bacteriology*. 1-28. doi: 10.1007/978-0-387-68233-4_1

Malgioglio, G., Rizzo, G. F., Nigro, S., Lefebvre Du Prey, V., Herforth-Rahmé, J., Catara, V., et al. (2022). Plant-microbe interaction in sustainable agriculture: the factors that may influence the efficacy of PGPM application. *Sustainability* 14 (4), 2253. doi: 10.3390/su14042253

Mangrio, G. Q., Gilal, A. A., Rajput, L. B., Hajano, J. U. D., and Gabol, A. H. (2023). Performance of pheromone and light traps in monitoring and management of tomato leafminer, *Tuta absoluta* (*Lepidoptera: Gelechiidae*). *J. Saudi Soc. Agric. Sci*. 22 (5), 288-29. doi: 10.1016/j.jssas.2023.01.004

Markakis, E. A., Tjamos, S. E., Antoniou, P. P., Paplomatas, E. J., and Tjamos, E. C. (2016). Biological control of Verticillium wilt of olive by Paenibacillus alvei, strain K165. *BioControl* 61 (3), 293-303. doi: 10.1007/s10526-015-9669-0

Mawarda, P. C., Le Roux, X., Dirk van Elsas, J., and Salles, J. F. (2020). Deliberate introduction of invisible invaders: A critical appraisal of the impact of microbial inoculants on soil microbial communities. *Soil Biol. Biochem*. 148, 107874. doi: 10.1016/j.soilbio.2020.107874

McMurdie, P. J., and Holmes, S. (2013). Phyloseq: an R package for reproducible interactive analysis and graphics of microbiome census data. *PloS One* 8 (4), e61217. doi: 10.1371/journal.pone.0061217

Mhatre, P. H., Karthik, C., Kadirvelu, K., Divya, K. L., Venkatasalam, E. P., Srinivasan, S., et al. (2019). Plant growth promoting rhizobacteria (PGPR): A potential alternative tool for nematodes bio-control. *Biocatalysis Agric. Biotechnol.* 17, 119–128. doi: 10.1016/j.bcab.2018.11.009

Migunova, V. D., and Sasanelli, N. (2021). Bacteria as biocontrol tool against phytoparasitic nematodes. *Plants*. 10 (2), 389. doi: 10.3390/plants10020389

Mohanty, P., Singh, P. K., Chakraborty, D., Mishra, S., and Pattnaik, R. (2021). Insight into the role of PGPR in sustainable agriculture and environment. *Front. Sustain Food Syst*. 5, 667150. doi: 10.3389/fsufs.2021.667150

Molinari, S., and Leonetti, P. (2023). Resistance to plant parasites in tomato is induced by soil enrichment with specific bacterial and fungal rhizosphere microbiome. *Int. J. Mol. Sci.* 24 (20), 15416. doi: 10.3390/ijms242015416

Mondal, S., Halder, S. K., Yadav, A. N., and Mondal, K. C. (2020). Microbial consortium with multifunctional plant growth-promoting attributes: future perspective in agriculture. *Advances in plant microbiome and sustainable agriculture: functional annotation and future challenges* 2020, 219-258. doi: 10.1007/978-981-15-3204-7_10

Ndereyimana, A., Nyalala, S., Murerwa, P., and Gaidashova, S. (2019). Pathogenicity of some commercial formulations of entomopathogenic fungi on the tomato leaf miner, *Tuta absoluta* (Meyrick) (*Lepidoptera: Gelechiidae*). *Egypt J. Biol. Pest Control* 29 (1), 70. doi: 10.1186/s41938-019-0184-y

Nicolopoulou-Stamati, P., Maipas, S., Kotampasi, C., Stamatis, P., and Hens, L. (2016). Chemical pesticides and human health: the urgent need for a new concept in agriculture. *Front. Public Health*. 2016 (4), 148. doi: 10.3389/fpubh.2016.00148

Nicotra, D., Ghadamgahi, F., Ghosh, S., Anzalone, A., Dimaria, G., Mosca, A., et al. (2024). Genomic insights and biocontrol potential of ten bacterial strains from the tomato core microbiome. *Front. Plant Sci.* 15, 1437947. doi: 10.3389/fpls.2024.1437947

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., et al. (2022). *vegan: Community Ecology Package. R package version 2.6-4. Community ecology package 2.6-4*.

