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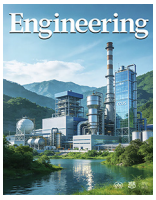

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Reducing Soil Moisture Fluctuations Significantly Improves Crop Yield and Quality: Insight into Multiomics in Soil–Plant Systems

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ABSTRACT

Agricultural water scarcity is increasingly conflicting with demands for both crop yield and crop nutritional quality, yet current irrigation strategies are failing to achieve synergistic improvements. This study explores how reducing soil moisture fluctuations (SMFs) affects crop yield and quality, using tomato plants under three irrigation treatments: fast wetting (FW), medium wetting (MW), and slow wetting (SW). We analyzed soil moisture dynamics, yield, fruit quality, soil bacteria, and plant molecular responses. Slowing the wetting process significantly improved tomato yield by 10%–20% and increased vitamin C and lycopene content by 10%–17% and 7%–29%, respectively, while reducing the irrigation quota by 30%–35%. The results showed a significant increase in the relative abundance of Myxococcota and Chloroflexi, while the relative abundance of Actinobacteria significantly decreased. Functional prediction showed that the abundance of aerobic chemotrophic heterotrophy was suppressed, whereas nitrate reduction was promoted. Based on a joint analysis of transcriptomics and metabolomics, several genes encoding key enzymes (*GME*, *DHAR*, *IDH1*, *crtB*, and *crtH*) in the pathways of ascorbic acid, lycopene, and organic acid cycles were significantly affected. Structural equation modeling (SEM) revealed that the stabilized soil moisture directly increased microbial community diversity and soil fertility, which subsequently activated transcriptional pathways associated with nutrient assimilation and antioxidant biosynthesis. This cascade of biological responses ultimately mediated improvements in crop productivity and quality. These findings challenge the conventional understanding of wet-dry cycles in irrigation. Reducing SMFs offers a practical approach to simultaneously improving water-use efficiency, crop yield, and fruit quality, with potential applications in sustainable agriculture.

1. Introduction

Global population growth is expected to increase the demand for agricultural products by 70% by 2050 [1]. Simultaneously, the growing need for nutritional and healthy foods has stimulated the public's demand for high-quality crop products [2]. Nevertheless, industrial and urban expansion will result in a further estimated reduction of 25%–40% in agricultural water usage [3], which will exacerbate the ongoing conflict between agricultural water scarcity and the pursuit of food security and quality [4]. Agriculture is already responsible for 70% of all water withdrawn from aquifers, streams, and lakes. Achieving the synergistic goals of water conservation, yield increase, and quality improvement has become a critical global challenge that urgently needs to be addressed for sustainable human development.

In recent years, regulated deficit irrigation (RDI) techniques that reduce water usage without compromising production have been rapidly developed. However, under current intensive water-management practices, drastic water fluctuations can disrupt the stability of rhizosphere microbial communities, impairing their functional activity in organic matter (OM) mineralization and

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nitrogen–phosphorus transformation [5]. Meanwhile, repeated drying-rewetting cycles may activate plant stress signaling pathways, triggering a metabolic reallocation of resources from growth-related genes to stress-responsive genes [6]. Furthermore, root perception of intermittent water deficits may induce long-term suppression of key fruit-development pathways through epigenetic regulation [7]. Therefore, there is still a need for an irrigation strategy that is both cost-effective and capable of synergistically achieving water conservation, yield improvement, and quality enhancement. Notably, spatiotemporal regulation of irrigation parameters may offer a breakthrough to this dilemma. Studies have indicated that regulating the frequency of soil moisture alterations and water content through diverse irrigation techniques can exert a significant influence on crop yield or quality improvement [8,9]. Under a constant total irrigation volume, increasing the drip irrigation frequency can significantly increase biomass and yield in crops such as cotton by maintaining soil moisture stability [10,11]. However, excessive high-frequency drying-wetting cycles may conversely suppress root development [12]. Maintaining a constant volumetric water content would appear to be a more suitable irrigation strategy for the production of high-quality crops than using fluctuating irrigation [13]. These findings suggest that precisely regulating the dynamic combination of irrigation frequency and flow rate may achieve the synergistic effects of water conservation, yield increase, and quality improvement. However, existing studies have predominantly focused on isolated analyses of single parameters or single systems, and no systematic investigation of the coupling mechanisms among water fluctuation patterns, rhizosphere microenvironments, and plant transcriptional metabolics has been carried out.

