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Synergistic interplay between arbuscular mycorrhizal fungi and fern manure compost tea suppresses common tomato phytopathogens and pest attacks on-farm

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Actually, there are intensive efforts towards eco-friendly integrated agricultural management measures to control plant diseases and pests. One of the most promising approaches is the use of arbuscular mycorrhizal fungi (AMF) in combination with organic biopesticides such as eagle fern manure (FM) compost tea. However, their effects have been mainly studied independently from each other. The potential interactions between belowground plant-associated microorganisms such as AMF and aboveground foliar application of biopesticide to mitigate common tomato phytopathogens and pests remain untapped, particularly under on-farm conditions. In a randomized complete block design, the impact of inoculating tomato seedlings with a selected AMF consortium and beyond that the impact of mycorrhized plants receiving three different doses of FM compost tea (0%, 5%, and 10%) on the control of tomato-specific plant diseases and pests and subsequently on the crop yield were examined. The present study demonstrated a sevenfold increase in the rate of mycorrhizal root colonization (from 10% to 70%) in tomato plants that received the combined application of AMF and 10% FM compost tea compared to the control plants that did not receive AMF inoculum and FM compost tea. The combination of AMF and FM compost tea application led to positive synergistic effects that promoted beneficial effects in suppressing the incidence and severity of common tomato diseases and pests. The magnitude of these synergistic effects increased with AMF inoculation and FM compost tea dosage, culminating in greater suppression of tomato plant diseases and pests and, moreover, in an increase in fruit yield compared to control plants. The combination of AMF and 10% FM compost tea revealed a higher suppressive ability against most pathogens and insect attacks. This was evidenced by a 71.3% and 94.7% total reduction in incidence and severity, respectively, compared to control plants.

This is the first time that pre-inoculation of AM, combined with FM compost tea application, has been reported as a potential biocontrol alternative to suppress common tomato pathogens and pests while increasing cherry tomato yields sustainably.

KEYWORDS

cherry tomatoes, arbuscular mycorrhizal fungal inoculants, fern manure compost tea, tomato diseases, bio-protection, crop production

Introduction

Globally, the deleterious impact of plant diseases and pests on crop yields is unequivocal, causing annual losses amounting to USD $220 billion, equivalent to 20%–30% of the total global harvest (Chakraborty and Newton, 2011). This pervasive challenge poses a significant threat to global crop production and food security on a planetary scale (Chakraborty and Newton, 2011; FAOSTAT, 2017). Tomato (*Lycopersicon esculentum* Mill) is a highly valued vegetable crop worldwide, offering a wide range of fruit types with diverse uses (Mfombep et al., 2016; María et al., 2019). Cherry tomatoes, for instance, are a type of tomato with a sweet taste commonly consumed in salads but rarely found in supermarkets globally and especially in shopping centers in Cameroon, where they can fetch attractive prices for producers (Mfombep et al., 2016; María et al., 2019). The demand for tomatoes is increasing, driven by the growing urban population seeking healthy and balanced diets rich in antioxidants; vitamins A, B, C, and E; fiber; and minerals (Shankara et al., 2005; Daniel et al., 2012; Achancho, 2013; Ignace et al., 2015). The red pigment in tomatoes, known as lycopene, possesses antioxidant properties that can potentially protect against cancer (Grubben and Denton, 2004; Morard, 2013).

The global production of tomatoes remains below consumer demand due to several abiotic and biotic adverse factors (FAOSTAT, 2017). Diseases and pests can be major biotic factors that affect the quality and size of the fruit (Blancard et al., 2009; Simo et al., 2019). Abiotic factors such as unfavorable weather conditions, poor crop management, and poor soil quality can also influence tomato growth and yield (Bationo et al., 2006; Rocha, 2009). Bacterial wilt caused by *Ralstonia solanacearum* and unhealthy soils are the most significant limiting factors that can result in substantial yield losses ranging from 70% to 100% in tropical agriculture (Mahbou, 2010; Nwaga et al., 2010; Mfombep et al., 2016). To mitigate these losses, farmers often use mineral fertilizers and pesticides that not only are expensive, but also pose health risks to humans, belowground and aboveground organisms, and the environment (Thakore, 2006; Nicolopoulou-Stamati et al., 2016).

Arbuscular mycorrhizal fungi (AMF) are a widespread group of mutualistic soil-borne fungi that colonize the roots of most (90%) terrestrial plant species including tomato plants (Smith and Read, 2008; Fortin et al., 2008; Brundrett and Tedersoo, 2018). AMF provide water, nutrients, and appreciable ecosystem services to plants (Smith and Read, 2008; Brundrett and Tedersoo, 2018; Lutz et al., 2023). For example, it was shown that the use of AMF as biofertilizers resulted in a 70% reduction in phosphate fertilizer expenditures and a 30% to 40% reduction in nitrogen and potassium fertilizers (Johnson and Menge, 1982; Fortin, 2013). Some studies showed that inoculation of microbial inoculants such as mycorrhizal fungi into soils may result in improved crop growth and yields in the range of 50% to 200% compared to non-inoculated controls (Nwaga et al., 2004; Nwaga et al., 2010; Li et al., 2022; Lutz et al., 2023). AMF may also alter and suppress the evolution and dissemination of several common diseases (Pozo et al., 2010; Weng et al., 2022). AMF, for example, significantly reduced bacterial wilt caused by *R. solanacearum* and downy mildew caused by *Phytophthora infestans* as well as the susceptibility of tomato to *Alternaria solani* under field and greenhouse conditions (Mvele et al., 2002; Fritz et al., 2006; Nwaga et al., 2010). Recent studies showed that pre-inoculation of AMF primed and induced systemic tomato disease defense in controlled experiments (Song et al., 2015; Dey and Ghosh, 2022). However, current agricultural practices, such as high pesticide inputs, are likely to inhibit AMF growth, leading to suboptimal mycorrhizal root symbiosis in many agricultural systems (Ipsilantis et al., 2012; Bowles et al., 2016; Okiobe et al., 2022). The benefit associated with microbial inoculants is commonly provided through their colonization of the host plant roots, and most often, bioinoculant density in the rhizosphere greatly determines their efficacy (Bowles et al., 2016). Farmers have considered fostering AMF colonization through reduced tillage or by inoculating the seeds/seedlings before transplantation (pre-inoculation) or agricultural soil after transplantation (post-inoculation) (Nwaga et al., 2010). Pre-inoculating seedlings with AMF provides a competitive advantage to introduced AMF for plant-root colonization and nutrition in comparison to post-inoculation and resident AMF (Nwaga et al., 2010; Song et al., 2015; Bowles et al., 2016). However, the effectiveness of these inoculation techniques in protecting crops against diseases and increasing crop yields through mycorrhizal plant symbiosis establishment is not well studied so far (Song et al., 2015; Dey and Ghosh, 2022).

The use of biopesticides has emerged as a promising agricultural biocontrol strategy as they have many benefits. Biopesticides can be generally classified into three categories based on their origin; either they derive from living organisms such as microorganisms or they derive from organic plant and animal products such as green manure, compost, or farmyard manure (Thakore, 2006; Chandler et al., 2011; Leng et al., 2011). Plant-derived substances, such as essential oils and compost tea, have been demonstrated to have multifaceted biopesticidal properties with notable effectiveness in pathogen and pest suppression (Koné et al., 2010; On et al., 2015; Campanelli et al., 2018; Simo et al., 2019). Previous studies have highlighted the insecticidal, insect repellent, and acaricidal potentials of plant-derived oils on vegetable crops (Camara, 2009; Mostafa et al., 2014; Kanko et al., 2017; Asmae et al., 2018; Simo et al., 2019). Fermented plant extracts, also called compost tea, are plant-based preparations to treat plant pests and diseases or to increase the plant resistance against predators by stimulating their defense system (Deravel et al., 2014). Some studies have demonstrated that applying compost tea can significantly reduce diseases such as early blight, gray mold, and powdery mildew (Koné et al., 2010; On et al., 2015; Campanelli et al., 2018). Mala et al. (2019) proved that applying diluted aqueous eagle fern (*Pteridium aquilinum*) extracts at a concentration of 20% led to a notable reduction in lettuce diseases compared to the untreated control. Although these studies suggested that compost tea has the potential to be an effective biocontrol tool for tomato plant diseases, the effectiveness of compost tea, however, varied depending on the type of disease, the type of compost used, the brewing method, and application rate. Moreover, studies investigating the effects of biopesticide such as eagle fern manure (FM) compost tea combined with the impact of beneficial root-colonizing plant symbionts have been largely overlooked so far.

Although biopesticides have been shown to potentially protect aboveground plant compartments, some compost teas or aqueous plant extracts also showed limited effects on belowground or soil-dwelling plant pathogens (Kone et al., 2010; Diabaté et al., 2014; Mala et al., 2019). There is limited research on the effectiveness of FM compost tea on belowground processes, particularly the soil microbiome or even soil-dwelling plant pathogens (Mala et al., 2019; Pilla et al., 2023).

The integration of the coexistence of belowground beneficial soil symbiotic microorganisms, capable of colonizing roots to improve soil nutrient uptake and preventing the intrusion of soil-dwelling plant pathogens with the aboveground or foliar application of FM compost tea, holds promising potential for the enhancement of both soil and plant health. This offers a compelling avenue for the biocontrol of pests and disease outbreaks (Weng et al., 2022). The effects between FM compost tea application and AMF inoculation remain shrouded regarding whether this interplay engenders deleterious or positive synergistic effects on the establishment of tomato plant symbiosis through the improvement of mycorrhizal root colonization, as well as potential additive or synergistic impacts on the mitigation of plant diseases and pests. Existing investigations into AMF symbiosis and plant–pathogen interactions have predominantly revolved around the influence of single AMF species in isolation and their interactions with other microbial inoculants or fertilizers (Nwaga et al., 2010; Kohler et al., 2015; Chen et al., 2022). Moreover, most of these studies have been conducted within controlled environments or sterile nursery soil-less systems within greenhouse conditions (Weng et al., 2022). Therefore, it becomes imperative to delineate the optimal application rate of FM compost tea to harness the maximum benefits of AMF symbiosis with tomato plants in vegetable cropping systems under real on-farm conditions. The main objective was to assess how the combined effect of AMF and different FM compost tea application doses would interact to influence tomato plant-root symbiosis and crop yield by promoting tomato plant defense.

