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Yield Increase in Strawberry Cultivated in Feather Compost Via The Application of Humic Substances Related to Rhizo Spheric Bacterial Community Shifts

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Abstract

Strawberries were cultivated in feather compost (DF) treated with DF-extracted humic substances (HSs), liquid chemical fertilizer (CF), CF + HS, or no fertilizer (blank). Higher strawberry yields were found in the HS and CF + HS treatments than in the CF and Blank. After the final strawberry harvest, rhizo spheric bacterial composition was determined in the four samples using next-generation sequencing. The abundance of *Terrimonas* increased in HS; *Dokdonella, Steroidobacter, Altererythrobacter* and *Rhodanobacter* increased in CF+HS; *Acidibacter* increased in CF; and *Thermomonas, Sphaerisporangium* and *Truepera* increased in Blank. Based on STAMP analysis, in comparison with Blank, the abundance of *Nitrospira lenta, Pseudomonas putida, Sphingobium czechense, Actinomadura glauciflava* and *Leptonemaillini* increased in HS, and the abundance of *Arenimonas composti* and *Caldimonas manganoxdans* increased in CF + HS. Compared with CF, *Arenimonas composti, Calidmonas manganoxidans* and *Bdellovibrio bacteriovorus* increased in CF + HS. HS treatment with or without CF can increase the abundance of rhizospheric bacteria with reported functions, such as aromatic compound degradation (*Terrimonas, Dokdonella, Altererythrobacter*), microalgal flocculation (*Terrimonas*), nitrification (*Nitrospira lenta*), hydrolysis of urea (*Nitrospira lenta*), denitrification (*Terrimonas, Dokdonella, Rhodanobacter*), inhibition of Fusarium (*Terrimonas, Dokdonella*), control of plant pathogens (*Rhodanobacter, Pseudomonas putida, Bdellovibrio bacteriovorus*), and promotion of plant growth (*Altererythrobacter, Rhodanobacter, Pseudomonas putida*).

Keywords: Feather compost; Soilless culture medium; Humic substance; Strawberry; Bacterial community

Abbreviations: HSs: Humic Substances; CF: Chemical Fertilizer; TSS: Total Soluble Solid; NGS: Next-Generation Sequencing; NMDS: Nonmetric Multidimensional Scaling; DBDE: Decabromodiphenyl Ether; PQQ: Pyrrolo Quinoline Quinone; PGPR: Plant Growth-Promoting Rhizobacterium; PHB: Poly(3-Hydroxybutyrate)

Introduction

In Taiwan, strawberries are produced during the winter season and are popular because of their high nutrient content, good flavor, and ease of consumption. The strawberry cultivation area in Taiwan is approximately 509 ha in 2021. Because plant nutrient management and pest control measures are challenged by extreme climatic changes and soil degeneration, an increasing number of farmers are planting strawberries in soilless culture media in greenhouses. Peat is a commonly used culture medium for strawberry production; however, considering the cost and carbon emissions generated during peat transport and utilization, the development of an alternative culture medium produced from agricultural wastes as raw materials is needed. For example, by using degradation-resistant feather and spent mushroom wastes as composting raw materials, a medium with long-lasting fertility can be produced as a soilless culture medium for the production of cherry tomatoes and melons without the need for additional fertilization [1,2].

In agricultural fields, humic substances are important bio stimulants with multiple functions, such as stimulating plant growth, controlling plant pests, and increasing plant resistance to abiotic stress [3,4]. Application of humic substances to improve strawberry production and quality via foliar application [5,6] or as a combined treatment with rhizobacteria [7] has been reported. The application of humic substances changes soil rhizosphere microbial diversity [8], and the increased abundance of microbial communities can be related to positive crop productivity

outcomes, such as increases in the yield of continuously cropped peanuts [9], potatoes [10] and wheat [11]. Humic substances from different sources have different effects when applied; for example, humic substances extracted from compost are more effective than lignite-extracted substances in stimulating plant growth [12] and increasing phosphorous availability in Oxisols [13].

In this study, we aimed to understand whether strawberry yield could be increased via strawberry cultivation in feather compost treated with humic substances sourced from the same compost, and to clarify whether the observed changes in the bacterial communities were positively correlated with strawberry productivity.

Materials and Methods

Humic substance preparation and carbon content analysis

Duck feather compost (DF) was manufactured at the Taichung District Agricultural Research and Extension Station. Humic substances were extracted from the DF following the method described by Azcona et al. [14] with some modifications. Sixty grams of air-dried DF was mixed with 340 mL of 0.1 M NaOH in a1L Erlenmeyer flask covered with aluminum foil and shaken for 24 h at 120 rpm. The supernatants containing humic substances (HS) were separated from the solid fraction by centrifugation at 11,000 × g for 15 min. The carbon percentage of the HS was determined using a TOC analyzer (Element arvario Max C).

Strawberry production in greenhouse

The characteristics of the strawberry cultivar Aroma are everbearing, semi-upright growth, green leaves, and a medium density of foliage with white petals. The fruit has a red conical shape and shows a pink flashing and core with a distant scent and sweet fruity flavor. The fruit sugar content is approximately 8-10 °Brix.