Based on previous research, we hypothesized that slowing the wetting process and reducing soil moisture fluctuations (SMFs) would create an optimal environment for microbial colonization, promoting greater diversity and functionality. This would improve soil fertility, which enhances plant transcription and metabolism related to nutrient uptake, ultimately boosting fruit yield and quality—the main goals of this study. To test this hypothesis, we used microbial 16S ribosomal RNA (rRNA) amplicon sequencing, fruit RNA sequencing (RNA-seq) transcriptomics, and untargeted metabolomics to determine the effects of different wetting processes on ① soil water distribution characteristics and fruit yield and quality; ② the soil microbiome and soil fertility; and ③ crop quality-related transcription and metabolic pathways. Finally, we carried out an integrated multiomics analysis to explore the mechanisms by which soil wetting processes influence crop yield and quality (Fig. 1). This research could increase global food security and promote sustainable agriculture by providing an innovative irrigation strategy that improves crop yields and quality while conserving water.

2. Materials and methods

2.1. Experimental design and treatment

In this study, the variety of tomato used was *Solanum lycopersicum* L., cultivar Zhefen 702 (Vegetable Research Institute of Zhejiang Academy of Agricultural Sciences, China). Tomato seedlings were transplanted in the spring and autumn in greenhouses at the Tongzhou Experimental Station of China Agricultural University (39°36′–40°02′N, E116°32′–116°56′) from March 2021 to July