The following three hypotheses were investigated in this study: (1) Pre-colonizing tomato seedlings with AMF will increase the rate of mycorrhizal root colonization, while combining AMF pre-colonized plants with different FM compost tea application doses will further enhance these positive synergistic effects. (2) The influence of independent effects or the emergence of synergistic interactions between AMF pre-inoculation and FM compost tea application will induce changes in soil nutrient contents that further promote tomato growth and yield, in contrast to control plants (Nwaga et al., 2010). Finally, (3) the independent effects or the interactions of belowground AMF root colonization and aboveground FM compost tea bioprotective properties will promote additive or synergistic adverse effects, which further enhance higher suppressive abilities in the incidence and severity of tomato-specific plant diseases and pests in contrast to some reports that focused only on independent effects (Pozo et al., 2010; Song et al., 2015; Mala et al., 2019).

The specific objectives of this study were to (1) explore the nature of the interactions between dual and independent applications of AMF pre-inoculation and FM compost tea on tomato plant symbiotic parameters, including mycorrhizal root colonization and spore density; (2) examine the effects of FM compost tea application on tomato plant growth and yield, and how the presence of AMF pre-inoculation influences these tomato plant performances; and (3) assess the influence of the combined effects of AMF pre-inoculation and FM compost tea on the incidence and severity of tomato-specific plant diseases and pests, as well as potential relationships between plant symbiotic and health parameters.

The coexistence of consortia of AMF and FM compost tea to promote plant defense of tomato plants has never been explored. This investigation endeavors to shed light on the intricate dynamics of these interactions within the real-world vegetable cropping system, offering insights into the potential of this approach for sustainable crop management and yield optimization.

Materials and methods

Experimental site

The experimental field trial was carried out from March to June 2016 in the Center Region of Cameroon, Yaounde Capital, Department of Mefou-Akono in Mbankomo, in Nomayos quarter

(3° 47' 37.8" N 11° 27' 9.7" E, Alt = 694 m). Nomayos exhibits a Guinean equatorial climate typified by a bimodal precipitation pattern characterized by two rainy and two dry seasons. The average annual temperature and precipitation are approximately 25°C and 1,750 mm, respectively. As this study was conducted for a specific period, we also included monthly meteorological climate data for the duration of the experimental agricultural season (Supplementary Material, Figure S7). Tomatoes were cultivated during the minor rainy season, which spans from March to June, as it provides ideal growing conditions for tomato production.

Biological material

Most studies that examined the AMF effects used single species like *Rhizophagus irregularis* and *Funneliformis mosseae*, which do not represent the diversity of AMF community in agricultural soils (Deja-Sikora et al., 2023; Lutz et al., 2023). Therefore, a mixture of different AMF species was used to better cover the natural occurring diversity of AMF under field conditions Liu et al. (2009). The AMF inoculum comprised five selected species (*Glomus hoi, Rhizophagus intraradices, Scutellospora gregaria, Gigaspora margarita*, and *Glomus clarum*). The AMF species originated from the Bank of Soil Microbiology Laboratory resource collection of the Biotechnology Centre, University of Yaounde I, Nkolbisson, Cameroon. These are usually propagated with Sorghum host plants in pots containing sterile substrate. This AMF consortium is well described and has been largely used as an AMF biofertilizer for many experiments in the nursery and on farms (Nwaga et al., 2004; Nwaga et al., 2010).

As an organic biopesticide, a new formulation of FM compost tea, manufactured by SOPAL, a Cameroonian company, was used. In comparative evaluations against conventional manure compost teas, it was discerned that the aqueous extracts derived from this biopesticide, specifically harnessed from eagle ferns, showed a reduced effectiveness when employed in isolation and in combination with other plant-based biopesticides (Koné et al., 2010; Mala et al., 2019). Combining such a biopesticide with AMF presents an intriguing opportunity for improving plant protection and crop yields. FM was custom-crafted from eagle fern (*P. aquilinum*) manure compost tea, in contrast to aqueous extracts procured from fresh ferns (Koné et al., 2010; Mala et al., 2019). According to the company, the FM was prepared using modified methods proposed by Zaccardelli et al. (2012) and Pane et al. (2012), ensuring a comprehensive and well-controlled process for producing the semi-aerated fern compost tea. Briefly, the leaves, stems, and roots of the fern were collected from a 5-year-old fallow in the Center Region, Cameroon, to ensure the acquisition of mature plant materials for compost tea production (Mala et al., 2019). The next step involved diluting 15 kg of composted fern leaves, stems, and roots with 100 L of dechlorinated water within a 100-L container to avoid the occurrence of root or foliar phytotoxicity (Pane et al., 2012). A black soap solution was added at 0.1% as a wetting agent to enhance the effectiveness of the tea. The mixture was allowed to rest for 15 days to facilitate the maturation process. Maintaining an airtight seal on the container was imperative to encourage the proliferation of microorganisms, and the ambient room temperature of 25°C was chosen to stimulate microbial activity within the mixture. Once a week, the container was opened, and the mixture was manually agitated for 30 min. This periodic aeration was pivotal in ensuring the optimal development of the compost tea over the 15-day maturation period. Upon completion of the maturation process, the fermented tea underwent filtration. The FM-liquid phase suspension was transferred into 50-L containers ready for field application. Finally, FM was chemically defined/adjusted to a pH of 7.45, 700 mg/mL nitrogen (N), 1.34 mg/mL copper (Cu), and 8 mg/mL iron (Fe) as major elements and other oligo-elements. The final concentrations at 5% and 10% FM were also calculated (see Table S3, Supplementary Material). N, Cu, and Fe were analyzed as described in Pane et al. (2016). In particular, metal concentrations were determined in the FM extracts using an ICP-OES Spectrometer (iCAP 6000 Series - Thermo Scientific, Waltham, MA, USA).

Experimental trial

To choose our Cherry tomato (*Lycopersicon esculentum*) variety, a preliminary pot experiment was performed at the University of Yaounde I to determine the mycorrhizal dependency and plant biomass production of five tomato varieties (Mbogning, 2017). The results showed that the variety Brin de Muguet performed better in terms of biomass yield and mycorrhizal dependency compared to the other varieties [Petit rouge de Bale, Délice des Jardiniers, and Cerise Rouge, Local Cherry variety from the Research Institute of Agricultural Development (IRAD) at Abong-Mbang OMPARED, Est Cameroon]. This variety is susceptible to bacterial wilt, mildew blight, and pest attacks (Mbogning, 2017). The seeds originated from AGROSEMENS Company, Switzerland. The tomato varieties had more than 90% germinating capacity with a short development cycle varying from 65 to 90 days.

The experimental trial was established in a randomized complete block design in a tomato cropping system with Brin de Muguet variety. Two main factors were addressed: (1) the AMF status and (2) the dosages of FM compost tea (Figure S3). To investigate the effects of AMF abundance and FM compost tea application under on-farm field conditions, two levels of AMF (with and without AMF inoculum) and three dosages of FM compost tea (0%, 5%, and 10%) were carried out, resulting in six different treatments: (1) control plants: 0% AMF and 0% FM compost tea; (2) 5% of FM compost tea without AMF; (3) 10% of FM compost tea without AMF; (4) AMF seedling inoculation without FM compost tea; (5) AMF seedling inoculation with 5% of FM compost tea; and (6) AMF seedling inoculation with 10% of FM compost tea. These six treatment combinations were grouped into experimental units replicated three times, corresponding to three blocks. Each block consisted of 4 m × 5 m with 25 tomato plants per combination of treatment, three times repeated, resulting in a total of 450 (6 × 25 × 3) individual tomato plants.

As the success of root colonization of the additionally supplied AMF under field conditions can be limited and sometimes depends on the competition with indigenous mycorrhizal fungi and field conditions, tomato seeds were pre-inoculated with an AMF consortium to strengthen the root colonization rate of supplied AMF relative to local AMF species (Nwaga et al., 2010; Song et al., 2015). Therefore, a prenursery experiment was established to grow pre-colonized tomato seedlings prior to their cropping on the field trial. The tomato seeds were previously surface sterilized using 1% chloride for 10 min and 70% ethanol for 30 s and rinsed with deionized water after each step to remove any contaminants and unwanted microorganisms. One part of the tomato seeds was pre-inoculated with our selected mixture of AMF and sown under a sterilized soil–sand mixture (1:1). The remaining seeds receive no AMF inoculum and served as control plants. Briefly, a part of the sterilized substrate was placed in a germinating plastic box with 96 alveolar wells as control treatments, which were covered with plastic. The remaining portion was filled into the alveolar wells of the germinating boxes. We made a 3-cm small hole in each well and inoculated one tomato seed with 5 g of the AMF consortium (Nwaga et al., 2010). The AMF consortium comprised 30 spores/g in sterilized soil–sand carrier and hyphae with 30%–40% in colonized root pieces (Nwaga et al., 2010; Mbogning, 2017). The seedlings were left to grow over 2 weeks in a climate chamber. After 2 weeks, colonized AMF seedlings were thinned one by one and transplanted in the fields according to the treatments.

FM compost tea was diluted at 5% and 10% according to the treatments. We used 10 L of diluted FM compost tea per treatment and sprayed 0.14 L/per plant on the leaves and around the shoot collar to facilitate the drift of biopesticide in the roots and the rhizosphere. FM compost tea was applied 1 week after the on-farm transplantation of seedlings and afterwards each week for 2 months.

Collection and analysis of field experimental parameters

Analysis of soil properties

To explore whether AMF pre-inoculation and FM compost tea application affected soil physicochemical properties, representative rhizosphere samples were taken from each treatment and freshly conveyed to the Laboratory of Soil Analysis of the Environmental Chemistry Department (LABASCE) from the Agronomic Faculty of Agricultural Sciences of the University of Dschang in Cameroon. Soluble phosphorus was estimated by Bray II (Bray and Kurtz, 1945). Physical properties of soils (texture including sand and clay, and organic matter) were evaluated at the end-point harvest to determine whether the inoculation with AMF and/or the application FM compost teas changed the soil properties. Supplementary information for determining the other soil parameters can be found in the Supplementary Material (Table S1).