Strawberry plantlets (cultivar 'Aroma') via stolon generation in soft plastic basin containers (volume 160 mL) filled with peat were transplanted into pots (4.5 L) with DF as the culture medium combined with the following treatments: (1) no further fertilization (blank), (2) drenching with 0.5% fertilizer as Taifer instant chemical fertilizer NO.43 (N-P2O5-K2O=15-15-15) (chemical fertilizer, CF), (3) drenching with 50 mg-C of HS per L (HS), and (4) drenching with 50 mg-C of HS per L in 0.5% Taifer instant fertilizer NO.43 (CF+HS). One strawberry plant was planted in each pot. Each treatment group contained five replicate pots, and, except for treatment (1), 200 mL of liquid fertilizer was added per pot on days 20th, 32nd, 46th and 66thdays after strawberry seedlings were planted. The strawberry cultivation time was from December 18, 2020, to April 9, 2021, average monthly air temperature (18.9°C, 15.1°C, 17.8°C, 20.4°C and 23.0°C), average monthly maximum air temperature (23.1°C, 20.7°C, 23.8°C, 25.3°C and 27.7°C) and average monthly minimum air temperature (16.2°C, 10.9°C, 13.9°C, 17.2°C and 19.5°C) were recorded by AMS-TDARES. average air temperature in greenhouse was approximately 1.5°C higher than outside from December to April. During cultivation, irrigation water (pH8.3 and EC 0.29 mS/cm) was applied thrice per day. Strawberry fruits were harvested from February 1 to April 9 and analyzed for fruit weight, total soluble solid (TSS), acidity, fruit number, and cumulative yield per pot. The TSS of the fruit juice was determined using a Palette digital refractometer (PR-101α, ATAGO). The acidity of fruit juice was determined by titration of diluted fruit juice (1:10 deionized water extract) containing the indicator phenolphthalein with 0.1 MNaOH. The reaction endpoint was determined by color change.

Nutrients in the DF Compost

The Three replicates of compost samples were oven-dried at 70 °C. Dry samples were ground and digested with H_2SO_4 and H_2O_2 [15]. The nitrogen content was analyzed using microdiffusion methods [16], and the phosphorus content was analyzed using a colorimetric method [17]. The potassium, calcium, and magnesium contents were analyzed using atomic absorption spectrophotometry. Micronutrients were extracted with 1 M HCl [18] and analyzed using atomic absorption spectrophotometry. Water-soluble nutrients were analyzed using a 1:10 deionized water extraction, following the abovementioned methods.

Bacterial diversity analysis in rhizospheric culture media

After the final strawberry harvest, the rhizo spheric culture medium in each treatment was mixed thoroughly to form one sample, and four samples were sent to TRI-I Biotech Inc. for bacterial diversity analysis using next-generation sequencing (NGS).

DNA isolation, amplification, and sequencing

Total DNA was extracted using a DN easy Power Soil kit (QIAGEN), following the manufacturer's instructions. The quality of the extracted DNA was confirmed using 1.2% agarose gel electrophoresis. PCR amplification of microbial 16S rDNA gene fragments were performed in the V3-V4 region by using the primers 341F (CCTACGGGNGGCWGCAG) and 805R (GACTACHVGGGTATCTAATCC) with 25 µlof reaction solution (0.5 µl of 1 U/µl KAPA HiFi DNA polymerase, 0.75 µl of 10 mM KAPA dNTP mix, 5.0 µl of 5X KAPA HiFi Fidelity buffer, 0.75 µl each 341F and 805R primer and 2 ng of DNA). The PCR cycling conditions included an initial denaturation at 95 °C for 3 min, followed by 25 cycles of 98 °C for 20 s, 57.5 °C for 20 s, 72 °C for 20 s, and extension at 72 °C for 3 min, followed by a final hold at 4 °C. The second phase of PCR was performed after tagging the library with universal primers and Illumina-indexed bar code sequences in the 341 F primer (bar code sequence for blank sample was CACgTCTA, HS sample was ACTCTCCA, CF sample was AgCTAgTg, and CF + HS sample was ACTATCgC) and 805R primer. The PCR Master Mix contained 0.75 µL each of 10 µM forward and reverse primers,0.75 µl of 10 mMdNTP, 5 µl of 5X KAPA HiFi Fidelity Buffer, 0.5 µl of 1 U/µl KAPA HiFi DNA Polymerase, 10 ng of amplicon

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and water to a total volume of 20 µl. PCR products were pooled and purified using AM Pure XP beads (Beckman Coulter, Inc.). The samples were separated by 2% agarose electrophoresis to target an approximately 500 bp band for purification using a MinElute Gel Extraction Kit (QIAGEN). The library was then loaded onto an Illumina MiSeq platform for paired-end sequencing (2 × 301 bp).

Taxonomy profiling and community analysis

Quality control of sequencing data was performed using CLC Genomics Workbench v10. The absolute numbers of sequences observed for the individual sequence lengths in the base pairs were calculated. The number of sequences that featured individual PHRED scores in 64 bins, from 0 to 63, was determined. The quality score of each sequence was calculated as the arithmetic mean of the base quality. The sequence and quality score data were extracted from fast q files, the reverse complement of the reverse read was created, and the reads were joined into contigs. Data processing for generating effective reads was performed using MiSeq SOP, and assembled reads were assigned to corresponding samples using default parameters. Then, reads shorter than 408 bp or longer than 555 bp were removed (approximately 95% of the reads were retained), chimeric sequences identified by the UCHIME algorithm were removed, and all reads were then classified using a Bayesian classifier with the Silva database (release 128). All the effective reads from all samples were clustered into operational taxonomic units (OTUs) based on 97% sequence similarity using USEARCH. If 51% or more reads in an OTU belong to the same taxon (ex. species), the taxon was chosen for the taxonomic classification of OTU. If the number was < 51%, the calculation was replicated at a higher taxonomic level (ex. genus). Taxonomic profiling of the samples at different taxonomic levels and the corresponding area and bar plots were created using QIIME.

