ORIGINAL ARTICLE

Relationship between pepper (*Capsicum annuum* L.) root morphology, inter-root soil bacterial community structure and diversity under water–air intercropping conditions

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Abstract

Main conclusion **The combination of water and gas at an aeration rate of 15 mg/L and irrigation amount of 0.8 Ep significantly promoted the root morphology, inter-root soil bacterial community structure and diversity of pepper, enhanced the structure of molecular symbiotic network, and stimulated the potential ecosystem function.**

Abstract Poor aeration adversely affects the root morphology of pepper (*Capsicum annuum* L.) and bacterial community. It is critical to understand the effects of water–air interactions on root morphology and bacterial community structure and diversity. A randomized block experiment was conducted under the two aeration rates of dissolved oxygen mass concentrations, including A: 15 mg/L, O: 40 mg/L, and C: non-aeration as control treatment, and two irrigation rates of W_1 and W_2 (0.8 Ep and 1.0 Ep). The results showed that aerated irrigation had a significant effect on the root morphology of pepper. Compared with treatment CW_1, treatment AW_1 increased root dry weight, root length, root volume, and root surface area by 13.63%, 11.09%, 59.47%, and 61.67%, respectively ($P < 0.05$). Aerated irrigation significantly increased the relative abundance of Actinobacteria, Gemmatimonadetes, Alphaproteobacteria, Gemmatimonas, Sphingomonas, and KD4-96 aerobic beneficial bacteria. It decreased the relative abundance of Proteobacteria, Monomycetes, Bacteroidetes, Corynebacterium, Gammaproteobacteria, Anaerolineae, Subgroup_6, MND1, Haliangium, and Thiobacillus. The Pielou_e, Shannon and Simpson indexes of treatment AW_1 were significantly higher than treatments OW_1 and CW_1. The results of the β-diversity of bacterial communities showed that the structure of soil bacterial communities differed significantly among treatments. Actinobacteria was a key phylum affecting root morphology, and AW_1 treatment was highly correlated with Actinobacteria. Molecular ecological network analysis showed a relatively high number of bacterial network nodes and more complex relationships among species under the aeration of level 15 mg/L and 0.8 Ep, as well as the emergence of new phylum-level beneficial species: Dependentiae, BRC1, Cyanobacteria, Deinococcus-Thermus, Firmicutes, and Planctomycetes. Therefore, the aeration of 15 mg/L and 0.8 times crop-evaporation coefficient can increase root morphology, inter-root soil bacterial community diversity and bacterial network structure, and enhance potential ecosystem functions in the rhizosphere.

Keywords Aerated irrigation · Bacterial molecular symbiotic network · High-throughput sequencing · Pepper · Root morphology

Abbreviations
NMDS   Non-metric dimensional scaling
RDA   Redundancy analysis

Introduction

Peppers are the most common food on the table, and they are the second largest vegetable crop after cabbage in China and are rich in vitamin A, vitamin C, capsaicin and capsanthin. The growth of pepper is neither drought-resistant

nor flood-tolerant, and is more suitable for growing in an environment with moist soil. Loose soil is conducive to the development of pepper roots, and permeable soil is conducive to pepper root respiration and can enhance root activity. The root system, the main organ of absorbing water and nutrient, plays an important role in growth and development (Zhang et al. 2021). Drip irrigation under plastic film is an efficient irrigation technique for greenhouse crops, has a high-water use efficiency, but it is easy to form a continuous saturated wet front near the drip head (Bhattarai et al. 2006, 2008), leading to hypoxia in the root zone (Pendergast et al. 2013). In addition, crop roots preferentially grow near the drip head (Machado et al. 2003). At the same time, root growth is very sensitive to soil oxygen stress. Oxygen stress leads to insufficient plant energy supply, which in turn restricts water and nutrient uptake by the root system and ultimately limits crop growth (Takeshi and Julia. 2004; Horchani et al. 2010). Mulching impedes soil CO_2 emission and disrupts the dynamic balance system of soil O_2 replenishment and diffusion (Li et al. 2011), further intensifying crop root zone hypoxia and affecting aboveground growth (Else et al. 2001). To alleviate this problem, water-fertilizer-air mixture bubbles are delivered to the root zone soil through aerated irrigation technology to improve soil aeration in the root zone of mulch drip irrigation (Bhattarai et al. 2005, 2006), which increase crop quality and yield potential (Lei et al. 2019a, b). Rhizosphere aeration facilitates improvement of gas environment in the root zone of the crop, increasing vigor and absorption capacity of tomato root (Niu et al. 2012). Aerated irrigation stimulates root elongation, and root growth secures canopy expansion, increasing light interception and photosynthetic efficiency (Pendergast et al. 2013) and yield (Zhu et al. 2017).

Soil microorganisms are important indicators of soil fertility and soil health (Bardgett and Putten 2014). They are mainly composed of soil bacteria, archaea and fungi, which are widely distributed in inter- and non-inter-rooted soils, and their diversity and abundance play a key role in regulating ecosystem functions such as organic matter decomposition, productivity, soil carbon dynamics and nutrient cycling (Wagg et al. 2014; Laforest-Lapointe et al. 2017; Bastida et al. 2018). The growth and reproduction of soil microorganisms require suitable temperature, humidity, aeration, and other certain environmental conditions (Zhou et al. 2022). It has been shown that coupled water-fertilizer-air drip irrigation improves soil aeration, increases soil dissolved oxygen levels, and maintains good soil permeability (Zhou et al. 2020)- Biomass and activity of aerobic and parthenogenic anaerobic bacteria are also well improved, while biomass and activity of specialized anaerobic bacteria are suppressed (Xu et al. 1998; Imlay 2002). The increase in soil dissolved oxygen content can avoid soil acidification due to material reduction in a low-oxygen environment, accelerate the decomposition of organic matter in the soil, promote the activation of soil fast-acting phosphorus and potassium, improve the effectiveness of soil phosphorus and potassium, and increase soil fertility (Burke et al. 2011; Bowles et al. 2014).

Molecular ecological network analysis can be used to explore changes in microbial interactions or reactions in intercropped soils (Deng et al. 2012). Zhu et al. (2022) found more connected lines of bacterial communities and a more stable network structure in aerated subsurface drip irrigation treatment. Zhou et al. (2020) found that aerated treatment had a higher positive connectivity compared with the symbiotic control network. In addition, dissolved oxygen gradients also strongly affect soil microbial community networks (Muhammad et al. 2021). The turnover of material in the soil will inevitably lead to changes in plant performance (Chen et al. 2019; Zhu et al. 2019). Therefore, we hypothesized that soil aeration might alter soil microbial community structure and indirectly affect plant root morphology and pepper yield. It has been shown that altering the amount of aerated air will change the microbial composition, structure, and diversity of the inter-rooted soil, ultimately influencing plant root morphology (Li et al. 2020, a, b).

So far, few studies have been reported on the sensitivity of vegetable crops and soil bacteria in clay loam soils to soil aeration and irrigation water, and how this sensitivity affects soil bacterial communities and root morphology. This information is of great importance especially in greenhouse conditions. The main objective of this study was to examine changes of bacterial community structure and diversity of pepper root and morphology under different aeration rates and irrigation amounts. Therefore, we assessed the impact of soil bacterial community composition as well as structure and diversity using high-throughput sequencing technology and further analyzed the relationship between changes in soil bacterial communities and pepper root morphology, thus providing evidence to support the above hypothesis. Hence, it is of great significance to determine the relationship between soil bacteria change and root morphology under different aeration rates and irrigation water volumes for improving nutrient transport and yield.