Evaluation of specific agronomic parameters

Aboveground biomass was sampled by harvesting the entire shoot at the end-point harvest after 3 months of cultivation. After harvesting tomato shoots, fresh weight and shoot diameter were recorded, and samples were oven-dried at 65°C for at least 72 h until a constant weight was achieved and used to determine the dry weight. A small fraction of fresh roots were sampled to determine the root colonization rate. The fruit parameters and plant yield were assessed manually by counting and weighing fruits as well as by harvesting all commercially ripe fruits once a week commencing on 9 March 2016 and terminating on 30 June 2016. The total mass and the yield of tomato plants were measured from 30 fruits per treatment. The cumulative crop yield for each treatment was calculated at the end-point harvest.

Analysis of symbiotic parameters

To evaluate the treatment effects on tomato root colonization rates, a representative tomato root fraction per treatment was stained at the Biotechnology Centre with 0.05% Trypan Blue according to a modified staining protocol (Brundrett et al., 1994). Root pieces were cleared in 10% KOH at 80°C for 30 min, washed with tap water three times, acidified in 1% HCl at room temperature, and stained for 15 min in 0.05% Trypan Blue at 80°C. AMF root colonization rate was quantified at 200× magnification using the magnified intersections method (200 intersects per sample) (Mc Gonigle et al., 1990). AMF structures—arbuscules, hyphae, and vesicles—were recorded separately. The total percentage of AMF root colonization rate was calculated. The average number of AMF spores/g of soil was determined according to Schenck (1982) and Brundrett et al. (1994).

Evaluation of pathogenic parameters

The incidence and severity of tomato plant diseases and pests were estimated daily from the first week when symptoms emerged. The disease incidence was evaluated and calculated as the percentage of infected plants over the total number of plants in each treatment. The disease incidence (I) was defined on a scale of 0 to 100% according to the following formula (Akhter et al., 2015):

$$\text{Incidence}\,(\%) = \frac{\text{number of infected plants or fruits}}{\text{total number of plants or fruits}} \times 100$$

To evaluate the degree to which pathogens and insects infected the number of leaves or surface area of the fruits, the infected plants were categorized on a scale of 1–5 as follows: c1 = 1%–5%, c2 = 5%–15%, c3 = 15%–35%, c4 = 35%–67.5%, c5 = 67.5%–100% (number of infected leaves or surface area of infected fruits). The disease severity was calculated for a batch of 10 plants (or 10 fruits) for each treatment according to a modified formula from Akhter et al. (2015):

$$\text{Disease severity}\,(\%) = \frac{10(\mathbf{n}c1 + 2\mathbf{n}c2 + 5\mathbf{n}c3 + 10\mathbf{n}c4 + 20\mathbf{n}c5)}{\mathbf{n}\,(\text{infected plants or fruits})} \times 100$$

Statistical analysis

To unravel the influence of AMF plant symbiosis and its interaction with FM compost tea on plant disease resistance, insect attacks, and crop yield under farm conditions, a series of linear mixed-effects (LME) models, including main effects and random effects, were carried out. The main effects were inferred to categorical predictors, including AMF and FM compost tea, while random effects were inferred to blocks because our treatments were allotted randomly to the experimental units within each block. All performed models included fixed interaction terms in order to primarily evaluate the potentially occurring combined effect of AMF inoculation and FM compost tea application. To reduce the between-block variance bias, the LME models were fitted preferably by the restricted maximum likelihood (REML) method. The LME models sequentially included the dependent variables, including AMF root colonization and spore density, plant growth and yield parameters, disease incidence and severity, and then the categorical predictors. Analysis of variance (ANOVA) statistics were extracted from these LME models to assess the effects of AMF and FM compost tea treatments and their combination terms at $p < 0.05$. To partially visualize potential relationships between AMF parameters and plant disease parameters that were assayed in the experiment, we plotted simple linear regression fitted by LME. At the same time, correlograms were generated to address possible Pearson correlations between variables. Additionally, a principal component analysis (PCA) was carried out to identify treatment-related clusters and the variance of the assayed AMF and disease parameters. All response variables were tested with Shapiro–Wilk and Levene's homogeneity tests to meet the assumptions of normality and homoscedasticity of variance and transformed if not, respectively. Our models were fitted using the LME function in the Lme4 R package. All analyses were performed in R version 3.0.2 (R Core Team, 2013).

Results

Effectiveness of the independent effect of AMF seedling inoculation on tomato plant growth and health

The investigation on the effectiveness of seedling inoculation with the AMF consortium yielded compelling results across multiple response variables. Furthermore, higher increases in AMF root colonization and spore density were detected when the tomato seedlings were inoculated with the AMF consortium compared to control plants that did not receive AMF and FM compost tea applications (Figure S1). Pre-inoculating tomato seedlings with the AMF consortium induced a fourfold increase in root colonization from 10% to 40% compared to non-inoculated plants and without FM compost tea application.

To assess the influence of AMF colonization on tomato plant performances, a comprehensive examination of soil properties was undertaken (Table S2). The analysis of soil properties indicate sandy clay oxisols with low pH. Rhizosphere soils subjected to the inoculation of tomato seedlings with AMF displayed a reduction of 1.6-fold in exchangeable cations, specifically calcium ions (Ca^{2+}), diminishing from 2.08 to 1.28 milliequivalents per 100 grams (meq/100 g). In contrast, substantial increases of 16-fold for magnesium ions (Mg^{2+}) and 2.47-fold for available phosphorus were evident in rhizosphere of tomato plants treated with FM compost tea compared to untreated plants. These increments varied from 0.16 to 2.56 meq/100 g for Mg^{2+} and from 6.33 to 15.66 mg/100 g of soil for available phosphorus in FM compost tea-treated tomato soils, differing from rhizosphere soils that did not undergo AMF inoculation and FM compost tea application.

The independent effects of AMF inoculation significantly increased most horticultural parameters including the number of flowers ($p < 0.001$), the number of fruits ($p = 0.02$), the volume of fruits ($p < 0.001$), the diameter of fruits ($p = 0.01$), and tomato plant yield ($p < 0.001$) compared to control tomato plants that did not receive AMF or FM compost tea (Figures 1 and 2, Table 1, and Table S1, Model parameters).

Moreover, the inoculation of tomato seedlings with AMF led to a decrease in disease incidence ($p < 0.001$) and disease severity ($p < 0.001$) of plant pathogens and pest attacks compared to the untreated control. This mitigation was underscored by a substantial 53.8% and 46.7% total reduction in incidence and severity, respectively, relative to control plants (Figures 3 and 4).

Effectiveness of the independent effect of FM compost tea application on tomato plant growth and health

Tomato plants treated with FM compost tea showed a significant increase in mycorrhizal root colonization ($p < 0.001$) and spore density ($p < 0.001$), underscoring the positive influence of the tea on AMF abundance. The application of FM compost tea alone induced a twofold increase (from 10% to 20%) in the root colonization of tomato plants from the indigenous mycorrhizal communities compared to control plants that did not receive FM compost tea and which were not inoculated with the AMF consortium (Supplementary Material, Figure S1). These positive beneficial effects were evidenced by a 50% and 78% increase in indigenous mycorrhizal root colonization and spore density, respectively, compared to untreated tomato plants. The application of 10% FM compost tea relatively decreased spore density compared to 5% FM compost tea concentration.

Unlike the AMF inoculation, rhizosphere soils subjected to the application of FM compost tea demonstrated 1.46- and 1.48-fold increases in exchangeable cations for both Ca^{2+} and Mg^{2+}, respectively, increasing from 2.08 to 3.04 or 3.08 meq/100 g for either 5% or 10% FM dosages, respectively, relative to untreated rhizosphere soils. In contrast to AMF-inoculated plants, there were no changes in available phosphorus levels here. They remained within the range of 6.33 to 6.57 mg/100 g of soil for either 5% or 10% FM compost tea applications compared to rhizosphere soils that did not undergo AMF inoculation or FM compost tea application.

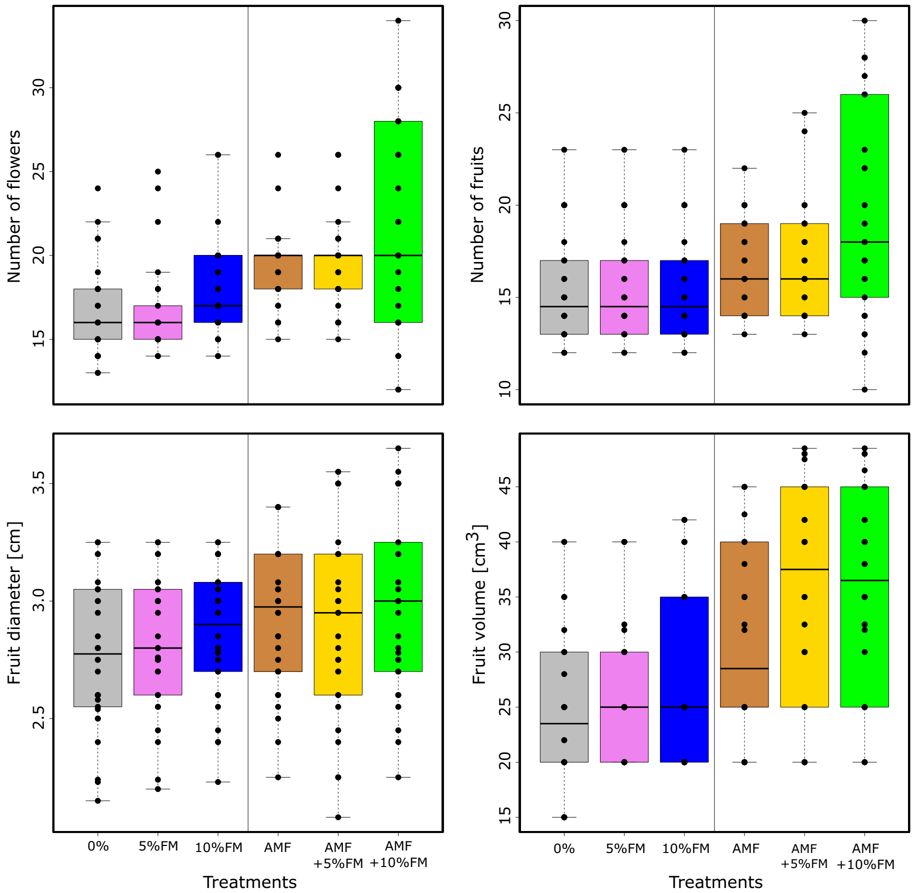

FIGURE 1
Effects of inoculation of tomato seedlings prior to planting with a consortium of five different arbuscular mycorrhizal fungi (AMF) and the addition of either 5% or 10% fern manure (FM) compost tea on plant growth parameters including the number of flowers (top left), the number of fruits (top right), the fruit diameter (bottom left), and the fruit volume (bottom right). Treatment abbreviations: (1) control plants: 0% AMF and 0% FM; (2) 5% of FM compost tea without AMF; (3) 10% of FM compost tea without AMF; (4) AMF seedling inoculation without FM compost tea; (5) AMF seedling inoculation with 5% of FM compost tea; (6) AMF seedling inoculation with 10% of FM compost tea. Jittered points are individual measurements—*n* in all cases equals 25. Model statistics are found in detail in Table 1 and Table S1.