Results

Strawberry fruit characteristics and yield

The pH, EC, C/N, N, P, K, Ca, Mg, Cu, Mn, Zn and Fe contents of the DF were 7.3, 4.6(1:0) dS/m, 12.8, 32 g/kg, 9 g/kg, 22 g/kg, 27 g/kg, 11 g/kg, 7.4 mg/kg, 296.7 mg/kg, 167.7 mg/kg and 976.7 mg/kg, respectively. The water-soluble nutrients in DF were NH_{4+} (230 mg/kg), NO_{3-} 2,274 mg/kg), P (641 mg/kg), K (16,608 mg/kg), Ca (2,473 mg/kg), Mg (1,779 mg/kg, Cu 0.3 mg/kg, Mn 2.4 mg/kg, Zn 0.9 mg/kg and Fe 2.9 mg/kg. The humic substance (HS) extracted from the DF with 8.4 mg-C per mL of extract was used to prepare a 50 mg-C/L solution with or without liquid chemical fertilizer (CF) for application in strawberry production. Strawberry fruit characteristics are shown in Table 1. Compared to the blank, which received no further fertilization, CF treatment alone did not increase strawberry yield; however, HS with or without CF increased strawberry yield. The TSS/acid ratio of strawberry fruit increased after HS treatment but decreased with CF+HS treatment.

Taxonomic profiling of bacterial metagenomic sequences

Next-generation sequencing of partial 16S rRNA genes based on taxonomic profiling revealed bacterial diversity in the four rhizo spheric samples: blank, HS, CF, and CF+HS. The V3-V4 hypervariable region of the 16S rRNA gene of the microbiome was sequenced using the Illumina MiSeq System. The total raw data in pairs were 51,486 in the blank, 52,239 in HS, 51,978 in CF, and 51,176 in CF + HS. A total of 47,081 OTUs were analyzed and identified to belong to 57 phyla, 266 classes, 494 orders, 763 families, 1,539 genera, 2,539 species, and others that were unclassified. The OTUs in the blank, HS, CF, and CF + HS groups were 11,992, 10,946, 12,697, and 11,446, respectively.

The distributions of the common and unique species in each group are shown in Figure 1. A total of 1,377 species were shared by all four groups, and 8,327, 7,194, 8,616, and 7,418 species were unique in the blank, HS, CF, and CF + HS groups, respectively.

The ten most abundant bacterial genera are listed in Table 2. In the blank, the genera, in descending order, were *Streptomyces, Thermomonas, Sphaerisporangium, Actinomadura, Chryseolinea,* and *Truepera. Actinomadura* showed the greatest increase in rhizo spheric bacterial abundance following HS application, followed by *Terrimonas, Streptomyces* and *Dogia*. With CF application, uncultured Deltaproteobacteria were the most abundant, followed by Streptomyces, Dongia, Acidibacter and Hyphomicrobium. Dokdonella was the most abundant genus in the CF+HS group, followed by *Steroidobacter, Altererythrobacter, Chryseolinea, Rhodanobacter, Hyphomicrobium* and *Streptomyces. Thermomonas, Sphaerisporangium, Truepera, Terrimonas, Acidibacter, Dokdonella, Steroidobacter, Altererythrobacter* and *Rhodanobacter* were not shared among the four treatment groups. Only Streptomyces was present in all four groups. Some abundant genera, such as *Actinomadura, Chryseolinea, Dongia* and *Hyphomicrobium*, coexisted in specific samples.

Rarefaction plots indicated that the four groups had similar bacterial diversity (high levels; Figure 2). Nonmetric multidimensional scaling (NMDS) analysis showed that the blank and CF+HS groups were closely clustered, as they shared identical OTUs; however, the bacterial species in the CF group were uniquely distributed and qualitatively deviated from the other three groups (Figure 3).

Comparison of bacterial community structure and significant differences

Compared with the blank, greater bacterial percentages of *Nitrospiralenta, Pseudomonas putida, Sphingobium czechense, Actinomadura glauciflava* and *Leptonema illini* were present in the HS group; *Arenimonas composti* and *Caldimonas manganoxdans* were present in the CF + HS group; *Pilimeliaanulata, Pedomicrobium americanum, Nitrospira lenta, Turneriella parva,* and *Zavarzinella formosa* were present in the CF group.

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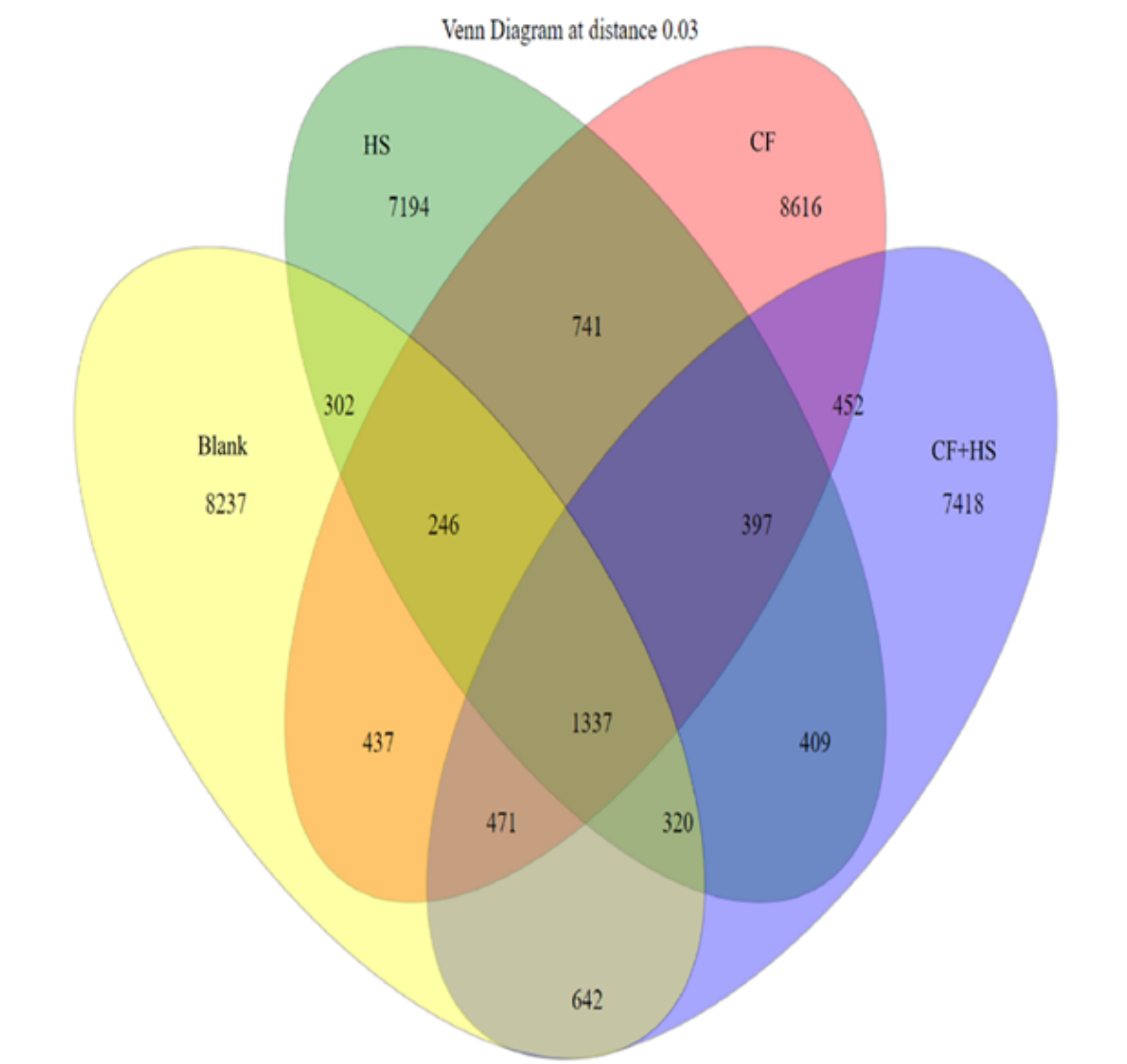