Materials and methods

Experimental site

The experiments were carried out in a modern greenhouse on the Agricultural Efficient Water Use Experimental Farm of North China University of Water Resources and Hydropower in Zhengzhou, Henan Province (34°47′23″N, 113°47′41″E). The total greenhouse area was 537.6 m^2, with an opening of 4 m and a span of 9.6 m. The greenhouse was

equipped with fans and wet curtains on the south and north sides to regulate the temperature and air humidity (Fig. 1). The test soil type was clay loam with soil capacity of 1.25 g/cm^3 and field quality water holding rate of 23.4%. The basic nutrient status of the soil was 38.87 mg/kg alkaline nitrogen, 3.42 mg/kg exchangeable potassium, 9.98 mg/kg available phosphorus, 21.54 g/kg organic matter, and 7.12 pH.

Experimental materials and management

The test crop was pepper (*Capsicum annuum* L.) of the variety "Yu Yi Fresh Spice No.8" (Henan Zheng'an Seedling Technology Co. Zhengzhou City, Henan Province, China). Pepper seedlings with 8 and 10 leaves were transplanted on 11 September 2019. Sufficient water was supplied at the time of planting, and polyethylene film was covered on the 12th after transplanting. The pot bucket was cylindrical, 30 cm in diameter, 40 cm in height, 30 cm in planting spacing, 70 cm in row spacing. Ten barrels were lined up in a fully buried row to simulate the light and temperature of the crop in the field. The irrigation was applied using an underground drip irrigation system with a Netafim (Netafim Irrigation, Tel Aviv, Israel) drip head placed at a depth of 10 cm below soil surface (the space between the drip head and the root system is shown in Fig. 2) and a rated flow rate of 2.5 L/h.

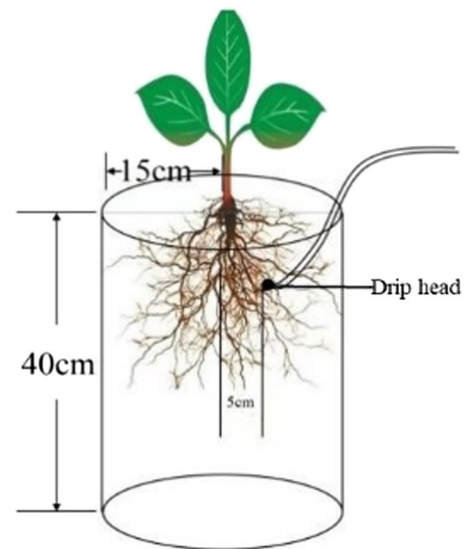Two aeration rates (dissolved oxygen mass concentration 15 mg/L and 40 mg/L, respectively)were set and

Fig. 2 Schematic diagram of the root system and dripper space

non-aeration irrigation (dissolved oxygen mass concentration 5 mg/L) was used as control treatment (Zhou et al. 2019) and 2 irrigation rates (0.8 Ep and 1.0 Ep) were used for a randomized block design, with a total of 6 treatments. The experimental design is shown in Table 1.

The aeration rates of dissolved oxygen mass concentrations of 15 mg/L and 40 mg/L were prepared using a
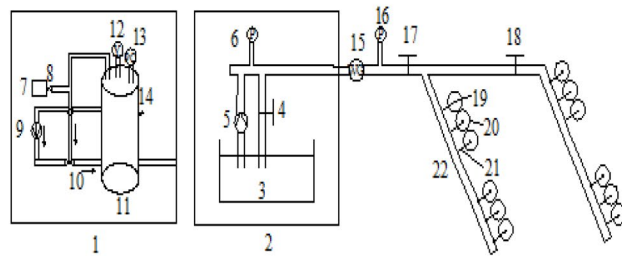
Note:
1-Circulating aeration unit
2-Comparison of water supply units
3-water-storage tank
4-Gate valve 1
5-Pump 1
6-Pressure gauge 1
7-Oxygen tank
8-Pressure reducing valve
9-Pump 2
10-Venturi
11-Pressurized water tank
12-Exhaust safety device
13-Pressure control device
14-Dissolved oxygen controller
15-Water meter
16-Pressure gauge 2
17-Gate valve 2
18-Gate valve 3
19-Pressure compensated drip tip
20-Earth column
21-Water supply capillary
22-Water supply mains

Fig. 1 Appearance of greenhouse and subsurface drip irrigation layout diagram

Table 1 Experimental design

Treatment	Aeration rate/ (mg L^{-1})	Irrigation levels	Nitrogen rate/(kg ha^{-1})
CW_1	5	0.8 Ep	300
CW_2	5	1.0 Ep	300
AW_1	15	0.8 Ep	300
AW_2	15	1.0 Ep	300
OW_1	40	0.8 Ep	300
OW_2	40	1.0 Ep	300

A and O denote aeration rate of 15 and 40 mg/L (dissolved oxygen) treatments; C denote non-aeration treatment; W_1 and W_2 are 0.8 Ep and 1.0 Ep, corresponding to low and high-water amount treatments, respectively; Ep is the evapotranspiration from the water surface of Φ601 evaporation dish

Table 2 Irrigation amount during crop growing season

Irrigation time	Day after trans-planting /d	Irrigation amount/mm	
		W_1	W_2
Sep 27, 2019	17	10.88	13.60
Oct 4, 2019	24	10.24	12.80
Oct 10, 2019	30	9.92	12.40
Oct 17, 2019	37	8.88	11.10
Oct 24, 2019	44	9.76	12.20
Nov 2, 2019	53	10.56	13.20
Nov 12, 2019	63	8.48	10.60
Nov 21, 2019	72	8.96	11.20
Nov 27, 2019	78	8.40	10.50
Dec 4, 2019	85	6.88	8.60
Dec 11, 2019	92	5.76	7.20
Dec 20, 2019	101	7.36	9.20
In total		106.08	132.60

venturi air injector Mazzei 484 (Mazzei Corp, Bakersfield, CA, USA) and a micro-nano bubbler of Aquamarine Technology (50 Hz, Yixing Aquamarine Technology Co., Ltd.), respectively. The venturi air jetter uses the water storage pipeline, circulating water pump, venturi air jetter and other equipment to adsorb air for aeration through pressure difference. Irrigation starts when the dissolved oxygen mass concentration of irrigation water reaches 15 mg/L. Aquamarine micro-nano bubble generator uses the principle of variable pressure adsorption separation to prepare pure oxygen, which can be circulated through the external water storage tank to prepare the target dissolved oxygen concentration in micro-nano bubble water. The water supply trunk was connected at the outlet end of circulating aeration, and the pressure gauge and water supply meter were connected. Irrigation started when the dissolved oxygen mass concentration in irrigation water reached 40 mg/L. Non-aeration irrigation treatment used the first water supply unit for water supply, and the mass of dissolved oxygen in groundwater was about 5 mg/L. The initial water supply pressure was controlled by the initial pressure gauge at 0.10 MPa. The lower limit of irrigation in the experiment was determined according to a tensiometer (Type 12 split tensiometer, Institute of Agricultural Irrigation, Chinese Academy of Agricultural Sciences) buried at a depth of 5 cm from the radial direction of the plant (Lei et al. 2021). The lower limit of soil substrate potential was controlled at (-30 ± 5) kPa, determined by soil moisture monitoring at a burial depth of 20 cm (Wan et al. 2019). The irrigation volume was calculated as follows (Lei et al. 2019a, b):

$$W = S \cdot E_P \cdot K_P$$

where, W is the irrigation amount during 2 irrigation events, L; S is the planting bucket area, m^2; E_P is the evaporation from Φ601 evaporation dish in 2 irrigation intervals, mm; K_P is the crop-evaporation dish coefficient, W_1 when taking 0.8Ep, W_2 when taking 1.0Ep. Both irrigation time and irrigation volume are shown in Table 2.