The independent influence of FM compost tea on tomato plants had a substantial impact on various horticultural parameters, leading to a significant enhancement in floral abundance ($p< 0.001$), fruit volume ($p< 0.001$), fruit diameter ($p = 0.01$), and overall tomato plant yield ($p< 0.001$). However, the effects of individual FM compost tea applications were not significant for the number of fruits ($p > 0.05$) and secondary shoot ($p > 0.05$). These effects were observable when contrasting with control tomato plants devoid of AMF and FM compost tea (Figure 1 and 2, Table 1, and Table S1, Model parameters).

Moreover, the application of FM compost tea led to a decrease in disease incidence ($p< 0.001$) and disease severity ($p< 0.001$) of plant pathogens and pest attacks compared to the untreated control. This mitigation was evidenced by a substantial 18.8% and 40% total reduction in the incidence of tomato plant diseases for either 5% or 10% FM compost tea dosages, respectively, compared to untreated plants. Additionally, there was a substantial 93.3% and 97% total reduction in the severity of tomato plant diseases for 5% and 10% FM compost tea concentrations, respectively, relative to control plants (Figures 3 and 4). The results also showed that the application of FM compost tea had higher and lower mitigating effects for severity and incidence, respectively, relative to AMF inoculation.

Synergistic effects of AMF seedling inoculation and FM compost tea application on tomato plant growth and health

The combined application of both AMF and FM compost tea demonstrated superior effects on the performance and health of tomato plants compared to their individual applications. The combined effects of AMF and FM compost tea were significant on root colonization ($p = 0.004$) and spore density ($p< 0.001$) (Table 1 and Table S1). The combined effects of AMF inoculation and FM compost tea application significantly fostered AMF root colonization from 10% to 70% relatively to non-treated plants (Figure S1). The application of both AMF and a 10% dosage of FM compost tea resulted in a sevenfold synergistic increase in mycorrhizal root colonization rates, demonstrating superior

TABLE 1 Report of the general ANOVA model statistics subtracted from the mixed-effects linear models to disentangle the effects of AMF and fern manure (FM) and their interplay (AMF × FM) on tomato agronomic crop parameters, symbiotic parameters, and plant disease response parameters.

Treatments	AMF		FM		Combination (AMF × FM)	
Crop parameters	*F*	*P*	*F*	*P*	*F*	*P*
Number of flowers	35.85	***	6.59	**	0.74	ns
Secondary shoot	76.68	***	2.74	ns	3.12	.
Number of fruits	22.87	***	4.47	ns	4.47	*
Fruit diameter	5.85	*	1.04	*	0.14	ns
Volume fruits	44.25	***	4.56	*	0.47	ns
Tomato yield	16.75	***	6.57	**	1.07	ns
Symbiotic parameters						
Spore density	854.65	***	75.17	***	293.59	***
Root colonization	453.10	***	40.27	***	5.75	***
Disease parameters						
Incidence	664.24	***	111.25	***	3.97	*
Severity	46.91	***	30.23	***	4.86	*

Exact model statistics can be found in detail in Table S1 in the Supplementary Material.
Highly significant: 0 "***" and 0.001 "**", significant 0.01 "*", marginal 0.05 "."
Non-significant: ns and 1 at p< 0.05.

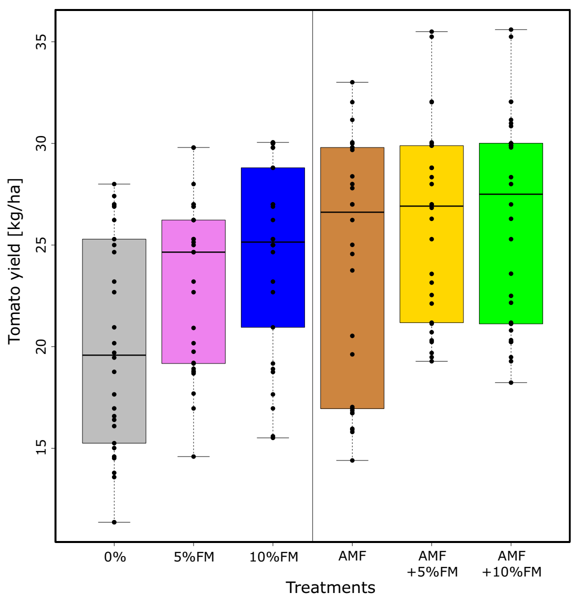

FIGURE 2
Effects of inoculation of tomato seedlings prior to planting with a consortium of five different arbuscular mycorrhizal fungi (AMF) and the addition of either 5% or 10% fern manure (FM) compost tea on the tomato yield. Treatment abbreviations: (1) control plants: 0% AMF and 0% FM; (2) 5% of FM compost tea without AMF; (3) 10% of FM compost tea without AMF; (4) AMF seedling inoculation without FM compost tea; (5) AMF seedling inoculation with 5% of FM compost tea; (6) AMF seedling inoculation with 10% of FM compost tea. Jittered points are individual plant measurements—*n* in all cases equals 25. Model statistics are found in detail in Table 1 and Table S1.

performance compared to other treatments. The same effects were found for AMF spore density when tomato plants were treated with AMF and 5% or 10% FM compost tea. However, supplying both the AMF consortium and FM compost tea resulted in a decrease in AMF spore density relative to AMF-inoculated plant at the end-point harvest (Figure S1).

The inoculation with AMF and the FM compost tea and the individual applications differently affected the physicochemical soil properties (Table S2). Unlike the FM compost tea, rhizosphere soils subjected to the combined application of AMF and FM compost tea demonstrated a 1.62-fold decrease in Ca^{2+}, but 6- and 1.63-fold higher increases in Mg^{2+} and available phosphorus levels, respectively, compared to control plants. In contrast to FM compost tea-treated plants, there was a notable increases in soil available phosphorus levels in the combined application, but these levels were lower than those depicted in AMF treated-plants (Table S2). Overall, the addition of the AMF consortium and the application of FM compost tea had a significant effect on the tomato plant growth (Figure 1 and Table 1) and tomato yield response parameters (Figure 2 and Table 1) relative to the untreated controls at the end-point harvest. The combined effects of AMF inoculation and FM compost tea application were not significant for most plant growth parameters, except for the number of fruits (AMF × FM, $p = 0.02$) and secondary shoot (AMF × FM, $p = 0.04$) (Table 1 and Table S1, Model parameters). However, significant effects of either AMF inoculation or FM compost tea application were found for most plant growth parameters. The sole inoculation with AMF or the AMF inoculation in combination with 5% or 10% FM compost tea had an enhancing effect regarding the tomato plant yields compared to the other treatments (Figure 2, Model 2). The

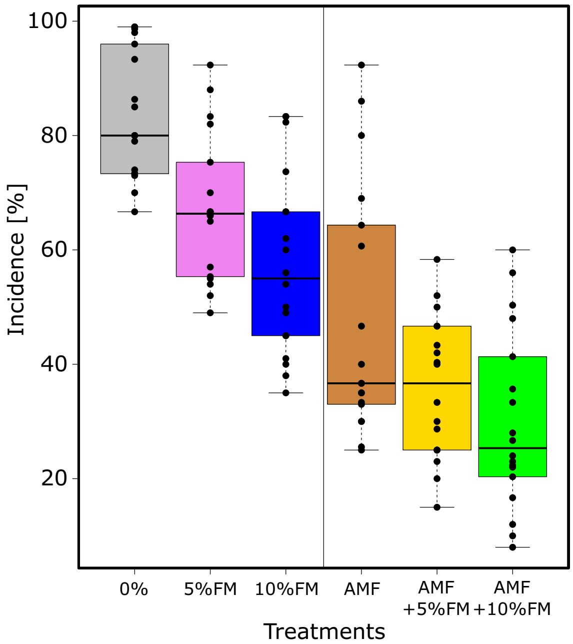

FIGURE 3
Effects of inoculation of tomato seedlings prior to planting with a consortium of five different arbuscular mycorrhizal fungi (AMF) and the addition of either 5% or 10% fern manure (FM) compost tea on the disease incidence. Treatment abbreviations: (1) control plants: 0% AMF and 0% FM; (2) 5% of FM compost tea without AMF; (3) 10% of FM compost tea without AMF; (4) AMF seedling inoculation without FM compost tea; (5) AMF seedling inoculation with 5% of FM compost tea; (6) AMF seedling inoculation with 10% of FM compost tea. Jittered points are individual plant measurements —*n* in all cases equals 25. Model statistics are found in detail in Table 1 and Table S1.