The number of species in group CF is 12697
The number of species in group HS is 10946
The number of species in group CF+HS is 11446
The number of species in group Blank is 11992
The number of species shared between groups CF and HS is 2721
The number of species shared between groups CF and CF+HS is 2657
The number of species shared between groups CF and Blank is 2491
The number of species shared between groups HS and CF+HS is 2463
The number of species shared between groups HS and Blank is 2205
The number of species shared between groups CF+HS and Blank is 2770
The number of species shared between groups CF, HS and CF+HS is 1734
The number of species shared between groups CF, HS and Blank is 1583
The number of species shared between groups CF, CF+HS and Blank is 1808
The number of species shared between groups HS, CF+HS and Blank is 1657
The total richness of all the groups is 37219

Figure 1: Venn diagram of bacterial species identified among the four samples.

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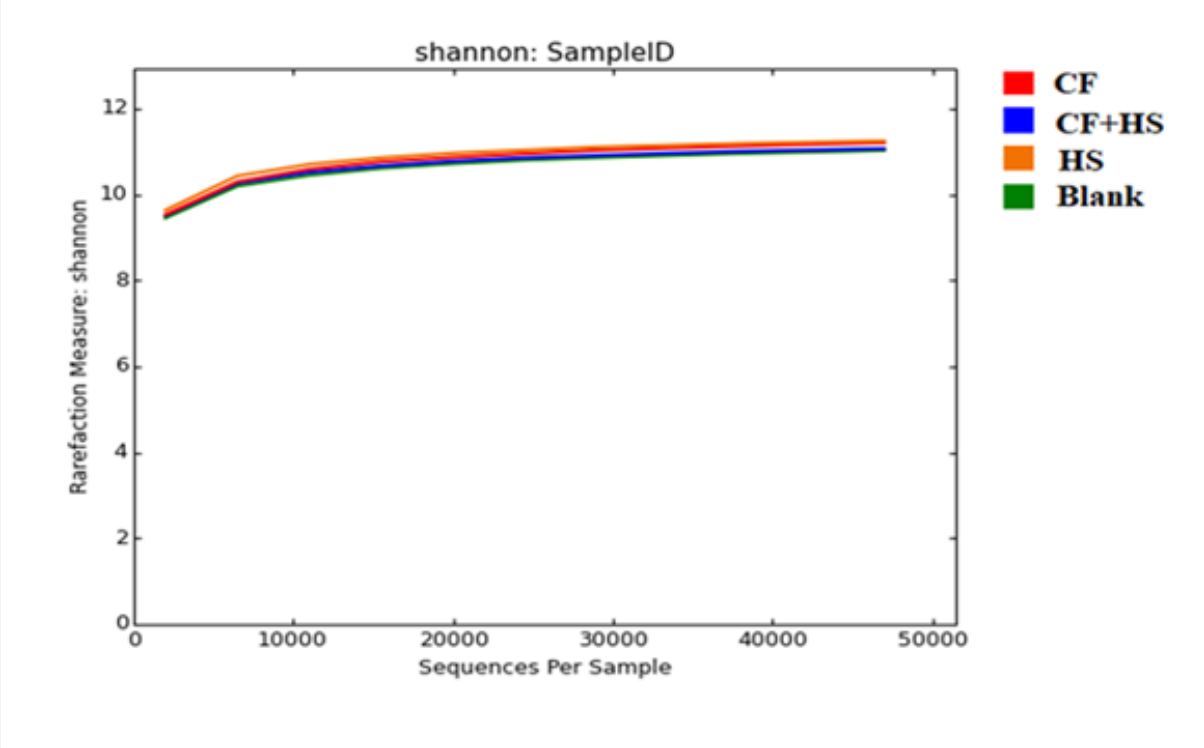

Figure 2: Rarefaction plots showing that the four groups had similar bacterial diversity.