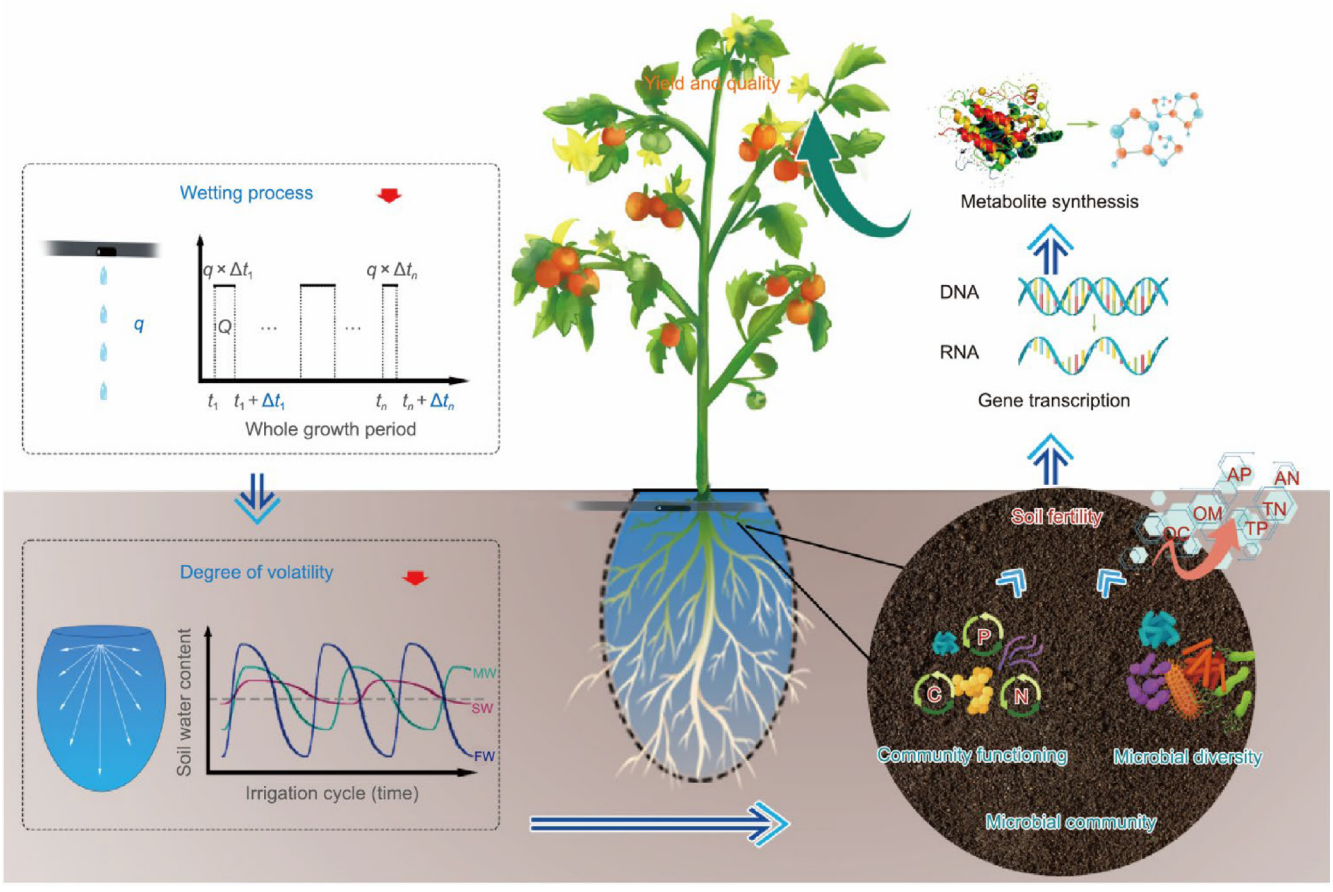

Fig. 1. Experimental design and scientific hypothesis. Q represents the total volume of water irrigated during each irrigation event, *q* is the amount of water irrigated per unit time, and Δ*t* is the duration of each irrigation event. OC: organic carbon; TP: total phosphorus; TN: total nitrogen; AP: available phosphorus; AN: available nitrogen.

2021 and from July 2021 to November 2021, respectively. The climatic conditions of the experimental site, along with basic soil fertility information, are provided in Table S1 in Appendix A.

We controlled the upper and lower irrigation limits based on different wetting processes and set up three treatments—namely, a fast wetting (FW) process, medium wetting (MW) process, and slow wetting (SW) process—using furrow, drip, and micro-wetting irrigation systems (Fig. S1 in Appendix A). To accurately control the wetting processes and enable the imposition of different irrigation strategies, automated irrigation systems based on solenoid valves and intelligent soil moisture sensors (Insentek Co., Ltd., China) were used. The amount of irrigation per time was calculated as follows:

$$Q = (\theta_2 - \theta_1) \times H \times R \times S$$

where Q is the total volume of water irrigated during each irrigation event (m^3); θ_2 and θ_1 are the maximum soil water content and measured soil water content, respectively; H is the depth of the planned wet soil layer (0.2, 0.3, and 0.4 m in seedling, flowering and fruiting, and expansion and maturity, respectively [14]) (Table S2 in Appendix A); R is the soil wetting ratio, which refers to the volume ratio of the wetted soil to the total soil within the planned wetting layer; and S is the area of the plot (10.5 m^2). We controlled for the same planned depth of the wetting front and the same irrigation limits across all treatments, thereby ensuring that there were no significant differences in the volume of the wetted soil bodies and the average water content within the wetted soil bodies among the treatments (Fig. S2 in Appendix A).

Differences in irrigation intensity per unit of wetted volume across a body of soil are defined as the wetting process, which characterizes the spatial and temporal variation in water content within the wetted volume of soil under irrigation. The wetting process can be quantified by the average quantity per time-volume (AQTV), measured in $m^3 \cdot m^{-3} \cdot h^{-1}$. Lower AQTV values correspond to a gentler wetting process, with less spatial heterogeneity in soil moisture distribution. The wetting process is calculated as follows:

$$\mathrm{AQTV} = \frac{Q}{V \times \Delta T}$$

where V is the volume of wetted soil (m^3), and ΔT is the duration of irrigation (h).