Pacios-Michelena, S., Aguilar González, C. N., Alvarez-Perez, O. B., Rodriguez-Herrera, R., Chávez-González, M., Arredondo Valdés, R., et al. (2021). Application of streptomyces antimicrobial compounds for the control of phytopathogens. *Front. Sustain Food Syst*. 5, 696518. doi: 10.3389/fsufs.2021.696518

Padmanabhan, P., Cheema, A., and Paliyath, G. (2015). "Solanaceous fruits including tomato, eggplant, and peppers," in *Encyclopedia of Food and Health* 24-32. doi: 10.1016/B978-0-12-384947-2.00696-6

Paravar, A., Piri, R., Balouchi, H., and Ma, Y. (2023). Microbial seed coating: An attractive tool for sustainable agriculture. *Biotechnol. Rep.* 37, e00781. doi: 10.1016/j.btre.2023.e00781

Pathak, V. M., Verma, V. K., Rawat, B. S., Kaur, B., Babu, N., Sharma, A., et al. (2022). Current status of pesticide effects on environment, human health and it's eco-friendly management as bioremediation: A comprehensive review. *Front. Microbiol*. 13, 962619. doi: 10.3389/fmicb.2022.962619

Picchi, V., Scalzo, R., Tava, A., Doria, F., Argento, S., Toscano, S., et al. (2020). Phytochemical characterization and *in vitro* antioxidant properties of four Brassica wild species from Italy. *Molecules* 25 (15), 3495. doi: 10.3390/molecules25153495

Popp, J., Pető, K., and Nagy, J. (2013). Pesticide productivity and food security. A review. *Agron. Sustain Dev.* 33, 243–255. doi: 10.1007/s13593-012-0105-x

Poveda, J. (2021). Trichoderma as biocontrol agent against pests: New uses for a mycoparasite. *Biol. Control.* 159, 104634. doi: 10.1016/j.biocontrol.2021.104634

Procopio, N., Ghignone, S., Voyron, S., Chiapello, M., Williams, A., Chamberlain, A., et al. (2020). Soil fungal communities investigated by metabarcoding within simulated forensic burial contexts. *Front. Microbiol.* 11, 1686. doi: 10.3389/fmicb.2020.01686

Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P., et al. (2013). The SILVA ribosomal RNA gene database project: Improved data processing and web-based tools. *Nucleic Acids Res.* 41 (D1), D590-D596. doi: 10.1093/nar/gks1219

R Core Team (2023). *R: A language and environment for statistical computing* (Vienna, Austria: R Foundation for Statistical Computing). R Foundation for Statistical Computing.

Rizzo, G. F., Al Achkar, N., Treccarichi, S., Malgioglio, G., Infurna, M. G., Nigro, S., et al. (2023). Use of bioinoculants affects variation in snap bean yield grown under deficit irrigation. *Agric. (Switzerland)* 13 (4), 865. doi: 10.3390/agriculture13040865

Rizzo, G. F., Bova, N., Emmanuello, E., Nigro, S., du Prey, V. L., Branca, F., et al. (2022). Efficacy of microbial consortia and natural compounds as seed treatment for tomato pathogen management, in: Acta Horticulturae. *Int. Soc. Hortic. Sci.* 1354, 253–260. doi: 10.17660/ActaHortic.2022.1354.33

Roda, A. L., Brambila, J., Barria, J., Euceda, X., and Korytkowski, C. (2015). Efficiency of trapping systems for detecting *Tuta absoluta* (*Lepidoptera: Gelechiidae*). *J. Economic Entomology* 108 (6), 2648–2654. doi: 10.1093/jee/tov248

Roopa, K. P., and Gadag, A. S. (2020). ". Importance of biopesticides in the sustainable management of plant-parasitic nematodes," in *Management of Phytonematodes: Recent Advances and Future Challenges*. (pp. 205-227). Singapore: Springer Singapore. doi: 10.1007/978-981-15-4087-5_9

Royston, P. (1995). Remark AS R94: A remark on algorithm AS 181: the W-test for normality. *Appl. Stat.* 44 (4), 547-551. doi: 10.2307/2986146