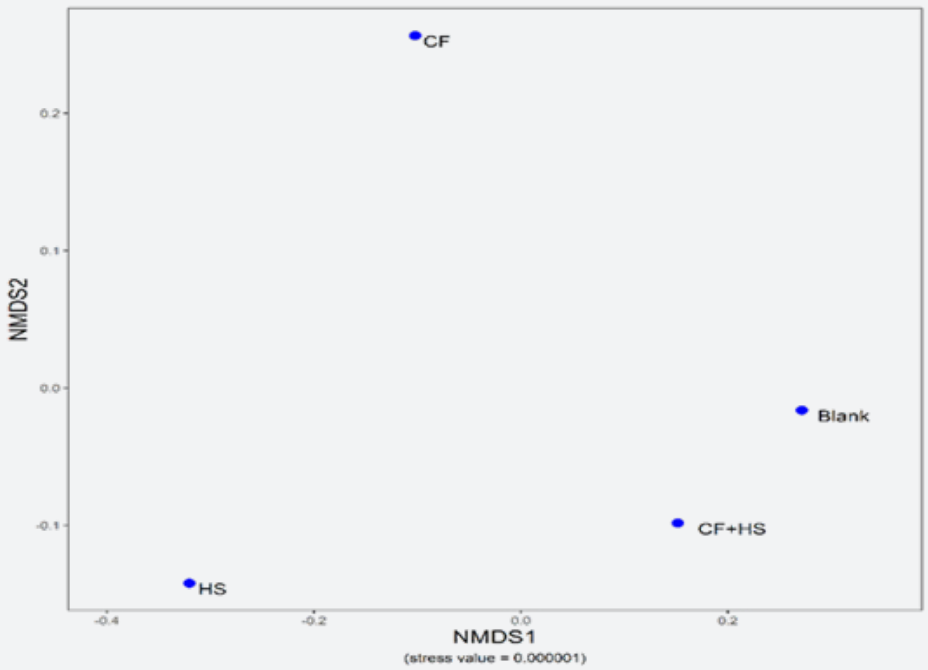

Figure 3: NMDS (nonmetric multidimensional scaling) analysis of bacterial communities among the samples by vegan (R package: v2.4-1).

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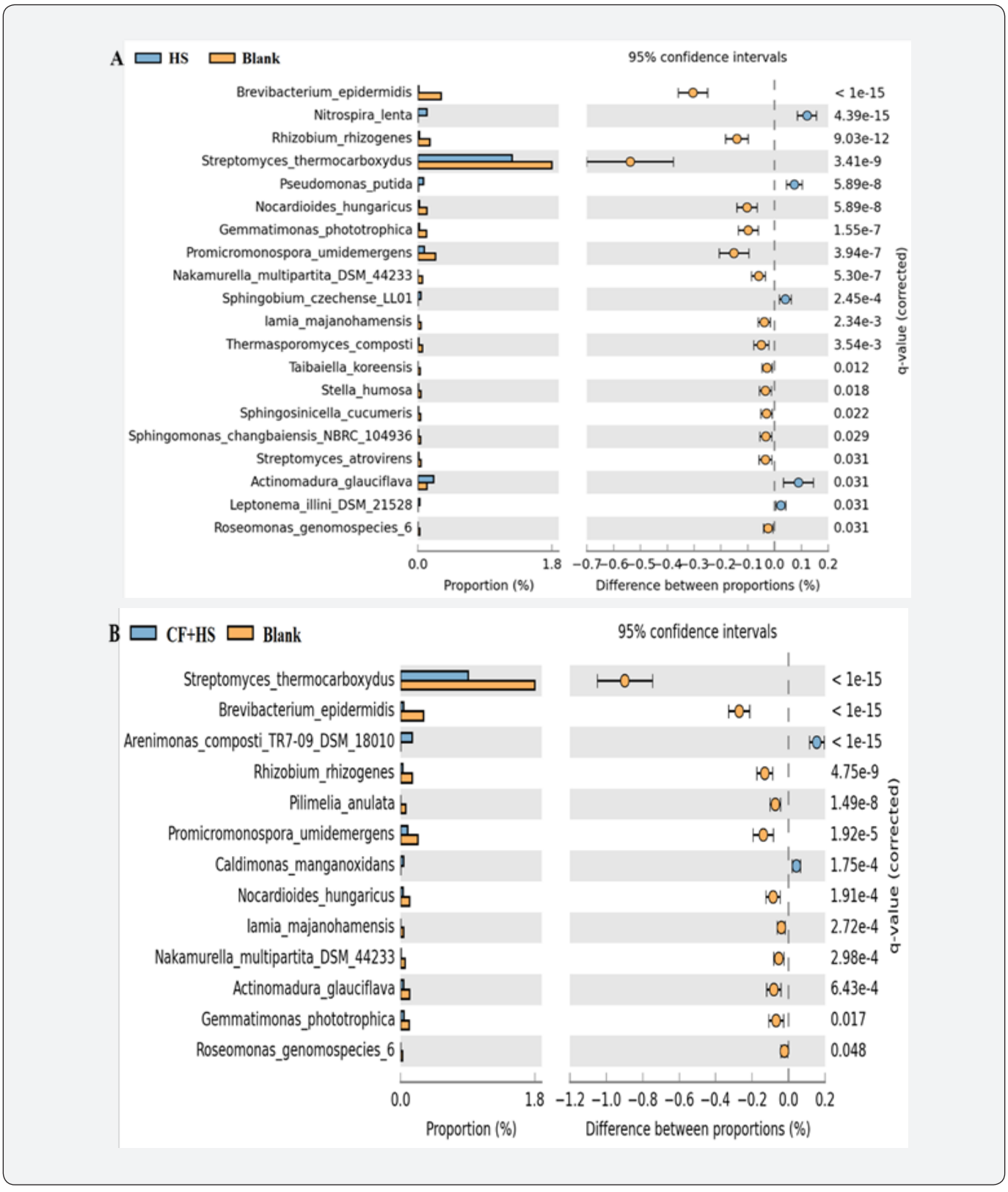
Compared with CF, the bacterial abundance of *Arenimonas composti, Calidmonas manganoxidans* and *Bdellovibrio bacteriovorus* was higher in the CF+HS group; *Actinomadura glauciflava* and *Pseudomonas putida* were higher in the HS group (Figure 4).