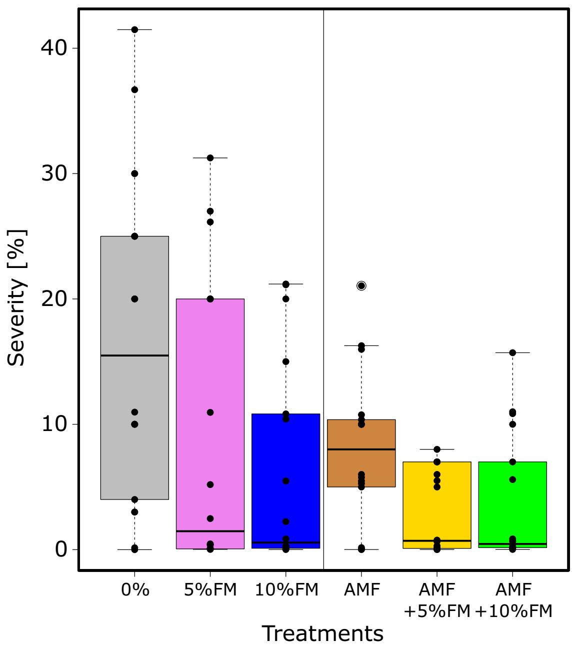

FIGURE 4
Effects of inoculation of tomato seedlings prior to planting with a consortium of five different arbuscular mycorrhizal fungi (AMF) and the addition of either 5% or 10% fern manure (FM) compost tea on the disease severity. Treatment abbreviations: (1) control plants: 0% AMF and 0% FM; (2) 5% of FM compost tea without AMF; (3) 10% of FM compost tea without AMF; (4) AMF seedling inoculation without FM compost tea; (5) AMF seedling inoculation with 5% of FM compost tea; (6) AMF seedling inoculation with 10% of FM compost tea. Jittered points are individual plant measurements —*n* in all cases equals 25. Model statistics can be found in detail in Table 1 and Table S1.

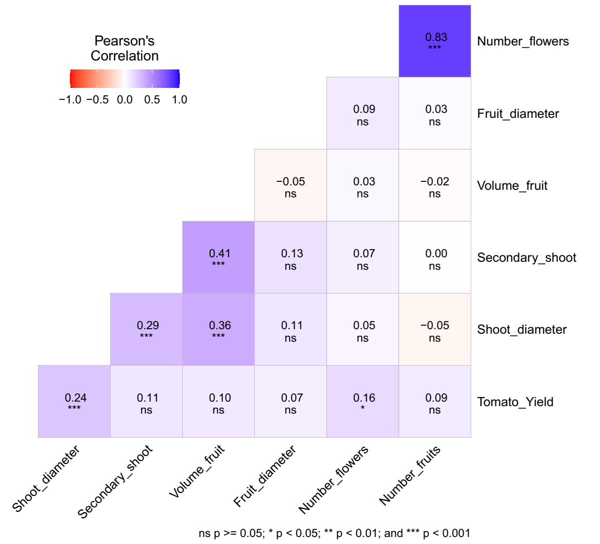

FIGURE 5
Pearson's correlogram of tomato plant growth and yield parameters highlighting the simple relationships between each other in farm settings. The blue color indicates positive correlations while red denotes negative correlations. Most of the plant response variables were positively correlated to each other; some correlations were significant and the others not. We observe that tomato plant yield positively correlated with all plant response variables that were assayed on-farm and the correlations with shoot diameter and number of flowers were significant.

tomato yield increased by approximately 8% when tomato seedlings were inoculated with AMF relative to non-inoculated plants, while there were no statistical differences between AMF + 5% FM and AMF + 10% FM compost tea.

To explore how plant growth parameters were related to each other and how they were altered by AMF inoculation and the addition of FM compost tea, a correlogram was generated (Figure 5 and Figure S6). The volume of fruits was negatively related to the number and diameter of fruits and positively correlated with the number of flowers as well as the secondary shoots and the shoot diameter. The yield of tomatoes positively correlated with all assayed plant variables, but only the correlations between the shoot diameter ($p< 0.001$) and the number of flowers ($p< 0.05$) were significant.

Compared to the independent effects of either AMF inoculation or FM compost tea additions, strong effects were found for the combination of both treatments in terms of reducing disease incidence ($p = 0.02$) and severity ($p = 0.01$) (Table 1). Disease incidence was significantly suppressed by 56% and 71.3% in tomato plants, which had received either AMF and 5% FM compost teas or AMF and 10% FM compost tea, respectively, compared to control plants (Figure 3). The same patterns were observed for disease severity, with approximately 95% total suppression by both AMF and 5% FM compost tea or AMF and 10% FM compost tea compared to the control plants (Figure 4). The combined application demonstrated robust synergistic effects, effectively mitigating the incidence and severity of tomato plants more strongly than their individual applications.

Prevalence of plant pathogens and pest attacks

Although the applied treatments significantly suppressed plant diseases and pest attacks, it was not possible to disentangle which disease type and pests contributed most to plant infection and damages in terms of severity and incidence percentages in the field. To reveal that, plant disease was added as a third fixed factor in the LME models (Figure 6). The importance of disease incidence ($p< 0.001$) and severity ($p< 0.001$) differed significantly across plant diseases and pest attacks. The incidence of mildew blight was significantly higher compared to the incidence of bacteria wilt and *Alternaria* blight as well as compared to pest attacks such as fruit worms and insect bites. In contrast, the severity of bacteria wilt was higher compared to that of mildew blight and *Alternaria* blight. At the same time, pest attacks were less severe in terms of symptom intensity on tomato plant development and fruits.

Potential relationships between AMF symbiosis and disease suppression

To explore the potential effects of AMF root colonization and spore density in the soil on plant disease resistance, linear regression was used (Figure 7). The enhancement of tomato root colonization due to AMF inoculation was negatively related to the incidence and the severity of plant disease and pest attacks compared to AMF spore density in the soil. AMF root colonization was positively correlated to the spore density, while it showed negative correlation to both the disease incidence and the disease severity (Figure 8 and Figure S6). Spore density, however, was moderately negatively correlated to disease incidence and severity (Figure 8 and Figure S6).

Variation in plant disease metrics relates to plant and soil AMF parameters

PCA allowed for exploring the variability of plant disease metrics including incidence and severity and AMF root colonization and spore density among samples, and for revealing the clusters of AMF and FM treatments in the mycorrhizal plant–disease interaction system (Figure 9). The FM compost tea treatments (0% FM, 5% FM, and 10% FM) that were clustered separately into AMF treatment and the combination of AMF and FM indicated that the applied treatments differently altered not only tomato plant diseases, severity, and incidence but also AMF root colonization and spore density. Disease incidence, spore density,

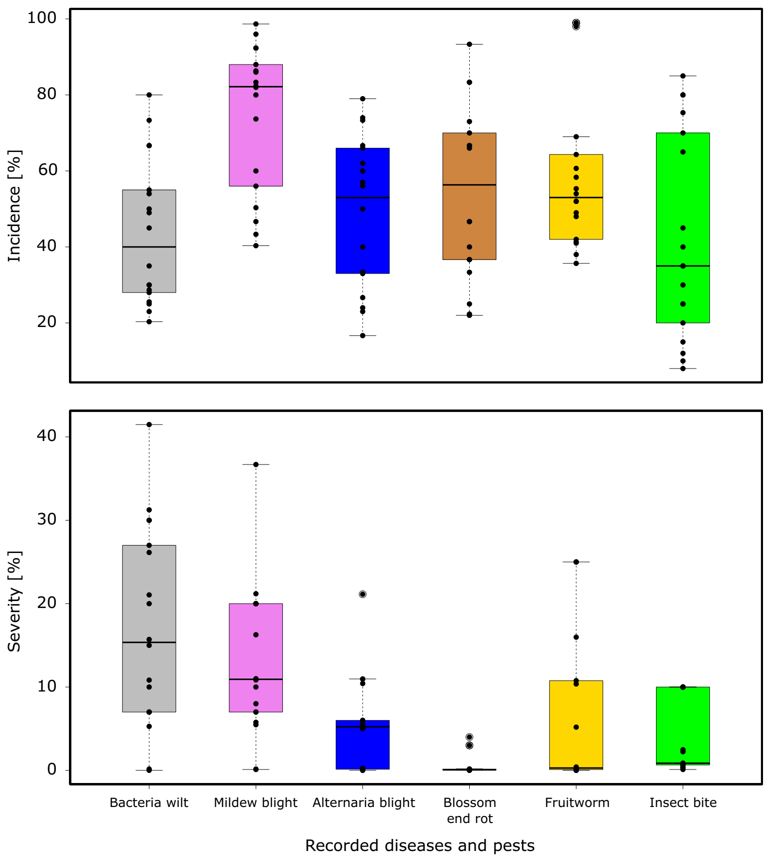

FIGURE 6
Prevalence of incidence and severity of the most common phytopathogens and insect attacks under on-farm conditions. To reveal how plant diseases varied in the plant-interaction pathogen system, we added in our LME models disease as a third fixed factor. Exact model statistics are found in Table S1, Model parameters.

and root colonization accounted for the majority of the variation, contributing to 63.6% of the explained variance in PC1. Meanwhile, severity contributed 18% of the variance and was associated with PC2 (Figure 9 and Figure S5).

Discussion

To reduce the current negative environmental impacts from agriculture (e.g., high amounts of external inputs of fertilizer and/or agrochemicals), there is an urgent need to develop new and more sustainable agronomic management measures. These novel techniques should *inter alia* improve soil health accompanied by an increase of plant resistance against diseases, thereby diminishing the reliance on pesticides and maintaining high agricultural productivity. So far, most studies related to the impact of AMF inoculants have broadly addressed either individual effects or synergistic effects with other microbial inoculants (i.e., of bacterial origin) on plant disease resistance against various pathogens (Nwaga et al., 2010; Simo et al., 2019). In comparison, this study investigated the synergistic effects of inoculating tomato seedlings with an AMF consortium coupled with a biopesticide based on FM compost tea on common tomato plant diseases and pests. Our findings show a significant synergistic effect of an induced AMF root colonization facilitated by the addition of FM compost tea, resulting not only in a pronounced enhancement of the crop yield, but also in a distinct suppression of specific tomato plant diseases and pest attacks under on-farm conditions. Therefore, this study underscores the unexploited potential of harnessing plant beneficial microorganisms, in this case AMF in combination with the FM compost tea to strengthen tomato defense mechanisms, while simultaneously providing a promising technique for sustainable and eco-friendly agricultural practices.