The fertilizers used in this experiment were urea (N content greater than or equal to 46%), calcium superphosphate (P_2O_5, P content greater than or equal to 16%), and water-soluble potassium sulfate (K_2O content greater than or equal to 52%). All phosphorus and potassium fertilizers were applied at the same rate. On the 24th, 37th, 44th, 53rd, 63rd, 72nd and 85th d after transplantation, nitrogen was applied in a ratio of 2:3:2:2:2:1, and the amount of N applied was 300 kg/ha.

Test indexes and methods

Root system indicators

During the flowering and fruiting stage, mature stage, and end stage, the pepper was removed entirely from the root as much as possible, placed in a mesh bag with a diameter of 0.5 mm, and soaked in water in the laboratory. After washing the roots, the surface was dried with absorbent paper and weighed for fresh weight. The obtained roots were placed in a transparent tray and filled with water to a depth of 10 mm. The transparent tray was scanned with an Epson Expression 1600 pro scanner to obtain a grayscale TIF image. The images were analyzed with a WinRHIZO Pro image processing system to obtain effective surface area (cm^2), root volume (cm^3), root length (cm), root tip, and root fork.

Yield

At the fruit ripening stage, five pepper plants were labelled to calculate the yield. The selected plants were healthy and free from diseases and pest attacks.

Inter-root soil sampling

For the sampling at different fertility stages, the above-ground part of the plant was cut off, and the root samples were taken out as a whole by excavating a rectangular area of 50×40 cm, and some soil samples were collected for the determination of soil chemical properties. Large pieces of soil between the roots were removed, and the soil attached to the roots was collected by shaking off vigorously. Then the visible root stubble was removed by brushing lightly with a brush and mixed thoroughly as inter-root soil samples, which were packed into sterile centrifuge tubes and stored in dry ice or $- 80$ °C liquid nitrogen for 16S rRNA high-throughput gene sequencing.

Soil DNA extraction and sequencing

The sample genomic DNA was extracted using an OMEGA M5635-02 kit, and the quality of DNA extraction was checked by 1.2% agarose gel electrophoresis, and the samples were diluted to 1 ng/μL in sterile water in a centrifuge tube. PCR amplification of the V3-V4 region of the bacterial 16S rRNA gene was performed using specific barcoded primers (barcodes) with diluted genomic DNA as a template. The common primer (F: ACTCCTACGGGAGGCAGCA R: TCGGACTACHVGGGTWTCTAAT) was selected for the V3-V4 region of the bacterial gene in pepper season. Reaction buffer 5 μL, $5 \times$ GC buffer 5 μL, dNTP (2.5 mm) 2 μL, Forwardprimer (10 μm) 1 μL, Reverse primer (10 μm) 1 μL, DNA Template 2 μL, ddH$_2$O 8.75 μL, Q5 DNA Polymerase 0.25 μL. PCR amplification conditions were: 98 °C initial denaturation for 2 min, 25–30 cycles including (98 °C, 15 s; 55 °C, 30 s; 72 °C, 30 s; 72 °C, 5 min). PCR products were mixed and purified, and library construction and sequencing were performed after purification.

Sequencing data analysis

The original DNA fragments of the community were double-end sequenced using the Illumina MiSeq sequencing platform. The original sequences screened by initial quality screening were divided into libraries and samples according to index and Barcode information, and barcode sequences were removed. Valid sequences were generated by QIIME2 software (Bolyen et al. 2019), and sequences were subjected to sequence quality control, denoising, concatenation and removal of chimeras and OTU clustering using the dada2 algorithm (Callahan et al. 2016), with each de-duplicated sequence generated after quality control as a feature sequence. The QIIME2 software was used to calculate the bacterial community structure and diversity. The Greengenes database (Release 13.8, http://greengenes.secondgenome.com/) (DeSantis et al. 2006) was selected for species annotation analysis of OTUs representative sequences and statistical sample community composition.

Statistical and bioinformatics analysis

SPSS 25.0 was used for variance analysis. Statistics software (SPSS Inc., Chicago, IL, USA) was adopted to measure differences of root morphology index among treatments at $P < 0.05$. Bacterial diversity was described by the Chao1, Pielou_e, Shannon and Simpson index, and estimated with QIIME2 software. Principal coordinates analysis (PCoA) was performed using unweighted UniFrac distance. Non-metric dimensional scaling (NMDS) calculations based on the Bray–Curtis distance were performed using the Vegan package of R software to show the differences among communities using the Bray–Curtis dissimilarity index. The smaller the stress value (Stress) of NMDS results, the better, and it is generally considered that the results of NMDS analysis are more reliable when the value is less than 0.2. Redundancy analysis (RDA) was performed using Canoco5 to investigate the relationship between root morphology and bacterial community structure. To better reveal the interactions of soil bacteria, this study used Cytoscape_v3.8.2 software to study the soil microbial community structure and function. The differences in soil ecosystem function between aerated and irrigated soils were evaluated.

The OUT table was filtered and normalized using the conet plug-in in Cytoscape_v3.8.2 software, and the threshold value was automatically selected by sorting the calculated results to select the value ranked 1000th from largest to smallest as the threshold value and retaining the $P < 0.05$ (or 0.01) results by Benjamin's test P value. 100 drop generations were performed to remove unstable correlations and dissimilarity results and retain the best results. The P values of correlation and dissimilarity were combined by Brown's method, respectively, and the edges that at least satisfy the correlation or dissimilarity greater than the set threshold and P less than 0.05 were retained to visualize the network and obtain the network structure graph and related information. Plots and data processing were performed using Excel 2016, CAD 2016, and Origin 2022b (Origin Lab Corp., Microsoft Corp., Redmond, MA, USA).

Results

Water–air intercropping enhances root morphology

Figure 3 shows the TIF diagram of the root system of each treatment. It can be seen that aerated irrigation has a significant impact on root morphology. The more developed the root system is, the higher the root density will be, the contact point between the root system and the soil will increase, which is conducive to the absorption of water and nutrients from the soil. Compared with the irrigation water amount of W_2, the number of lateral roots, root volume, root surface area, and root forks significantly increased. In addition, both irrigation and aeration rate had significant effects on the root morphology of pepper (Figs. 3 and 4). Treatment AW_1 increased root dry mass, root length, root volume, and root surface area by 12.23%, 11.60%, 21.22%, and 16.64%, respectively, compared with AW_2 ($P < 0.05$). Thus, moderate reduction in irrigation amount was of beneficial to root lengthening growth. The root dry weight of treatment AW_1 increased by 13.63% and 8.16% compared with CW_1 and OW_1, respectively, and that of treatment AW_2 increased by 10.16% and 8.17% in compared with CW_2 and OW_2, respectively ($P < 0.05$). Compared with CW_2, the root length of AW_2 and OW_2 treatment increased by 26.22% and 14.19%, respectively, while that of AW_1 treatment increased by 11.09% compared to OW_1 ($P < 0.05$), indicating that root growth does not increase all the time with the increase of aerated volume. The root volumes in treatments AW_1 and OW_1 significantly increased by 59.47% and 62.67% compared with CW_1, respectively. The surface area in treatment AW_1 significantly increased by 61.67% and 53.19% compared with CW_1 and OW_1, respectively. The root ratio in treatment AW_1 significantly reduced by 15.37% and 17.41% compared with CW_1 and OW_1, respectively ($P < 0.05$).

The interaction analysis (Fig. 4) showed that soil aeration had an extremely significant positive correlation ($P < 0.01$) with root dry mass, root volume, root surface area, and root ratio. Irrigation had an extremely significant positive correlation ($P < 0.01$) on root dry mass, root length, root volume and root ratio under the single factor. Under the interaction of two factors, soil aeration and irrigation had an extremely significant effect on root ratio ($P < 0.01$) and had a significant effect on root length ($P < 0.05$). The effect of the two factors on the root ratio was highly significant ($P < 0.01$) and had a significant effect on the root length and root volume ($P < 0.05$).