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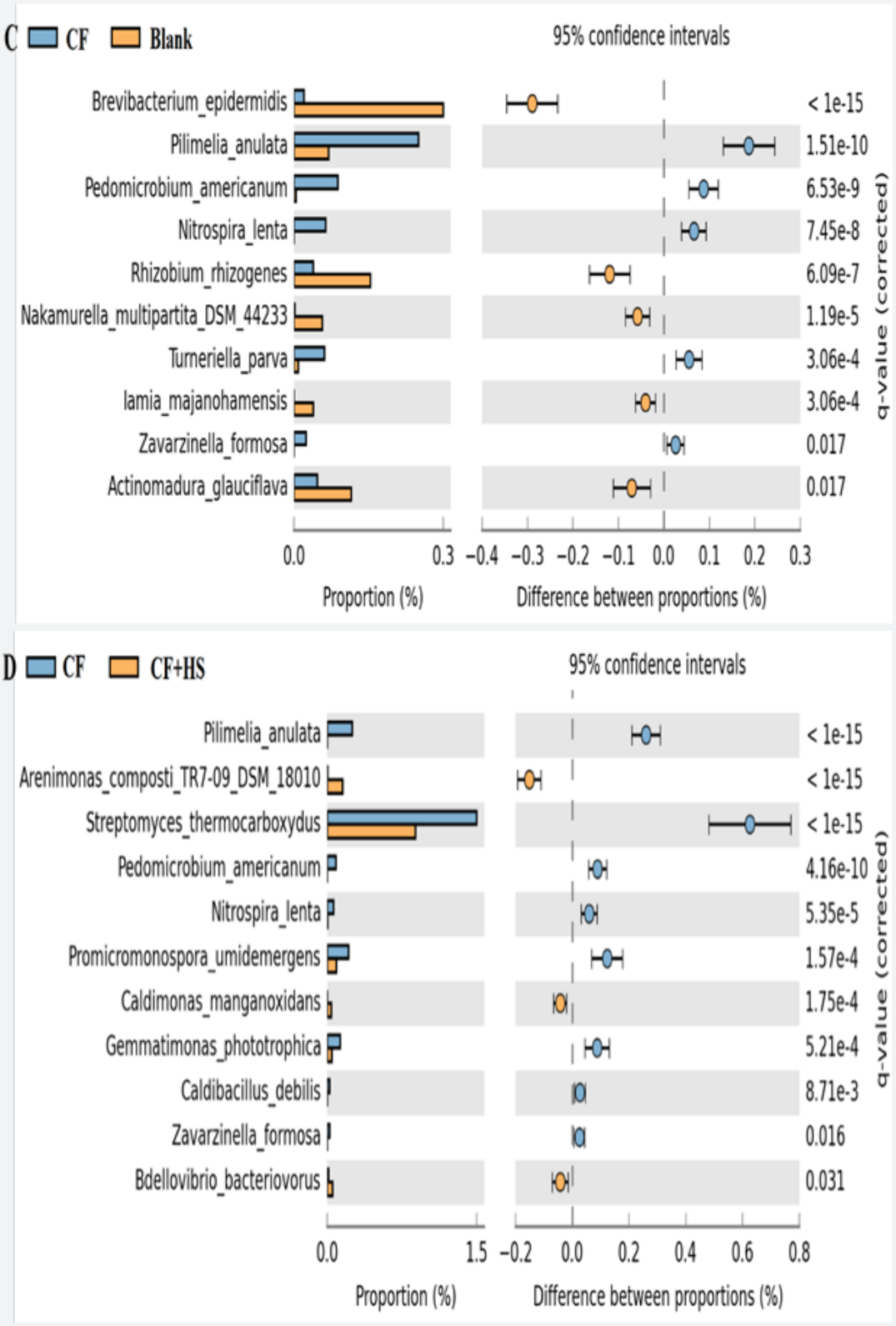

Figure 4: The comparison of taxa using STAMP V2.1.3. Corrected P values were calculated based on Fisher's exact test method using Story's FDR approach (P values < 0.05). The bar plot indicated in blue or orange shows a positive or negative difference between read proportions. Differences between samples (A:HS and Blank, B:CF+HS and Blank, C:CF and Blank, D:CF and CF+HS, and E: CF and HS) are shown at 95% confidence.

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Table 1: Strawberry fruit characteristics and yield in the experiment.

Treatment	Cumulative weight g	Fruit weight g	Fruit number	Fruit TSS/Acid	Fruit TSS Brix	Fruit Acid %
Blank	233.6b*	13.6a	17.6a	11.6ab	7.5ab	0.66a
CF	170.8b	15.2a	11.6b	11.2ab	7.0b	0.63a
HS	299.5a	14.1a	21.4a	12.8a	8.6a	0.67a
CF+HS	339.8a	15.9a	21.4a	10.3b	7.0b	0.69a

*Values followed by the same letters in each column are not significantly different at the 5% level (least significant difference).

Table 2: The top ten bacterial genera in strawberry rhizo spheric culture medium with the application of humic substances (HSs), chemical fertilizer (CF), CF+HS and with no further fertilization (blank).