Effect of FM compost tea on AMF root colonization success

Owing to the pervasive use of pesticides and conventional farming practices, the compromised status of mycorrhized agricultural crops represents a substantial impediment for an optimal harnessing of these plant-beneficial microorganisms (Smith and Read, 2008; Ipsilantis et al., 2012; Bowles et al., 2016; Okiobe et al., 2022; Lutz et al., 2023). In this regard, various inoculation techniques have been explored to address the challenge of low mycorrhizal colonization rates (Nwaga et al., 2010; Song et al., 2015; Bowles et al., 2016). For example, studies have reported that the application of single AMF species directly into agricultural soils often results in short-term, inadequate

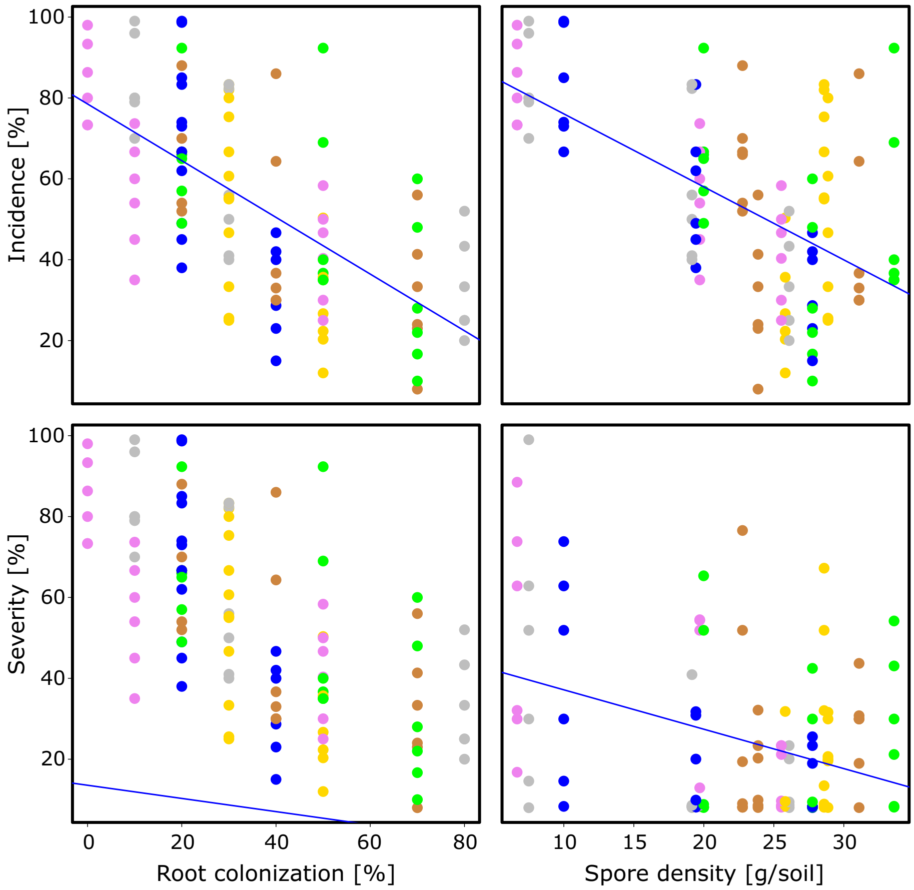

FIGURE 7
Relationships between disease incidence and severity and AMF symbiosis that were assayed at harvest; this includes root colonization rate (p< 0.001) on the left and spore density (p< 0.001) on the right side. We overlay the first-order best-fit ablines (blue) representing the simple relationship existing between our AM fungal predictors root colonization rate and spore density and plant disease response variables incidence and severity on-farm settings. The six different colors represent the six treatments that we established: Non-precolonized tomato plants without the addition of FM (0%,"peru"), with the addition of 5% FM ("gold") and 10% FM ("green"); and pre-colonized tomato plants by AM fungal propagules (AMF, "gray"), pre-colonized AM tomato plants with the addition of 5% (AMF + 5% FM, "violet"), and pre-colonized AM tomato plant with the addition of 10% (AMF + 10% FM, "blue"). Jittered points are individual plant measurements—n in all cases equals 25 per treatment. Model statistics are found in detail in Table 1 and Table S1.

colonization rates of the cultivated plants (Nwaga et al., 2010; Song et al., 2015; Bowles et al., 2016; Lutz et al., 2023). In contrast, the presented study pre-inoculated tomato seedlings with a consortium of five different AMF species. This approach was coupled with the application of a plant-based biopesticide based on FM compost tea in order to potentially enhance the beneficial effect of the AMF colonization in the crop performance and health. Our study revealed higher and longer-lasting levels of root colonization with AMF at the end-point harvest compared to control plants, indicating a sustained and positive synergistic effect of both the AMF inoculation of tomato seedling itself and the application of FM compost tea (Figure S1). This confirms the initial hypothesis stating that pre-inoculating tomato seedlings with AMF enhances mycorrhization rates and that combining AMF inoculation with the application FM compost tea would induce positive synergistic effects that further promote and facilitate the establishment of AMF symbiosis in tomato host plants. Although there are only a few studies reporting the impact of compost teas as a biostimulant (Pane et al., 2016; Pilla et al., 2023), the heightened AMF colonization rate of tomato roots found in this study can most probably be attributed to the application of FM compost tea. There are indications that FM compost tea potentially stimulates not only the AMF colonization but also the growth of AMF mycelium through the absorption by AMF of compost nitrogen-rich nutrients (Smith et al., 2011; Hodge and Storer, 2015; Pilla et al., 2023). Additionally, the applied FM compost teas also impacted the density of spores, particularly at 10% FM compost tea, which might possibly be related to increased accumulation of soil nutrients like nitrogen and phosphorus (Hodge and Storer, 2015). With few exceptions, studies on the effect of compost teas as biostimulants enhancing beneficial interactions in the soil–crop system are rarely available (Pilla et al., 2023).

Higher rates of root colonization are generally reported in many studies that used reductionist experimental approaches under controlled greenhouse conditions with sterilized soils and single AMF species to promote root colonization compared to realistic on-farm studies with an AMF consortium (Bowles et al., 2016; Rillig et al., 2018; Lutz et al., 2023). The presented study showed that FM

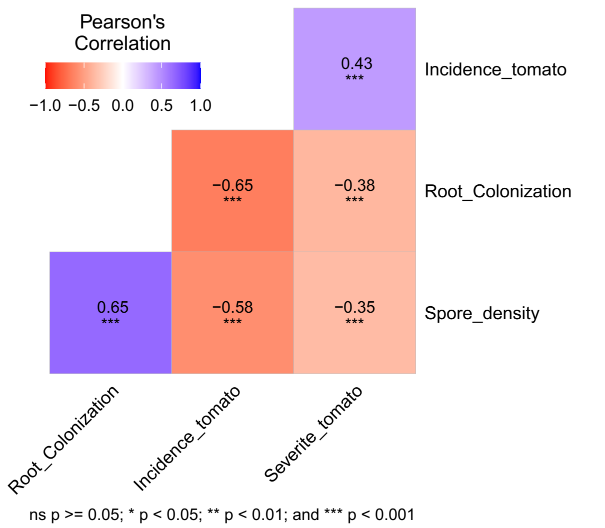

FIGURE 8
Pearson's correlogram of disease resistance response parameters and AMF symbiotic predictor variables including root colonization rate and spore density that were assayed in the field at harvest. The blue color indicates positive correlations, while red denotes negative correlations. We observe that the correlations were significant at *p*< 0.05 for all the variables and that the incidence and severity of tomato plants related negatively to estimated AM fungal predictors at harvest on farms.

compost tea can be considered a biostimulant that promotes the proliferation of mycorrhizal root colonization on-farm conditions. Hence, further investigations are needed, in order to comprehensively evaluate the thresholds for applicable compost tea concentrations that enhance both AMF sporulation and colonization, thereby exerting positive cascading effects on plant performance and health.

Independent effects on soil properties and crop performance

Many studies have reported that root colonization by AMF increased the concentration of various nutrients in plants that originated from the soil, thereby increasing the performances of plants, including plant growth and yield (Smith and Read, 2008; Nwaga et al., 2010; Li et al., 2022; Lutz et al., 2023). This study showed that higher tomato yields were achieved when tomato seedlings were inoculated with AMF, independently of the FM compost tea application (Figures 1 and 2 and Table S1, Model parameters). This indicates that high tomato yields were associated with high AMF root colonization. Our results unveiled a profound impact stemming from the independent effects of AMF inoculation on tomato seedlings, leading to a discernible influence on root colonization and the performance metrics and yield of tomato plants (Figures 1 and 2).

Furthermore, the observed increases in tomato growth parameters and yield following AMF seedling inoculation are closely linked to the AMF-induced changes in soil properties, indicating a dynamic interplay between tomato plant–microbe interactions and soil nutrient dynamics. The analysis of soils showed that the agricultural soil where tomato seedlings were planted is a tropical sandy clay oxisol, characterized by intrinsic soil health challenges, including elevated acidity levels. In such edaphic conditions, the pivotal role of AMF in influencing both soil properties and tomato plant hosts is high and imperative (Smith and Read, 2008; Nwaga et al., 2010; Brundrett and Tedersoo, 2018). The shifts induced by AMF in exchangeable cations like Ca^{2+} potentially fostered nutrient uptake by plant roots, thus influencing the overall tomato plant-root development. Furthermore, the increase in Mg^{2+} within the rhizosphere of AMF-inoculated plants suggested the plausible involvement of AMF in nutrient mobilization and cycling within the soil. AMF-induced increases in Mg^{2+} levels may

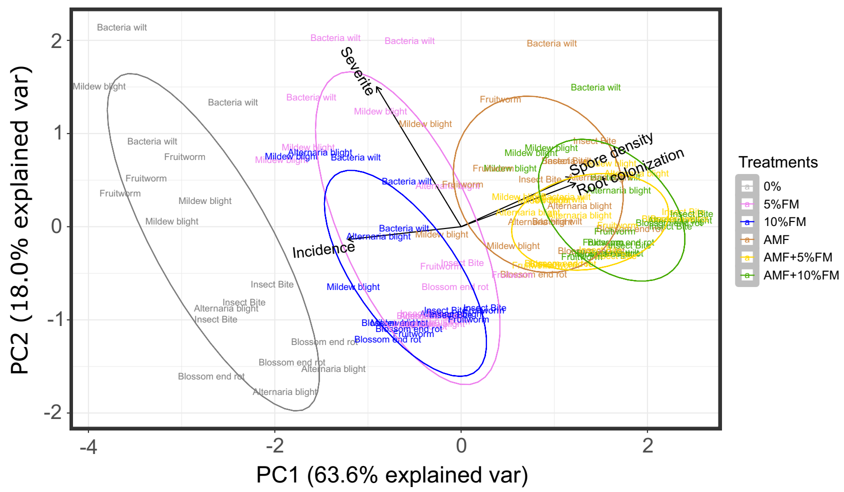

FIGURE 9
Principal component analysis of the tomato disease response parameters, including incidence and severity, tomato plant disease type, and AMF predictor variables, including root colonization rate and spore density that were assayed in the field at harvest and the effects of AMF and FM biological treatments that were applied on tomato plant on-farm. The first dimension explained 64% of the variance, while the second was 18%. The incidence, root colonization, and spore density contributed the most to the variation in the first dimension (PC1), while the severity was the sole contributor to the second dimension (PC2). Moreover, AMF root colonization and spore density negatively correlated to disease severity and incidence.

amplify photosynthetic processes and facilitate plant phosphorus uptake, critical for the flowering and fruiting stages in tomato plants (Smith et al., 2011; Lutz et al., 2023). Many studies have reported the role of AMF in facilitating the mobilization and uptake of soil macro- and micronutrients in oxisols, especially N and P, which are limiting macronutrients, thereby effectively promoting the growth of tomato host plants (Mvele et al., 2002; Nwaga et al., 2010; Smith et al., 2011; Chen et al., 2022; Deja-Sikora et al., 2023).