Correlation analysis between root morphology and yield

There were 10 pairs of significant or highly significant positive correlations and 5 pairs of highly significant negative correlations between pepper root morphological indicators and yield (Fig. 5). It can be seen that pepper yield showed highly significant positive correlations ($P < 0.01$) with root dry weight, root length, root surface area and root volume, and significant negative correlations ($P < 0.01$) with root ratio.

Fig. 3 TIF diagram of roots under different aerated treatments

(a) CW_1 (b) CW_2 (c) AW_1 (d) AW_2 (e) OW_1 (f) OW_2
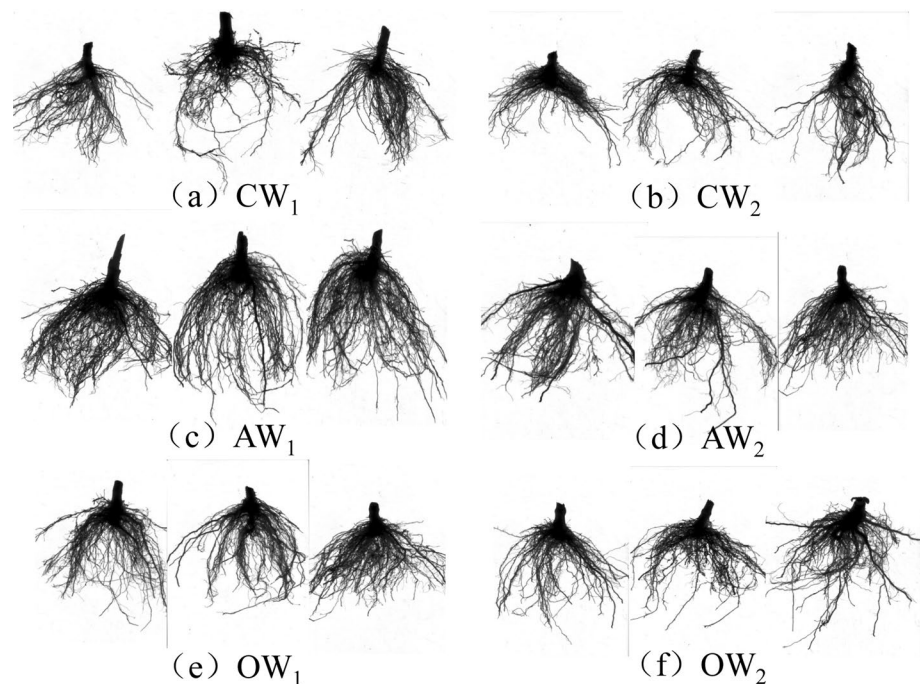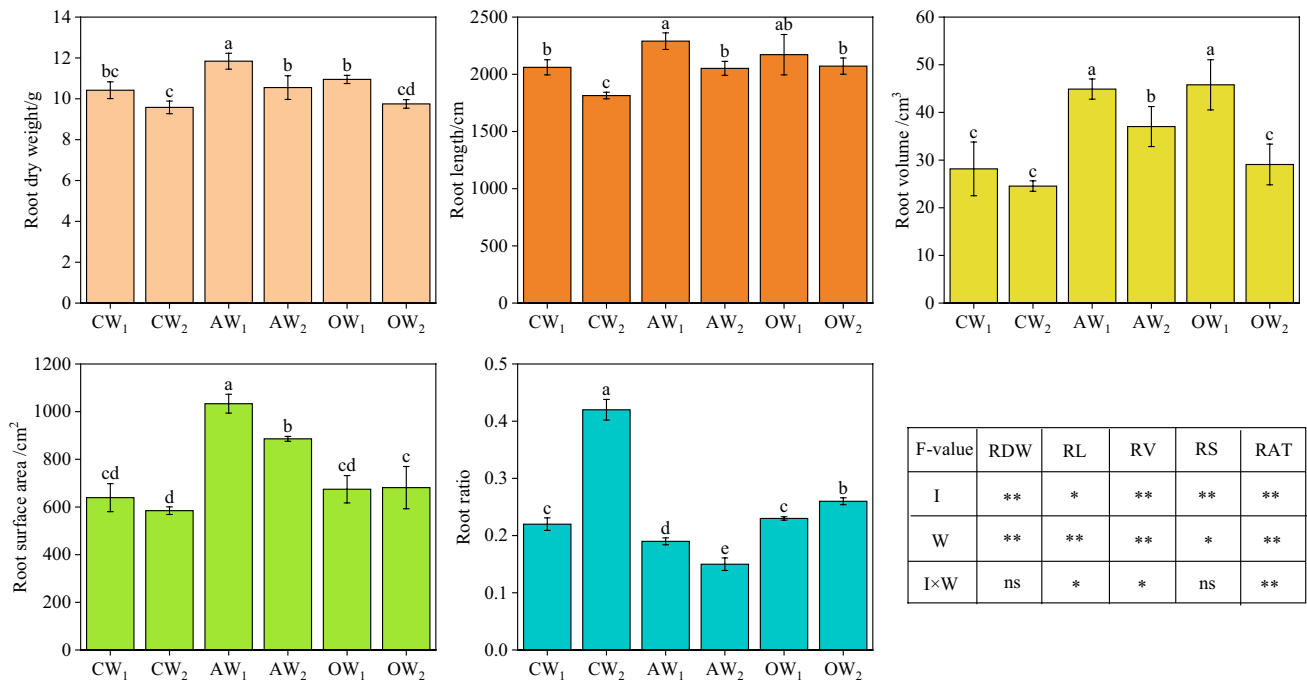
Fig. 4 Root indexes of different aerated irrigation treatments. I aeration rate, W irrigation amount, RDW root dry weight, RL root length, RV root volume, RS root surface area, RAT root ratio. Different lowercase letters after the data in the same column indicate significant differences at the $P < 0.05$ level (values are means $\pm$ SE, $n = 3$). * and ** indicate significant differences at the $P < 0.05$ and $P < 0.01$ levels, respectively

Fig. 5 Correlation analysis between root morphology and yield. RDW root dry weight, RL root length, RV root volume, RS root surface area, RAT root ratio. * and ** indicate significant differences at the $P < 0.05$ and $P < 0.01$ levels, respectively
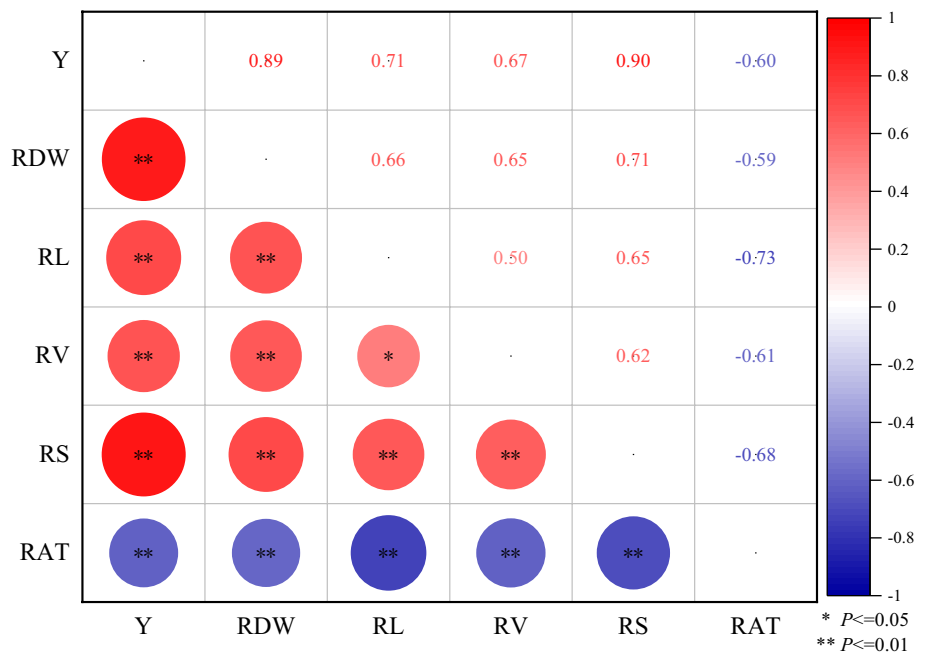
Water–air interactions affect the abundance of rhizosphere soil bacterial community structure