NO	Blank	HS	CF	CF+HS
1	Uncultured compost bacterium (913) OTU00001	Uncultured bacterium (1126) OTU00010	Uncultured delta proteobacterium (1893) OTU00111	Uncultured bacterium (718) OTU00023
2	Uncultured bacterium (698) OTU00026	Uncultured soil bacterium (778) OTU00136	Uncultured compost bacterium (571) OTU00001	Dokdonella (648) OTU00009
3	Uncultured bacterium (682 OTU00023)	Actinomadura (685) OTU00229	Uncultured soil bacterium (522) OTU00002	Uncultured soil bacterium (617) OTU00002
4	Streptomyces (592) OTU00035	Uncultured Chlamydiales bacterium (556) OTU00029	Uncultured delta proteobacterium (494) OTU00019	Steroidobacter (406) OTU00054
5	Thermomonas (480) OTU00007	Uncultured bacterium (551) OTU00017	Streptomyces (464) OTU00035	Altererythrobacter (396) OTU00217
6	Sphaerisporangium(467) OTU00094	Terrimonas (538) OTU00032	Uncultured soil bacterium (420) OTU00136	Chryseolinea (380) OTU00003
7	Actinomadura (459) OTU00229	Streptomyces (419) OTU00035	Dongia (381) OTU00005	Rhodanobacter (379) OTU00037
8	Chryseolinea (448) OTU00003	Dongia (410) OTU00005	Uncultured soil bacterium (379) OTU00075	Hyphomicrobium (371) OTU00020
9	Uncultured compost bacterium (434) OTU00004	Uncultured compost bacterium (293) OTU00001	Acidibacter (280) OTU00070	Uncultured Acidobacterium(315) OTU00115
10	Truepera (358) OUT00013	Uncultured compost bacterium (292) OUT00004	Hyphomicrobium (263) OTU00015	Streptomyces (304) OTU00035

Discussion

Even without additional fertilization, strawberries can be cultivated in feather compost (DF) because of the coexistence of ionic nutrients that can be immediately taken up by the plant roots and organic nutrients that can be degraded for a continuous release of amino acids and ionic nutrients. Without application of additional chemical fertilization in crop production can decrease carbon emissions from fertilizer manufacturing process that was benefit in sustainable agriculture. The high EC value (4.6 dS/m) of the DF compost did not inhibit strawberry growth, which could be due to the salt-alleviating effects of humic substances within the DF compost, as previously reported [19-21]. Strawberry fruits with deep-red peel color were collected to investigate characteristics; however, slight differences in fruit maturity would affect the characteristics. In this experiment, additional treatments with liquid chemical fertilizer (CF) did not increase the yield of strawberry; however, treatments with CF combined with 50 mg-C/L humic substances (HSs) increased strawberry yield, which could be due to the dual role of HS in stimulating crop production and increasing plant resistance to biotic and abiotic stresses [3,4]. In addition to the effects of the chemical interaction between humic substances and plant roots, compositional changes in microbial communities induced by HS are expected to affect strawberry growth.

The Venn diagram shows that each group had unique species, ranging from 7,194 to 8,216 in number, and only 1,337 species were shared by all four groups. Treatment with different nutrients increased the abundance of unique species in the individual groups, which was related to similar α-diversity but different β-diversity among the four samples.

The ten most abundant bacterial genera in each sample are listed in Table 2. In the blank, uncultured compost bacteria were the most abundant, followed by known genera, such as *Streptomyces, Thermomonas, Sphaerisporangium, Actinomadura, Chryseolinea,* and *Truepera*. With HS application, the top ten known rhizo spheric bacterial genera were *Actinomadura*, uncultured *Chlamydiales, Terrimonas, Streptomyces* and *Dongia*. On the one hand, some reports of human disease caused by *Actinomadura*

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and *Chlamydiales* have emerged; on the other hand, *Actinomadura graeca* has been reported to produce the macrocyclic antibiotic zelkovamycin [22].

The application of HS increased the abundance of *Terrimonas* relative to that in the other groups. Terrimonas has been reported to degrade decabromodiphenyl ether (DBDE) [23] and secrete extracellular substances that play a role in enhancing microalgae flocculation [24], inhibiting Fusarium plant pathogens [25] and inhibiting denitrification [26]. Humic substances composed of aromatic rings, such as phenylpropene, may increase the abundance of microbial populations, such as *Terrimonas*, which can degrade aromatic compounds. Previous research has shown that humic substances can induce soil aggregation and increase soil stability [27]. Because of the role of *Terrimonas* in microalgal flocculation [23], it can also improve soil aggregation, which might suggest that humic substances play a role in soil improvement, both through their chemical properties and by increasing the abundance of specific bacteria that can help in soil aggregation.

Humic substances can suppress *Fusarium oxysporum* by regulating the soil microbial community and increasing cucumber biomass [28]. In the aforementioned experiment, we found a possible connection between the application of HS and increased plant resistance to *Fusarium*. For example, HS increased Terrimonas abundance and has been reported to inhibit *Fusarium* [25]. Humic substances containing optimal functional groups for electron shuttling can improve denitrification and promote microbial denitrification [29], which can increase bacterial populations with denitrifying functions such as *Terrimonas*. The genus *Dogia* may not be a key factor in strawberry yield enhancement because its abundance was similar in the HS and CF groups.

Liquid chemical fertilizer combined with humic substances (CF + HS) increased the abundance of genera such as *Dokdonella, Steroidobacter, Altererythrobacter* and *Rhodanobacter* relative to the other groups. *Dokdonella* has been reported to increase banana resistance to the pathogen Fusarium [30], degrade polycyclic aromatic hydrocarbons, break down nitrogen-containing organic pollutants [31,32] and perform heterotrophic denitrification [33,34]. *Steroidobacter* was increased by wood sawdust (lignin) amendment [35] and has been reported to have functions such as sulfonamide (aromatic compound) degradation [36], control of the plant pathogen Fusarium [30,37] and denitrification of *Steroidobacter denitrificans* [38]. *Altererythrobacter* has been reported to promote plant growth [39] and to degrade aromatic, petroleum-aromatic, and lignin compounds [40-42]. The genus *Rhodanobacter* has been reported to have multiple functions, including denitrification [43], plant growth promotion [44] and plant disease control. For example, the application of urban waste compost reduced barriers to watermelon continuous cropping via an increase in the abundance of *Rhodanobacter* and a reduction in the abundance of the pathogen Mizugakiibacter [45]; *Rhodanobacter* and *Kaistobacter* were the dominant bacterial genera in healthy soil with a ginger disease incidence of <10% [46]; and *Rhodanobacter* showed antagonism to the soil-borne root-rot plant pathogen *Cylindrocladium spathiphylli* [47].