Unlike FM compost tea, inoculation of tomato seedlings with AMF increased soil-available phosphorus concentrations, which was associated with higher plant performances. This suggests that AMF-induced increases in plant phosphorus uptake might be the result of either AMF transfer of soluble phosphorus to tomato plants or AMF-induced increases in mobilization of immobilized soil phosphorus, but are not the result of FM compost tea application (Table S2). Our findings corroborate the previous studies emphasizing that AMF are best known for their efficacy in enhancing nutrient availability and uptake, especially phosphorus (Smith and Read, 2008; Nwaga et al., 2010; Smith et al., 2011; Brundrett and Tedersoo, 2018; Rillig et al., 2018; Lutz et al., 2023). The nexus between AMF-induced increases in plant growth parameters and yield following tomato seedling inoculation and the alterations in soil properties emphasizes the intricate and symbiotic association between tomato plants and AMF. However, these AMF mechanisms necessitate further investigation in this experiment.

A large body of literature has extensively explored the utilization of municipal compost waste and food compost teas in various agricultural contexts (Pane et al., 2012; Pane et al., 2016; Pilla et al., 2023). However, the existing scientific literature reveals a noticeable gap when it comes to the investigation of vegetable compost teas, particularly the effects of FM compost tea on tomato plants. Our results elucidated the distinctive impact of individual FM compost tea application on rhizosphere soil properties and tomato plant performances, providing valuable insights into its potential role in sustainable agriculture (Figures 1 and 2).

The independent influence of FM compost tea on tomato plants resulted in a remarkable improvement in most horticultural parameters including floral abundance, fruit volume, fruit diameter, and overall plant yield. These results are consistent with hypothesis 2. This highlights the biostimulatory influence of FM compost tea on vegetative and reproductive growth of tomato plants and yield. Likewise, foliar applications of compost teas have demonstrated substantial biostimulatory effects on diverse plant species, including *Abelmoschus esculentus*, melon, pepper, and tomatoes (Campanelli et al., 2018; Villecco et al., 2020; Pilla et al., 2023). These effects encompassed various morphological characteristics such as plant height, root length, leaf count, leaf area, and productivity. Additionally, physiological attributes such as chlorophyll content and photosynthetic rate have also experienced significant improvements following foliar applications of compost teas (Pane et al., 2016; Campanelli et al., 2018; Villecco et al., 2020; Pilla et al., 2023). However, the exact mechanisms by which manure compost tea-induced increases in plant growth parameters and yields remain incompletely understood. The mechanisms driving the observed effects might involve direct effects, that is, the direct contact of FM compost tea components including N and micronutrients with tomato plants. These components may have directly interacted with tomato plants and, subsequently, biostimulating plant growth and yield. Compost teas have demonstrated their capacity to biostimulate physiological status in tomato plants (Pane et al., 2012; Zaccardelli et al., 2012). In fact, the compost teas contain a large number of plant macronutrients (nitrogen, phosphorus, and potassium), micronutrients (e.g., copper, zinc, iron, and manganese), dissolved organic matter, and beneficial microorganisms (Zaccardelli et al., 2012; Pilla et al., 2023). Previous studies suggested that nutrients and the dissolved organic structures contained in compost teas were involved in the biostimulation processes of tomato plants (Pane et al., 2016; Villecco et al., 2020). However, it is crucial to note that, here, the number of fruits and secondary shoot development did not experience significant changes in response to individual FM compost tea applications (Figure 5). This suggests a selective impact of FM compost tea on certain growth aspects, highlighting the need for further investigation into the specific mechanisms governing these observed effects.

Moreover, these components may also interact with the rhizosphere of tomato plants, influencing soil quality and indirectly plant growth responses (Pane et al., 2016; Villecco et al., 2020; Pilla et al., 2023). Unlike AMF inoculation, FM compost tea application triggered significant increases in soil exchangeable cations (Ca^{2+} and Mg^{2+}). FM compost tea-induced soil ion alterations indicate potential indirect effects of FM compost tea, that is, the increase in nutrient availability and soil quality, contributing to the observed enhancements in plant growth parameters and yield. Noteworthy is the stability in soil-available phosphorus levels in FM compost tea rhizosphere-treated soils compared to control and AMF rhizosphere soils. This suggests that FM compost tea application influences soil quality via enhancing cation availability without altering soil phosphorus concentrations. This specificity in soil nutrient dynamics underscores the nuanced effects of FM compost tea on tomato plants.

While AMF primarily influences mycorrhizal associations and phosphorus availability, FM compost tea appears to modulate cationic dynamics without substantial changes in phosphorus levels. Hence, FM compost tea holds significant importance, especially considering that high levels of soil-soluble phosphorus have been demonstrated to impede the root colonization by AMF (Smith et al., 2011; Rillig et al., 2018). The observed higher yields in AMF-treated tomato plants compared to FM compost tea-treated tomato plants and control plants suggest that AMF are particularly important when soil health is low (Nwaga et al., 2010; Lutz et al., 2023). The distinctiveness in the response patterns of key growth parameters between the individual AMF and FM compost tea treatments suggests that they operate through different pathways —AMF acted as a microbial biofertilizer and FM compost tea acted as a biostimulant. This indicates their potential for synergistic effects on plant growth and yield when combined.

Independent effects on plant diseases and pest suppression

The field conditions revealed a significant prevalence of mildew blight compared to bacteria wilt and *Alternaria* blight, as well as pest attacks such as fruit worms and insect bites (Figure 6). Conversely, the severity of bacteria wilt surpassed that of mildew blight and *Alternaria* blight. Although pest attacks were less severe in symptom intensity on tomato plant development and fruits, the most prominent diseases affecting tomato plants were observed in the field.

The results revealed compelling evidence of the considerable impact of independent applications of AMF inoculation and FM compost tea on mitigating disease incidence and severity in tomato plants, emphasizing the potential of these biological treatments for integrated pest management strategies. The inoculation of tomato seedlings with AMF demonstrated a robust suppressive effect on both disease incidence and severity. The substantial 53.8% and 46.7% reductions in incidence and severity, respectively, highlight the effectiveness of AMF in conferring resistance against plant pathogens and pests (Hashem et al., 2021). The negative relationships between tomato disease metrics and AMF parameters support these results (Figures 7 and 8). The low levels of soil Ca^{2+} that were observed in AMF-treated plants compared to control plants might indicate that AMF might have promoted the uptake of Ca^{2+} by tomato plants. The enhanced uptake of Ca^{2+} by plants induced by AMF may contribute to the reduction of tomato plant diseases and pest attacks. It is largely known that calcium plays a crucial role in plant defense mechanisms, making the plants more resistant to pathogens and pests and potentially enhancing the plant's ability to ward off diseases and pest infestations. In this regard, some studies have demonstrated that root colonization by AMF not only provides benefits to the plant growth via soil nutrient uptake but also enhances plant resistance to diverse biotic stresses, including fungal pathogens (Fritz et al., 2006; Pozo et al., 2010), bacteria pathogens (Liu et al., 2007), and viruses (Maffei, 2014). These outcomes also align with existing literature on the positive influence of mycorrhizal associations in enhancing plant defense mechanisms or in modulating the plant's immune responses, creating an environment less conducive to diverse pathogenic attacks (Mvele et al., 2002; Nwaga et al., 2010; Pozo et al., 2010; Song et al., 2015; Dey and Ghosh, 2022; Weng et al., 2022). While the role of AMF as a biocontrol agent against insect pests has already been reported, it remains an area with limited empirical exploration and evidence (Vannette and Hunter, 2009; Weng et al., 2022).

Furthermore, as endomycorrhizal fungi, AMF occur rapidly inside the plant roots (with their arbuscules) and build a hyphae network around and outside the plant roots (Werner and Kiers, 2015; Lutz et al., 2023); this might have reduced the belowground capacity of microbial and faunal pathogens including the galls caused by nematodes that infect tomato roots (Figure S4, Mbogning, 2017). A range of studies reported that the pre-colonization of tomato plants with AMF plays a pivotal role in the suppression of nematodes (Veresoglou and Rillig, 2012; Vos et al., 2012; Gough et al., 2020; Lutz et al., 2023). However, further research is warranted to unravel the intricate AMF molecular mechanisms underlying the observed disease and pest reductions including microbial and faunal soil-borne pathogens.

Various studies have demonstrated the efficacy of applying manure compost tea to tomato plants in reducing the incidence of diseases caused by soil-borne pathogens such as *Fusarium* and *Verticillium* wilt, as well as foliar diseases like early blight and powdery mildew (Koné et al., 2010; Pane et al., 2012; On et al., 2015; Pilla et al., 2023). Despite this wealth of evidence, the precise mechanisms through which manure compost tea directly suppresses pathogens and pests remain not fully elucidated. It has been observed that the compost tea introduces beneficial microorganisms that either compete with or prey upon harmful organisms, or it biostimulates the natural defense mechanisms of plants (Koné et al., 2010; Pane et al., 2012; On et al., 2015).