The relative species abundance of rhizosphere soil bacterial communities in pepper treated with different aeration and irrigation water amounts at phylum and genus levels is shown in Fig. 6. The dominant phylum (mean relative abundance > 5%) of the soil bacterial community was
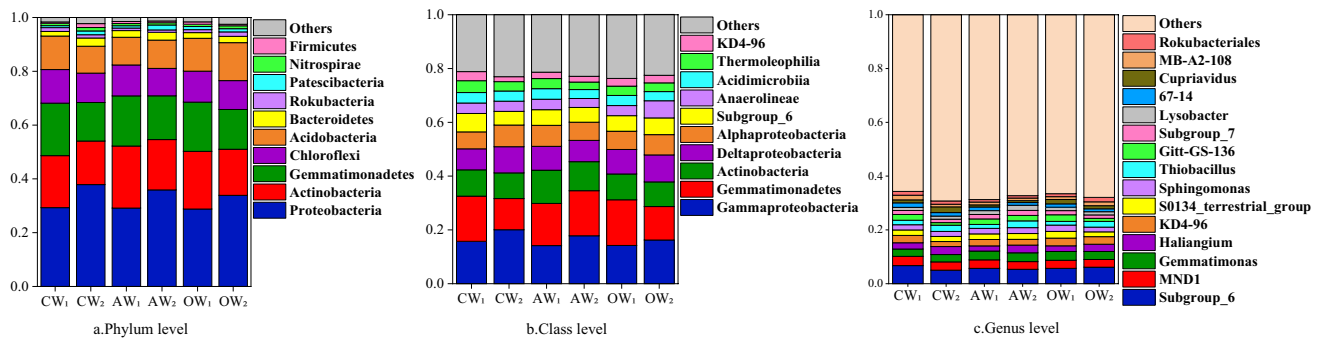
Fig. 6 Relative abundance of bacterial communities at the phylum, class and genus levels

Proteobacteria (mean 32.47%), Actinobacteria (mean 19.32%), Gemmatimonadetes (mean 16.98%), Chloroflexi (mean 11.23%), Acidobacteria (average 11.60%), accounting for 91.60% of the total number of species at the level of the total bacterial community phylum (Fig. 6a). The relative abundance of species at the bacterial community phylum level differed significantly among treatments with different aeration rate and irrigation amounts. Further analysis revealed that compared with W_1 level, W_2 treatment significantly increased the relative abundance of Proteobacteria, and CW_2, AW_2 and OW_2 treatments significantly increased it by 29.24%, 23.20% and 17.66% compared with CW_1, AW_1 and OW_1 treatments, respectively ($P < 0.05$). Compared with non-aeration irrigation, the relative abundance of Proteobacteria decreased significantly under aeration irrigation. The relative abundance of Actinobacteria under W_1 treatment was significantly higher than that under W_2 treatment and the relative abundance of CW_1, AW_1 and OW_1 treatments was increased by 19.21%, 23.33% and 25.03% ($P < 0.05$) compared with CW_2, AW_2 and OW_2 treatments, respectively. The relative abundance of Actinobacteria phylum significantly increased under aerated irrigation compared non-aeration irrigation ($P < 0.05$).

At the class level (Fig. 6b), the top five bacterial dominant groups in terms of relative abundance were Gammaproteobacteria (average 16.38%), Gemmatimonadetes (average 15.04%), Actinobacteria (average 10.21%) Deltaproteobacteria (average 8.91%) and Alphaproteobacteria (average 7.21%). The relative abundance of species at the bacterial community class level differed significantly between treatments of aeration and irrigation water. The relative abundance of Gammaproteobacteria in W_2 treatment was significantly increased compared with that in W_1 treatment, and that in CW_2, AW_2 and OW_2 treatment was significantly increased by 27.39%, 25.70% and 14.29% compared with CW_1, AW_1 and OW_1 treatment, respectively ($P < 0.05$). The relative abundance of Gammaproteobacteria in aeration irrigation treatment was significantly lower than that in non-aeration irrigation treatment. The relative abundance

of Gammaproteobacteria in CW_1 treatment was 11.11% and 10.83% higher than that in AW_1 and OW_1, and the relative abundance of Gammaproteobacteria in CW_2 treatment was 12.60% and 22.51% higher than that in AW_2 and OW_2, respectively. The relative abundance of Actinobacteria and Alphaproteobacteria in AW_1 treatment were significantly increased by 26.10% and 28.63%, 24.28% and 15.20% compared to treatments CW_1 and OW_1, respectively. Treatment CW_2 increased Anaerolineae by 13.35% and 11.50% in compared with treatment AW_2 and OW_2, respectively ($P < 0.05$).

The top 15 inter-rhizosphere soil bacterial genera were selected for taxonomic comparison (Fig. 6c). The dominant genera (relative abundance > 2%) in the community were Subgroup_6 (averagely 5.78%), MND1 (averagely 3.07%), Gemmatimonas (averagely 3.04%), Haliangium (averagely 2.48%), KD4-96 (averagely 2.46%), S0134_terrestrial_group (averagely 2.08%), Sphingomonas (averagely 2.03%). The amount of aeration and irrigation had significant effects on the relative abundance of inter-rhizosphere bacterial genus levels. Aerated irrigation in W_1 treatment significantly reduced the relative abundance of Subgroup_6, MND1, Haliangium and Thiobacillus, and significantly increased the relative abundance of Gemmatimonas and Sphingomonas. Aerated irrigation in W_2 treatment significantly reduced the relative abundance of MND1, Haliangium, and 67–14, and significantly increased the relative abundance of Subgroup_6 and KD4-96. Meanwhile, the relative abundance of Gemmatimonas, S0134_terrestrial_group, Sphingomonas, Thiobacillus, and Subgroup_7 increased first then decreased with the increase of aerated volume under the same amount of irrigation.

Water–air interactions affect the diversity of inter-root soil bacterial communities

The Pielou_e index, Chao1 index, Shannon index, and Simpson index were analyzed to assess the α-diversity of the inter-rhizosphere soil bacterial community under different aeration rates and irrigation amounts (Fig. 7). The Pielou_e