Previous studies have shown that the application of HS alone or in combination with other materials can control *Fusarium* disease in cucumber [48] and soybean [49], which is consistent with the findings of this study showing that the application of HS or CF + HS increased the abundance of *Terrimonas, Dokdonella* and *Rhodanobacter*, which have potential biocontrol functions. A higher abundance of the genus Hyphomicrobium was found in CF+HS than in CF. *Hyphomicrobium* has been reported to have denitrification capacity [50] and pyrroloquinolinequinone (PQQ) production [51]. PQQ can promote plant growth [52] and increase plant resistance to pathogens such as *Agrobacterium tumefaciens* and *Ralstoniasolanacearum* [9]; therefore, the combined application of chemical fertilizers and HS can be a potential method for increasing crop productivity.

Based on the taxa comparison (STAMP) results, HS treatment increased the abundance of *Nitrospiralenta, Pseudomonas putida, Sphingobium czechense, Actinomadura glauciflava* and *Leptonema illini* compared to the blank. *Nitrospira lenta* is a nitrite-oxidizing bacterium and is also able to hydrolyze urea to ammonium and CO2, facilitating nitrogen and carbon assimilation from urea [53]. Humic acid and fulvic acid can increase nitrite production but decrease the maximum nitrification rate [54], which can benefit nitrite-oxidizing bacteria, such as *Nitrospira lenta*. Previous research also showed that increasing the concentration of humic acid can result in the enrichment of *Nitrospira* in nitritation systems [55], which is consistent with our results showing that the application of HS to DF compost with a high concentration of ammonium ions can enrich *Nitrospira lenta*.

Pseudomonas putida is a plant growth-promoting rhizobacterium (PGPR) that can boost plant growth and prevent pathogenic disease development [56], which might be the reason the application of HS increased strawberry yield. The functions and roles of *Sphingobium czechense, Actinomadura glauciflava* and *Leptonema illini* in agricultural fields are not fully understood. For example, the plant interactions and outcomes of these three species are unclear.

Compared with the blank, chemical fertilizer combined with humic substances (CF + HS) increased the abundance of the species *Arenimonas composti* and *Caldimonas manganoxidans*. *Caldimonas manganoxdans* is a poly(3-hydroxybutyrate) (PHB)-degrading bacterium [57] that possesses genes for PHB production [58]; however, its function in promoting plant growth is not clear. Compared with the CF group, the abundance of *Arenimonas composti, Calidmonas manganoxidans* and *Bdellovibrio bacteriovorus* increased in the CF+HS group. *Bdellovibrio bacteriovorus* is a predatory bacterial species found in an environment that can attack gram-negative bacteria; therefore,

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it has the potential to be applied for plant disease control. For example, *Bdellovibrio bacteriovorus* strain SOIR-1 can effectively prey on *Pantoea* sp. and *Xanthomonas campestris* to control the rotting of onion and potato tubers [59].

In the experiment, the application of HS alone or in combination with liquid chemical fertilizer (CF + HS) increased specific bacterial populations with reported functions in degrading aromatic compounds, carrying out nitrification and denitrification, controlling plant pathogens, including Fusarium, and promoting plant growth. The abundance of specific bacteria with aromatic compound-degrading functions might increase when plants are grown in an environment with HSs composed of condensed phenylpropene and amino acids. The high concentrations of ammonium ions present in the DF compost can be used by nitrifying bacteria, and the denitrification reaction can be accelerated by HS, as HS provides an optimal chemical environment for electron shuttling [29]. HS may modulate plant physiology, resulting in the recruitment of microorganisms with biocontrol abilities [4].

Strawberries grown in different environments would have different bacterial compositions with different functions in the rhizosphere. For example, previous strawberry microbiome studies showed many nitrogen-fixing bacteria, such as Rhizobiaceae, Devosiaceae, Xanthobacteraceae, and Burkholderiaceae, were found in the rhizosphere soil of three strawberry cultivars (Monterey, Elsanta, and Sarselect) [60]. Strawberries cultivated in DF medium with high ionic nitrogen content (NH_{4+} 230 mg/kg, NO_{3-} 2,274 mg/kg) and organic carbon (41%), the communities of nitrogen-fixing bacteria would decrease, as previous research has shown that high ionic nitrogen in the environment can reduce the density of free-living rhizobia [61].

In this experiment, the DF compost-extracted HS increased strawberry yield. Previous studies have shown that humic substances sourced from compost can promote plant growth, suppress plant diseases, and regulate plant metabolism. For example, potassium humates can stimulate the vegetative growth of chicory [62]; humic acids extracted from vermicompost can enhance maize growth parameters and plasma membrane H+-ATPase activity [63]; and humic acids increase strawberry and pepper growth [64]. Additionally, humic acid-rich vermicompost can promote *Pisumsativum* growth by enhancing soil microbial communities, root nodulation, and mycorrhizal colonization [65]. Humic acids protect ornamental plants from soil-borne pathogenic fungi [66]. Fulvic acids decrease the severity of Fusarium disease severity [48]. Humic substances from green compost increase the bioactivity and antibacterial properties of the essential oils in basil leaves [67].

Conclusion

In the experiment, strawberry plants cultivated in DF compost treated with humic substances sourced from the DF compost with or without liquid chemical fertilizer increased yield owing to the possible functions of HS and its influence in changing rhizosphere bacterial composition.

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