Similarly, the application of FM compost tea displayed remarkable mitigating effects on disease incidence and severity. The substantial reductions of 18.8% and 40% in incidence and a remarkable 93.3% and 97% total reduction in the severity of tomato plant diseases, for both 5% and 10% FM compost tea dosages, underscore its potential as a biocontrol agent against plant pathogens and pests. Nevertheless, further investigations are warranted to unravel the specific mechanisms underlying the biocontrol properties of FM compost tea, contributing to a more comprehensive understanding of its role in promoting plant resilience against diseases and pests in this study.

Furthermore, the results indicate differential effects of AMF inoculation and FM compost tea application on disease parameters. While AMF inoculation showcased higher reductions in disease incidence, FM compost tea demonstrated superior efficacy in mitigating disease severity. The higher efficacy in reducing disease severity compared to AMF inoculation suggests that FM compost tea played a major role in suppressiveness. The effects of a single application of FM compost tea might have acted here as a biopesticide that limited the infection of foliar plant pathogens by suppressing them via a direct contact while AMF colonization effects might have limited the invasion of tomato roots by soil-borne pathogens. The differential effects observed between the two microbial and compost treatments suggest that both might play a complementary role in integrated pest management strategies. The combined application may provide a comprehensive approach for enhancing tomato horticultural parameters and plant resilience against diverse pathogens and pests.

Synergistic effects of AMF and FM compost tea

The combined effect of induced AMF root colonization enhanced by FM compost tea supply was not significant for most of the investigated horticultural plant parameters, indicating that both treatments are beneficial for different crop performance parameters, which synergistically promote the overall crop growth and finally the crop yield compared to their individual applications. Besides this, the synergistic effect of tomato seedling inoculation with AMF and the application of FM compost tea might have played an essential role in soil nutrient availability and plant nutrient uptake. This is supported here, as either the treatment with the sole inoculation with AMF or the combined treatments showed an increased pH value and a higher availability of soluble phosphorus, while both parameters were positively associated with increased fruit and yield (Figures 1 and 2 and Table S2). This result is in accordance with the second hypothesis stating that both the inoculation with AMF and the application of FM compost tea will induce changes in soil nutrient contents that further promote tomato growth and yield (Nwaga et al., 2010). The enhanced tomato yield in this study might have benefited from the effects of AMF root colonization and/or the mineral N derived from the FM compost tea enriched in the soil as in the tropical oxisols soil N and P, which are limiting growth factors for plant development (Nwaga et al., 2010; Li et al., 2022). Owing to the beneficial effects observed in the combined application on improved crop yields, the simultaneous utilization of AMF with FM compost tea is strongly recommended to enhance crop production. At this point, the question arises whether the inoculation of tomato seedling with AMF and the application of FM compost tea might have the potential to suppress plant disease and pest attacks.

Our findings suggest that the effectiveness of root colonization with AMF is strongly enhanced by the application of FM compost tea while the higher dosages of FM compost tea (10%) led to a higher AMF pre-colonization rate of tomato plants, which, in turn, effectively suppress the incidence and severity of tomato plant diseases and pest attacks (Figures 3 and 4). This result is consistent with the third hypothesis indicating that the combination of inoculating tomato seedlings with AMF and the application of FM compost tea would strengthen the suppressive ability of tomatoes compared to the untreated plants or each treatment independently. The individual impacts reveal that the enhanced root colonization by AMF likely played a pivotal role, surpassing soil-borne pathogen infections in the combined application when compared to the single foliar application of FM compost tea and control plants (Veresoglou and Rillig, 2012; Vos et al., 2012; Gough et al., 2020).

Besides the mentioned plant protection mechanisms by outcompeting the plant pathogens due to the root colonization with AMF, another explanation might be related to a better nutritional status of the plant derived from the addition of both treatments. This is supported by an increased availability of soluble phosphorus in the soil, particularly in the treatments that received AMF and FM compost tea (Table S2).

The potential mechanisms underlying the suppression of tomato phytopathogens and pests encompass a multifaceted interplay. First, the addition of FM compost tea might have acted as a biostimulant to improve AMF symbiosis by promoting systemic effects (Vos et al., 2012; Hashem et al., 2021; Weng et al., 2022). The observed total mitigation of blossom end rot, fruit worm severity, and insect bites can be ascribed not only to the emergence of positive synergistic effects, that is, increased AMF colonization of roots, but also to the occurrence of adverse synergistic effects, that is, the suppression of tomato plant diseases due to the biostimulation of tomato plants (Figures 4 and 6). Comparable findings have rarely been reported, e.g., by studies that focused on the influence of single AMF species (Fritz et al., 2006; Liu et al., 2007; Fiorilli et al., 2009; Pozo et al., 2010; Song et al., 2015) or the sole application of compost tea to induce systemic defense mechanisms (Pane et al., 2012; Pane et al., 2016).

Second, the combined applications might have acted here as biopesticides to suppress tomato plant disease and pest attacks via a direct contact. Compost teas that are known to possess repellent, insecticidal, and fungicidal properties could have played a major role here in mitigating plant disease and insect attacks compared to AMF (Figure 4) (Zaccardelli et al., 2012; Pane et al., 2016).

We think that the emergence of synergistic effects that led to the combined suppressive effects of tomato diseases and biostimulation of tomato plant symbiosis, including plant growth and crop yield, is directly due to the cooperation of bioprotective properties of FM (i.e., plant-based biopesticide extracts) and microbial biofertilizer capacities of AMF symbiosis. A limited body of research has shown that the combined application of AMF with other types of compost contributes to enhancing tomato plant vigor, growth, yield, and suppressiveness and resistance to leaf diseases (Maaloum et al., 2020; Rahou et al., 2021; Soussani et al., 2023). Our outcomes pinpoint that the co-application of AMF consortium and FM compost tea emerges as a superior biocontrol strategy that acted as biopesticides and biostimulants compared to their independent effects.

Overall, the synergistic biocontrol interaction of AM and FM compost tea demonstrated direct and indirect implications for enhancing tomato disease resistance (Deravel et al., 2014; Kohler et al., 2015; Dey and Ghosh, 2022). The direct effects include suppression of tomato plant diseases and pests with FM compost tea biopesticide and AMF colonization effects. The synergistic interplay between AMF and FM compost tea might have both together directly suppressed phytopathogens and pests through their multifunctional properties, meaning via direct contact of plant-based biopesticide extracts associated with the ability of AMF to rapidly pre-colonize the roots (Veresoglou and Rillig, 2012; Pane et al., 2016; Mala et al., 2019). The indirect effects include biostimulation of tomato plants by the combined application of AMF and FM compost tea acting as bio-effectors to promote tomato plant vigor and systemic resistance mechanisms (Cissokho et al., 2015; Pane et al., 2016; Asmae et al., 2018; Dey and Ghosh, 2022). These findings are supported by PCA, revealing distinct and complementary effects of AMF and FM compost tea on the intricate dynamics of tomato plant diseases and AMF symbiosis (Figure 9). The observed synergies likely contribute to unique clustering patterns, indicating that the combined application alters the system in a way not solely attributable to individual treatments but rather to their combination.

Our results offer valuable insights for optimizing agricultural practices, emphasizing the potential of synergistic interactions between AMF and FM compost tea in promoting tomato plant and soil health, disease resistance, and overall soil ecosystem dynamics. The dual application of AMF and FM compost tea constitutes a friendly approach to promoting different strategies for sustainable agricultural management, since they come from a natural source and their application not only promotes plant growth and AMF, but also induces plant resistance.

However, it is crucial to underscore the intricacy and multifaceted nature of delineating the direct effects stemming from both AMF inoculation and FM compost tea application, as opposed to their indirect impacts on the regulation of tomato plant resistance, within the scope of this field experiment. While we refrain from asserting the occurrence of molecular mechanisms, we proffer plausible mechanisms that could have contributed to the observed reductions in diseases and pests. We here further propose to perform microbiological analysis of FM compost tea and targeted mechanistic molecular experiments underpinned by advanced metagenomic, metatranscriptomic, and metabolomic tools. These mechanistic assessments aim to systematically disentangle the interrelated genes and functional genomic mechanisms through which the combined application of AMF and FM compost tea jointly upregulates plant defense genes and precipitates significant alterations in the metabolic profile of tomato plants, ultimately inducing enhanced disease resistance. Further research into the specific mechanisms driving these synergistic effects could enhance our understanding of sustainable agricultural strategies.

Conclusion

The potential synergies between AMF symbiosis and organic pesticides such as FM compost tea in enhancing plant disease resistance remain largely unexplored, particularly in the context of on-farm studies. We conducted a comprehensive on-farm investigation to unravel the intricate interactions between a blend of AMF inoculant and an organic biopesticide, FM compost tea, aiming to protect tomato plants against prevalent pathogens and insect pests. Our results showed that the combined application of AMF tomato seedling inoculation and FM compost tea induced beneficial synergistic effects that promoted significant increases in the mycorrhizal colonization rate of tomato plants and largely suppressed the incidence and severity of common plant diseases and insect attacks, surpassing the outcomes of control plants and individual applications. Moreover, the co-application of higher dosages of FM compost tea with AMF seedling inoculation performed significantly in terms of tomato disease resistance promotion, and this also translated to increased plant yield relative to control without AMF and FM compost tea addition or individual applications. This study advocates for innovative next-generation agricultural techniques that promote dual application of AMF and FM compost tea for optimizing the tomato-cropping system and enhancing soil health. Further studies are urgently needed to disentangle the role of AMF with organic biopesticide on plant defense-related enzymes and genes. We here offer a scientific–practical guiding light for biorational studies that could be leveraged as a new effective biocontrol alternative with broad-spectrum capabilities for the suppression of common tomato phytopathogens and insect attacks while enhancing tomato productivity sustainably.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

SO: Conceptualization, Data curation, Formal analysis, Methodology, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. DN: Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Visualization, Writing – original draft, Writing – review & editing. SM: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Visualization, Writing – original draft, Writing – review & editing. ST: Data curation, Formal analysis, Investigation, Methodology, Resources, Visualization, Writing – original draft, 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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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fhort.2024.1253616/full#supplementary-material

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