Fig. 7 Bacterial diversity index in rhizosphere soil. * and ** indicate significant differences at the $P < 0.05$ and $P < 0.01$ levels, respectively. Values are means $\pm$ SE, $n = 3$
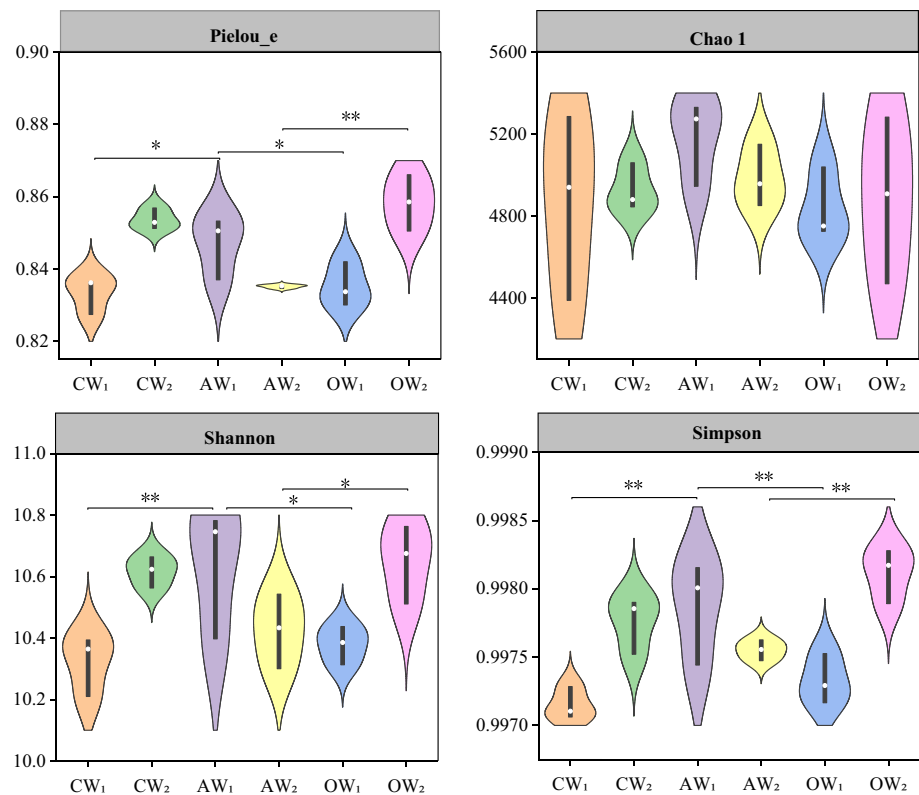
index (Fig. 7a), Shannon index (Fig. 7c) and Simpson index (Fig. 7d) of irrigation with aeration amount O (40 mg/L) and non-aeration C (5 mg/L), increased with the increase of irrigation volume. The Pielou_e index, Shannon index, and Simpson index decreased with the increase of irrigation water with aeration amount A (15 mg/L). Treatment AW_1 showed a significant increase in Pielou_e index, Shannon index and Simpson index compared with OW_1 and CW_1 treatments ($P < 0.05$). The results showed that the bacterial community diversity firstly increased and then decreased with the increase of aeration rate under low irrigation conditions, but firstly decreased and then increased with the increase of aeration rate under high irrigation conditions. The NMDS of bacterial community based on Bray–Curtis distance is shown in Fig. 8. There were highly significant differences in bacterial community composition between W_1 and W_2 treatments and aeration treatments, indicating that irrigation and aeration amounts significantly changed the community structure of soil bacteria (ANOSIM, $R = 0.9885$, $P = 0.001$).

## Redundancy analysis (RDA) of bacteria and roots

To investigate the relationship between root morphology and inter-root soil bacterial community, RDA was conducted to reveal the importance of the above root morphology and its effect on the inter-root bacterial community. The total

explanation of bacterial community on root morphology (Fig. 9) was 92.45%, and 77.95%, and 14.50% for RDA1 and RDA2, respectively. Among them, Nitrospirae ($P = 0.002$), Actinobacteria ($P = 0.006$), Bacteroidetes ($P = 0.016$), Patescibacteria ($P = 0.028$) and Firmicutes ($P = 0.05$) contributed significantly to the root morphological indexes, respectively. Actinobacteria showed a positive correlation with root length, root dry weight, root volume and root surface area, and AW_1 treatment had a higher correlation with Actinobacteria; Nitrospirae, Firmicutes and Patescibacteria showed a negative correlation with root length, root dry weight, root volume and root surface area, and CW_2 treatment revealed better correlation with Nitrospirae and Firmicutes, and Bacteroidetes had positive correlation with root surface area and negative correlation with root length, root dry weight, and root volume.

Water–air interactions enhance the complexity of bacterial symbiotic networks

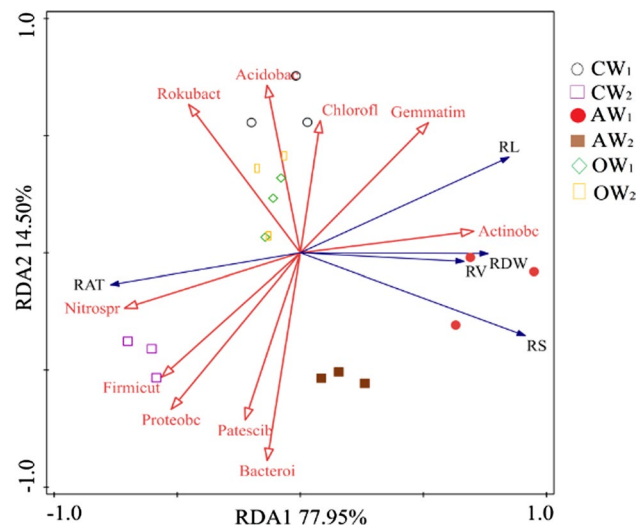To investigate the effects of different aerated rates and irrigation water volumes on the symbiotic form of soil microorganisms, we constructed a molecular ecological network of microorganisms based on a random matrix model (Fig. 10). To investigate the differences of microbial symbiotic networks under different aerated volume and irrigation volume, a total of six treatments were divided into five groups for comparison,