Saar, D. E., Polans, N. O., Sørensen, P. D., and Duvall, M. R. (2001). Angiosperm DNA contamination by endophytic fungi: detection and methods of avoidance. *Plant Mol. Biol. Rep.* 19 (3), 249-260. doi: 10.1007/BF02772897

Saleh, R., Bearth, A., and Siegrist, M. (2021). How chemophobia affects public acceptance of pesticide use and biotechnology in agriculture. *Food Qual Prefer* 91, 104197. doi: 10.1016/j.foodqual.2021.104197

Sandeep Kumar, J., Jayaraj, J., Shanthi, M., Theradimani, M., Venkatasamy, B., Irulandi, S., et al. (2020). Potential of standard strains of *Bacillus thuringiensis* against the tomato pinworm, *Tuta absoluta* (Meyrick) (*Lepidoptera: Gelechiidae*). *Egypt J. Biol. Pest Control* 30 (1), 123. doi: 10.1186/s41938-020-00326-w

Sarkar, S., Dias Bernardes Gil, J., Keeley, J., Möhring, N., and Jansen, K. (2021). *The use of pesticides in developing countries and their impact on health and the right to food* (Europe.eu: Policy Department for External Relations), ISBN: . doi: 10.2861/28995

Schmieder, R., and Edwards, R. (2011). Quality control and preprocessing of metagenomic datasets. *Bioinformatics* 27 (6), 863-864. doi: 10.1093/bioinformatics/btr026

Seo, H. J., Park, A. R., Kim, S., Yeon, J., Yu, N. H., Ha, S., et al. (2019). Biological control of root-knot nematodes by organic acid-producing lactobacillus brevis wikim0069 isolated from kimchi. *Plant Pathol. J. (Faisalabad)* 35 (6), 662. doi: 10.5423/PPJ.OA.08.2019.0225

Shafiei, F., Shahidi-Noghabi, S., and Smagghe, G. (2024). Effect of arbuscular mycorrhizal colonization on tomato defense metabolites and population parameters of *Tuta absoluta* (Meyrick). *Arthropod Plant Interact.* 18 (2), 339-351. doi: 10.1007/s11829-023-10035-4

Sharafzadeh, S. (2012). Effects of PGPR on growth and nutrients uptake of tomato. *Int. J. Adv. Eng. Technol.* 2, 27. ISSN: 2231-1963.

Sharma, A., Kumar, V., Shahzad, B., Tanveer, M., Sidhu, G. P. S., Handa, N., et al. (2019). Worldwide pesticide usage and its impacts on ecosystem. *SN Appl. Sci.* 1 (11), 1446. doi: 10.1007/s42452-019-1485-1

Shefali,, Kumar, R., Sankhla, M. S., Kumar, R., and Sonone, S. S. (2021). Impact of pesticide toxicity in aquatic environment. *Biointerface Res. Appl. Chem.* 11 (3), 10131-10140. doi: 10.33263/BRIAC113.1013110140

Silva, G. A., Queiroz, E. A., Arcanjo, L. P., Lopes, M. C., Araújo, T. A., Galdino, T. S. V., et al. (2021). Biological performance and oviposition preference of tomato pinworm *Tuta absoluta* when offered a range of Solanaceous host plants. *Sci. Rep.* 11 (1), 1153. doi: 10.1038/s41598-020-80434-7

Silva, A. C. L., Silva, G. A., Abib, P. H. N., Carolino, A. T., and Samuels, R. I. (2020). Endophytic colonization of tomato plants by the entomopathogenic fungus Beauveria bassiana for controlling the South American tomato pinworm, *Tuta absoluta*. *CABI Agric. Bioscience* 1 (1), 3. doi: 10.1186/s43170-020-00002-x

Smith, L. G., Kirk, G. J. D., Jones, P. J., and Williams, A. G. (2019). The greenhouse gas impacts of converting food production in England and Wales to organic methods. *Nat. Commun.* 10 (1), 4641. doi: 10.1038/s41467-019-12622-7

TariqJaveed, M., Farooq, T., Al-Hazmi, A. S., Hussain, M. D., and Rehman, A. U. (2021). Role of Trichoderma as a biocontrol agent (BCA) of phytoparasitic nematodes and plant growth inducer. *J. Invertebr Pathol.* 183, 107626. doi: 10.1016/j.jip.2021.107626