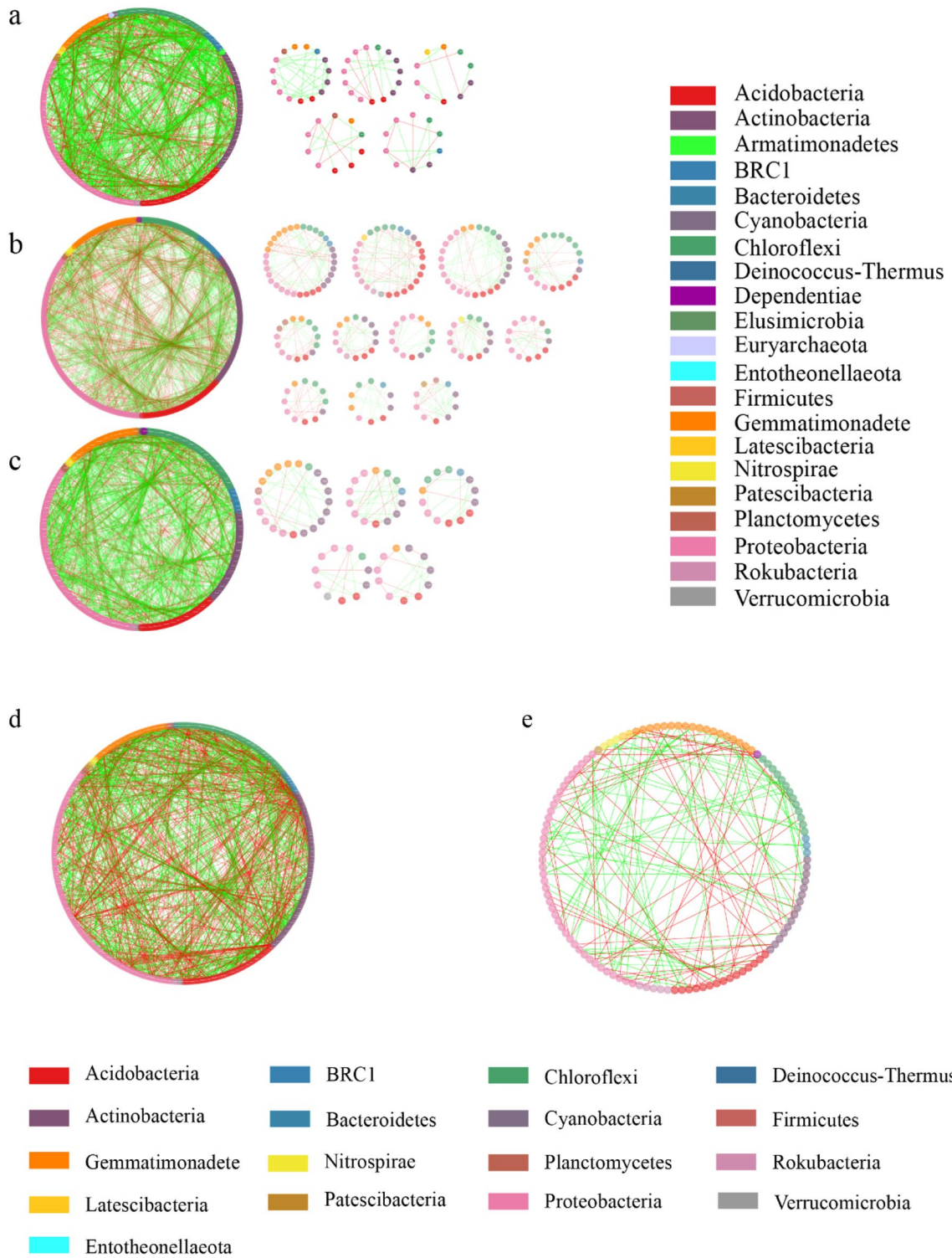**Fig. 8** NMDS of bacterial communities based on Bray–Curtis distance
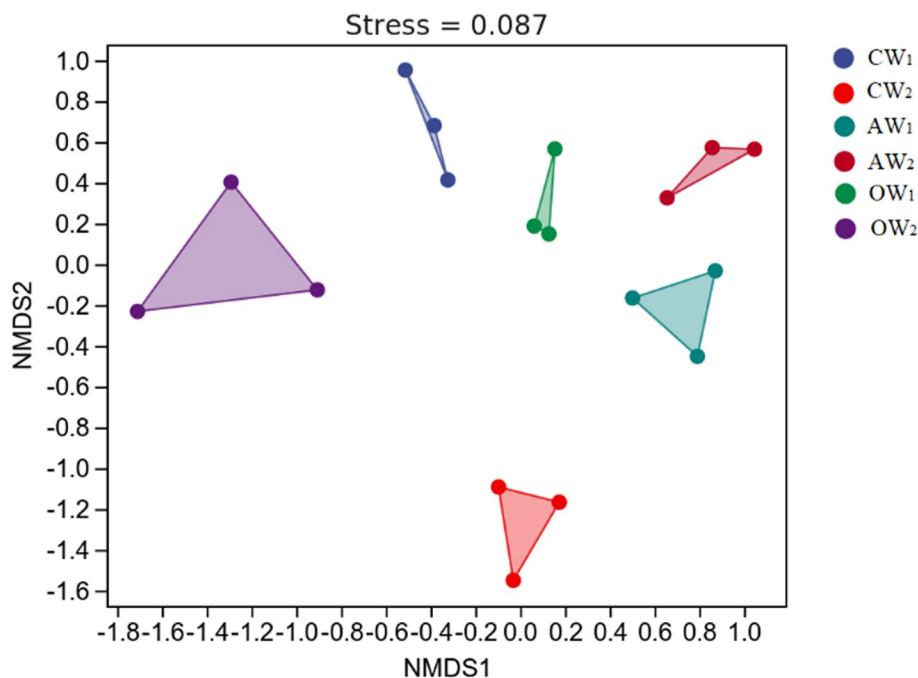
namely, non-aeration treatment C, aeration rate A (15 mg/L, dissolved oxygen mass concentration of irrigation water, hereafter) treatment, aeration rate O (40 mg/L) treatment, low water treatment W_1 and conventional irrigation treatment W_2. Table 3 shows the topological properties of the five networks constructed with 542, 673 and 582 nodes and 1561, 2376 and 1880 connections in treatments C, A and O, respectively. Treatment A had more bacterial network nodes and more complex interspecies relationships than C and O treatments. The number of subgroups with more than 10 nodes was screened

from pMENs, and the number of subgroups at the gate level in soils under treatments C, A and O were investigated, with 6, 13 and 6 subgroups, respectively, indicating that the symbiotic network structure of microbial networks was more complex under aerated irrigation. In treatments W_1 and W_2, there were 673 and 127 nodes, 1460 and 168 links, respectively. The number of bacterial network nodes in treatment W_1 was greater than that in treatment W_2, and the interspecies relationships were more complex. The number of nodes in the W_2 treatment was higher in the W_1 treatment. All five networks constructed in this study were dominated by negative correlations, indicating a strong competitive relationship between bacteria in each treatment.

As can be seen from Fig. 10, Proteobacteria is the dominant species in the five networks, and in contrast to the conventional subsurface drip irrigation, BRC1, Cyanobacteria, Elusimicrobia, and Euryarchaeota disappeared from the symbiotic network in treatment A, and one new phylum level species appeared: Dependentiae. In the O treatment symbiotic network, one new phylum-level species appeared: Entotheonellaeota. In the W_1 treatment symbiotic network, Entotheonellaeota disappeared and five new phylum-level species appeared: BRC1, Cyanobacteria, Deinococcus-Thermus, Firmicutes, and Planctomycetes.

Fig. 9 Redundancy analysis of root morphology and rhizosphere soil bacterial phylum. *RL* root length, *RS* root surface area, *RV* root volume, *RDW* root dry weight, *RAT* root ratio

Fig. 10 Phylogenetic molecular ecological networks (pMENs) of rhizosphere soil bacterial communities. **a** Non-aeration irrigation. **b** Aeration rate of 15 mg/L. **c** Aeration rate of 40 mg/L. **d** 0.8 Ep. **e** 1.0 Ep. The red line represents a positive relationship, and the green line represents a negative relationship

Table 3 Characteristic parameters of the molecular ecological network of soil microorganisms

Treatment	Number of nodes	Number of connections	Average connectivity	Average path length	Average aggregation coefficient
C	542	1561	6.158	7.592	0.411
A	673	2376	6.922	7.687	0.656
O	582	1880	6.990	8.204	0.471
W_1	673	1460	4.367	4.676	0.133
W_2	127	168	2.718	6.401	0.119

Discussion

Effect of water–air interactions on root morphology

The root system is a medium for nutrient transfer between the crop and the environment, and factors such as water, nutrients, and temperature in the soil can directly affect root growth and distribution, consequently affecting the growth and development of aboveground organs and morphological composition, and crop yield (Huang et al. 2019). In this study, compared with the non-aeration irrigation, aerated irrigation increased root morphology (except root ratio). The most significant effect of aerated irrigation was observed on the root surface area of pepper (Fig. 4). Root surface area increased by 61.67% ($P < 0.01$) compared to the non-aeration treatment, because adding oxygen in irrigation water improved soil aeration in the root zone, and alleviated hypoxic stress in the root zone (Wang et al. 2020), which resulted in increased root expansion and nutrient uptake (Sun et al. 2020). This method facilitated the transport of soil water and nutrient from the root zone to the aboveground part through the root system (Zhao et al. 2010; Ben-Noah and Friendman 2016), crop growth and increased fresh mass of above-ground plants, thus improving fruit yield, water use efficiency, and pepper quality. Previous studies also found that aeration improved the soil hypoxic environment in the root zone and increased crop root length, root vigor (Niu et al. 2012), root volume, and root tip numbers. The total root length and root surface area increased by 34.76–82.12% and 33.78–63.14%, respectively, compared with the non-aeration, and the increase in the number of forks and surface area increased the area of nutrient absorption in the soil (Li et al. 2020, a, b). As hypoxia induces a shift from normal respiration to anaerobic respiration, oxygen deprivation decreases the transport of oxidative phosphorylation electrons, reducing the production of adenosine triphosphate and reduced nicotinamide adenine dinucleotide phosphate NADP(H)$^+$ (Fukao and Bailey-Serres 2004). In general, hypoxia results in the arrest of aerobic respiration and quickly leads to energy deficiency in plants. It indicated that the aerated soil root zone provided more oxygen for aerobic root respiration, which increased the root length, the

surface area, and volume of the root system. The improvement in root growth indirectly affected the dry matter accumulation of the whole plant and improved crop yield and quality. This finding is consistent with previous studies (Botta et al. 2018).

Effect of water–air interactions on inter-root soil bacterial communities

The development of high-throughput sequencing technologies, especially 16S rRNA-based methods, has greatly improved the sensitivity and specificity of detecting different types of microorganisms (Xu et al. 2013; Knight et al. 2018). In this study, combined with high-throughput sequencing technology, it was concluded that aeration irrigation increased the relative abundance of rhizosphere bacterial dominance at the phylum, order and genus levels, and the relative abundance of Proteobacteria decreased with the increase of aeration volume. It has been found that Proteobacteria live in nutrient-rich environments, especially conditions with high net carbon mineralization rates (Yang et al. 2020). This study was conducted to sample and analyze the inter-root soil bacterial community at the end of crop fertility in pepper, and aerated irrigation provided a long-term high oxygen environment to the soil in the root zone throughout the growth stage. The soil environment around the root zone was well improved to accelerate nutrient cycling, and nutrients in the soil that are easily decomposed were either used by plants or lost in irrigation, resulting in a general reduction in the availability of nutrient substrates and limiting the growth of Proteobacteria. Thus, aerated irrigation significantly reduced the abundance of Proteobacteria in soil at the end of pepper fertility, which was consistent with the results obtained by Zhu et al. (2022), Zhou et al. (2022) and Sibanc et al. (2014). Phylum Firmicutes is a typical coprotrophic bacterium that converts cellulose and hemicellulose into smaller polysaccharides (Li et al. 2020) and produces budding spores against external harmful factors, making it extremely resistant (Dai et al. 2019). At the class level, aerated treatment significantly reduced the relative abundance of Gammaproteobacteria, and the increase in relative abundance may be related to the increased the supply of unstable

C substrates in the soil (Dai et al. 2019). Gammaproteobacteria contain a variety of plant pathogens (Eilers et al. 2010), so aerated irrigation reduced the relative abundance of Gammaproteobacteria, suppressed disease, and enhanced soil health. Meanwhile, aerated irrigation significantly increased the relative abundance of Nitrospirae, which has been shown to oxidize nitrite in the soil to nitrate and participate in soil nitrogen cycle (Gao et al. 2019). The results revealed that aerated irrigation could change the soil bacterial community alpha diversity and beta diversity. The results of PCoA analysis based on Bray–Curtis distance showed that there were significant differences in bacterial community diversity and structure between aerated irrigation treatment and control treatment.

Relationship between root morphology and the role of inter-root soil bacterial communities under aerated irrigation

The soil environment is a complex ecosystem, especially the root zone "soil environment-crop root system-microorganisms and enzymes" constitutes a closely linked dynamic system that interacts with each other (Santos et al. 2016). Different root growth had different effects on soil microstructure, soil nutrient transport distribution, soil microbial growth (Huan 2012), and soil enzymes (Garcia-Gil et al. 2000), which influence crop root growth and soil nutrient uptake and utilization. Most of the relationships between root characteristics and root influencing factors were positive. These results are in agreement with the findings of Khumoetsile and Dani (2000), concluding that interactions between plant roots, soil bacteria, and soil properties regulate plant performance by promoting or inhibiting soil-borne pathogens, soil organic matter decomposition, nutrient cycling and utilization. Studies have shown that actinomycetes have the ability to biocontrol various plant pathogens through various mechanisms (Hong-Thao et al. 2016). Actinomycetes are relatively abundant in the rhizosphere of healthy peppers, where they are known to inhibit the growth of several plant pathogens in the rhizosphere and produce extracellular enzymes that promote crop production and immunity by breaking down the complex mixture in the soil (Kong et al. 2022). In our study, an aeration rate of 15 mg/L showed a higher correlation with Actinobacteria. The vast majority of the Actinobacteria phylum were aerobic bacteria that promote the synthesis of crop growth factors and secrete antibiotics that promote crop growth and antagonize crop diseases. To better reveal the interactions of soil bacteria, this study used a molecular ecological network approach to determine the structure and function of soil microbial communities and assessed the differences in inter-root soil ecosystem function for water–air interactions. In the soil ecosystem, microorganisms coexist and interact

with each other in complex network structures (Chen et al. 2021). Highly associated microorganisms in modules may have similar ecological characteristics within the community (Kladivko 2001). In molecular ecological networks, the number of nodes, connections and average connectivities were used to indicate the size and complexity of the network, with higher average connectivity indicating the more complex relationship between network nodes (Li et al. 2020). The results of the symbiotic network in this experiment showed that the number of nodes was higher at the aeration rate of A (15 mg/L) and irrigation volume of W_1 (0.8 times the crop-evaporation dish coefficient), which had more similar ecological networks among species in the network (Banerjee et al. 2016), indicating that the inter-rhizosphere soil bacterial network was larger and the relationships among species were more complex in the low water volume treatment of aerated irrigation. A new phylum-level species, Dependentiae, emerged from the symbiotic network of treatment A. Dependentiae were found to be significantly associated with metabolites mainly related to linoleic acid metabolism (Li et al. 2022). Under high dissolved oxygen conditions, the connectivity, centrality and complexity of microbial network nodes increased significantly, indicating a decrease in the stability of the microbial network (Abbas et al. 2019). Microbial community structure and diversity were significantly altered by oxygen levels (Biggs-Weber et al. 2020). Adjusting the oxygen content of microhabitats using aerated subsurface drip irrigation (ASDI) induced changes in the taxonomic composition, network and function of soil microbial communities, thus affecting soil carbon and phosphorus. It could be inferred that when the external environment was disturbed, the aerated irrigation network might slow down the transmission of disturbances and keep its structure stable. A stable bacterial network could improve the diversity of bacterial communities involved in soil nutrient cycling (Hu et al. 2018), so that aerated irrigation had a more organized and diverse ecological functional group than conventional subsurface drip irrigated soils, enhancing the ability of soil microorganisms to utilize nutrients, improving the microscopic environment of arable land. Improved ecology and effective root growth increased facility crop yields. In this study, it was found that aerated irrigation inhibited inter-root bacterial community function and the enhancement of effective nutrient content under high dissolved oxygen values, thus increasing the yield.

Conclusion

Aerated irrigation significantly increased the root dry mass, root volume, and root surface area of pepper. When the optimal treatment was 15 mg/L of aeration rate and 0.8 times the crop-evaporation coefficient, the root dry mass, root

volume, and root surface area increased by 13.63%, 59.47%, and 61.67%, respectively, compared with CW_1 treatment ($P < 0.05$). The Pielou_e index, Shannon index, and Simpson index decreased with the increase of irrigation amount at the aeration rate of 15 mg/L. The NMDS analysis showed significant differences between different aerated rates and irrigation volumes. Redundancy analysis revealed that the contribution of Nitrospirae, Actinobacteria, Bacteroidetes, Patescibacteria and Firmicutes to the root morphological indexes was highly significant, with the highest correlation between AW_1 treatment and Actinobacteria. Actinobacteria showed a significant positive correlation with root length, root dry weight, root volume, and root surface area. According to the symbiotic network analysis, we found that there was an increase in the number of nodes between bacterial community species, in the complexity between species, and in the beneficial bacterial phylum under an aeration rate of 15 mg/L and 0.8 Ep.

Author contribution statement CJ: performed the data analyses and wrote the manuscript; HL: helped perform the analysis with constructive discussions; ZX and JC: contributed significantly to the analysis and manuscript preparation; PH: contributed to the conception of the study; SJL: revised the manuscript and polished the language. All authors reviewed and approved the final manuscript.

Data availability The data reported in this study are contained within the article.

Declarations

Conflict of interest None. All authors have approved the manuscript. I declare on behalf of all authors that the work described is original research that has not been published previously and is not under consideration for publication elsewhere, in whole or in part.

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