Tileubayeva, Z., Avdeenko, A., Avdeenko, S., Stroiteleva, N., and Kondrashev, S. (2021). Plant-parasitic nematodes affecting vegetable crops in greenhouses. *Saudi J. Biol. Sci.* 28 (9), 5428-5433. doi: 10.1016/j.sjbs.2021.05.075

Tkach, V. V., Kuzmin, Y., and Snyder, S. D. (2014). Molecular insight into systematics, host associations, life cycles and geographic distribution of the nematode family Rhabdiasidae. *Int. J. Parasitol.* 44 (5), 273-284. doi: 10.1016/j.ijpara.2013.12.005

Toju, H., Tanabe, A. S., Yamamoto, S., and Sato, H. (2012). High-coverage ITS primers for the DNA-based identification of ascomycetes and basidiomycetes in environmental samples. *PloS One* 7 (7), e40863. doi: 10.1371/journal.pone.0040863

Toscano, S., Ferrante, A., Branca, F., and Romano, D. (2021). Enhancing the quality of two species of baby leaves sprayed with moringa leaf extract as biostimulant. *Agronomy* 11 (7), 1399. doi: 10.3390/agronomy11071399

Treccarichi, S., Cali, R., Amari, M., Mortada, A., Felis, M. D., Achkar, N., et al. (2023). New tools for organic plant nutrition: microbial and aminoacid treatments for organic seed production of broccoli (*Brassica oleracea* var. *italica* Plenk.). *Acta Hortic.* 1365, 81-90. doi: 10.17660/ActaHortic.2023.1365.10

Tropea Garzia, G., Siscaro, G., Biondi, A., and Zappalà, L. (2012). Tuta absoluta, a South American pest of tomato now in the EPPO region: Biology, distribution and damage. *EPPO Bull.* 42 (2), 205-210. doi: 10.1111/epp.2556

Tudi, M., Li, H., Li, H., Wang, L., Lyu, J., Yang, L., et al. (2022). Exposure routes and health risks associated with pesticide application. *Toxics.* 10 (6), 335. doi: 10.3390/toxics10060335

Tudi, M., Ruan, H. D., Wang, L., Lyu, J., Sadler, R., Connell, D., et al. (2021). Agriculture development, pesticide application and its impact on the environment. *Int. J. Environ. Res. Public Health.* 18 (3), 1112. doi: 10.3390/ijerph18031112

Turner, S., Pryer, K. M., Miao, V. P. W., and Palmer, J. D. (1999). Investigating deep phylogenetic relationships among cyanobacteria and plastids by small subunit rRNA sequence analysis. *J. Eukaryotic Microbiol.* 46 (4), 327-338. doi: 10.1111/j.1550-7408.1999.tb04612.x

Upadhayay, J., Rana, M., Juyal, V., Bisht, S. S., and Joshi, R. (2020). "Impact of pesticide exposure and associated health effects," in *Pesticides in Crop Production: Physiological and Biochemical Action*. 2020, 69-88. doi: 10.1002/9781119432241.ch5

Urbaneja, A., González-Cabrera, J., Arnó, J., and Gabarra, R. (2012). Prospects for the biological control of *Tuta absoluta* in tomatoes of the Mediterranean basin. *Pest Manag Sci.* 68 (9), 1215-1222. doi: 10.1002/ps.3344

van Dijk, M., Morley, T., Rau, M. L., and Saghai, Y. (2021). A meta-analysis of projected global food demand and population at risk of hunger for the period 2010–2050. *Nat. Food* 2 (7), 494-501. doi: 10.1038/s43016-021-00322-9

Vasantha-Srinivasan, P., Park, K. B., Kim, K. Y., Jung, W. J., and Han, Y. S. (2025). The role of Bacillus species in the management of plant-parasitic nematodes. *Front. Microbiol.* 15, 1510036. doi: 10.3389/fmicb.2024.1510036

Ventura, M., Canchaya, C., Tauch, A., Chandra, G., Fitzgerald, G. F., Chater, K. F., et al. (2007). Genomics of actinobacteria: tracing the evolutionary history of an ancient phylum. *Microbiol. Mol. Biol. Rev.* 71 (3), 495-548. doi: 10.1128/mmbr.00005-07

Vinothini, K., Nakkeeran, S., Saranya, N., Jothi, P., Richard, J. I., Perveen, K., et al. (2024). Rhizosphere engineering of biocontrol agents enriches soil microbial diversity and effectively controls root-knot nematodes. *Microbial Ecol.* 87 (1), 120. doi: 10.1007/s00248-024-02435-7

Vishwakarma, K., Kumar, N., Shandilya, C., Mohapatra, S., Bhayana, S., and Varma, A. (2020). Revisiting plant–microbe interactions and microbial consortia application for enhancing sustainable agriculture: A review. *Front. Microbiol.* 11, 560406. doi: 10.3389/fmicb.2020.560406

Wang, Y., Pei, Y., Wang, X., Dai, X., and Zhu, M. (2024). Antimicrobial metabolites produced by the plant growth-promoting rhizobacteria (PGPR): *Bacillus* and *Pseudomonas*. *Advanced Agrochem.* 3 (3), 206-221. doi: 10.1016/j.aac.2024.07.007

Wang, M., Wang, Z., Guo, M., Qu, L., and Biere, A. (2023). Effects of arbuscular mycorrhizal fungi on plant growth and herbivore infestation depend on availability of soil water and nutrients. *Front. Plant Sci.* 14, 1101932. doi: 10.3389/fpls.2023.1101932

Wang, Y., Wang, L., Suo, M., Qiu, Z., Wu, H., Zhao, M., et al. (2022). Regulating Root Fungal Community Using Mortierella alpina for *Fusarium oxysporum* Resistance in Panax ginseng. *Front. Microbiol.* 13, 850917. doi: 10.3389/fmicb.2022.850917

Wanner, L. A. (2006). A survey of genetic variation in Streptomyces isolates causing potato common scab in the United States. *Phytopathology* 96 (12), 1363-1371. doi: 10.1094/PHYTO-96-1363

White, T. J., Bruns, T., Lee, S., and Taylor, J. (1990). "Amplification and direct sequencing of fungal ribosomal rna genes for phylogenetics," in *PCR Protocols*. 18 (1), 315-322. doi: 10.1016/b978-0-12-372180-8.50042-1

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis* (Springer-Verlag New York, Media).

Wu, M., Yan, Y., Wang, Y., Mao, Q., Fu, Y., Peng, X., et al. (2021). Arbuscular mycorrhizal fungi for vegetable (VT) enhance resistance to Rhizoctonia solani in watermelon by alleviating oxidative stress. *Biol. Control* 152, 104433. doi: 10.1016/j.biocontrol.2020.104433

Yang, R. H., Su, J. H., Shang, J. J., Wu, Y. Y., Li, Y., Bao, D. P., et al. (2018). Evaluation of the ribosomal DNA internal transcribed spacer (ITS), specifically ITS1 and ITS2, for the analysis of fungal diversity by deep sequencing. *PLoS One* 13 (10), e0206428. doi: 10.1371/journal.pone.0206428

Yao, X., Guo, H., Zhang, K., Zhao, M., Ruan, J., and Chen, J. (2023). Trichoderma and its role in biological control of plant fungal and nematode disease. *Front. Microbiol.* 14, 1160551. doi: 10.3389/fmicb.2023.1160551

Yüksel, E. (2022). Biocontrol potential of endosymbiotic bacteria of entomopathogenic nematodes against the tomato leaf miner, *Tuta absoluta* (Meyrick) (*Lepidoptera: Gelechiidae*). *Egypt J. Biol. Pest Control* 32 (1), 135. doi: 10.1186/s41938-022-00633-4

Zhou, B., and Li, X. (2021). The monitoring of chemical pesticides pollution on ecological environment by GIS. *Environ. Technol. Innov.* 23, 101506. doi: 10.1016/J.ETI.2021.101506

Zhou, X., Wang, J., Liu, F., Liang, J., Zhao, P., Tsui, C. K. M., et al. (2022). Cross-kingdom synthetic microbiota supports tomato suppression of Fusarium wilt disease. *Nat. Commun.* 13 (1), 7890. doi: 10.1038/s41467-022-35452-6