2.2. Fruit and soil sampling

Sampling and analysis of the fruit were carried out after the tomatoes had changed color and ripened. The total mass of all fruits from the first harvest to the end was taken as the total yield of tomatoes, which was converted using the area control method. Tomato fruit samples were collected during the peak fruiting period for quality assessment and transcriptomic and metabolomic testing. Eighteen tomatoes were randomly harvested from each treatment group and divided into six replicates, with three tomatoes per replicate. The sliced tomato fruit samples were divided into two portions. One portion was frozen at −20 °C for quality indicator analysis. Ascorbic acid, lycopene, and organic acids—key indicators of interest in this study—were determined using the 2,6-dichloroindophenol titration method (GB6195-86), ultraviolet (UV)-visible spectrophotometry, and sodium hydroxide titration, respectively. The other portion of the fruit samples was rapidly frozen in liquid nitrogen for 5 min and stored at −80 °C for subsequent transcriptomic and metabolomic analyses.

At the end of the experiment, six healthy plants were randomly selected from each treatment. The entire root systems of the plants were carefully excavated. The collected root samples were then sorted, labeled, placed into sterile sampling bags, and stored in sealed containers. The sterile sampling bags were immediately placed in a refrigerated biological sampling box and transported to the laboratory at approximately 0 °C for rhizosphere soil collection. The collected rhizosphere soil was divided into two portions. One portion was used for soil fertility indicators, including total nitrogen (TN) and total phosphorus (TP), which were determined by means of the Kjeldahl digestion method and the alkali fusion molybdenum-antimony (Mo-Sb) anti-spectrophotometric method, respectively. Available nitrogen (AN) and available phosphorus (AP) were determined using the alkaline diffusion method and the sodium bicarbonate extraction/Mo-Sb anti-spectrophotometric method. OM and organic carbon (OC) were determined using the potassium dichromate volumetric method and the potassium dichromate oxidation-spectrophotometric method, respectively. The other portion of the soil samples was rapidly frozen with liquid nitrogen and stored in an ultra-low-temperature freezer (−80 °C) for subsequent 16S rRNA high-throughput sequencing and analysis.

2.3. 16S rRNA amplicon sequencing

Microbial DNA was extracted from the rhizosphere soil using the E.Z.N.A. soil kit (Omega Bio-tek; Norcross, USA). The concentration and purity of the DNA were estimated using 1% agarose gel electrophoresis. The extracted DNA was diluted to 1 $ng \cdot \mu L^{-1}$ using sterile nuclease-free water. Using the diluted genomic DNA as a template, polymerase chain reaction (PCR) amplification of the V3–V4 variable region of the 16S rRNA gene was performed using specific primers. The PCR products were visualized using 2% agarose gel electrophoresis and then purified electrophoretically using 1×Tris–acetate–(ethylenediaminetetraacetic acid) EDTA buffer (TAE) and a 2% agarose gel after mixing equal amounts according to the concentration of PCR products. Finally, the 16S rRNA library was constructed using the Ion Plus Fragment Library Kit 48 reactions (Thermo Fisher Scientific, USA), and the PCR products were sequenced on the IonS5TMXL platform.

2.4. RNA isolation, library construction, and quality control (QC)

The total RNA was extracted using TRIzol (Invitrogen, USA), and the genomic DNA was removed using DNase I (TaKara, China). RNA quality was assessed using a 2100 Bioanalyzer (Agilent, USA) and ND-2000 spectrophotometer (NanoDrop Technologies, USA) to ensure suitability for transcriptome sequencing. RNA libraries were prepared with the TruSeqTM RNA Sample Preparation Kit (Illumina, USA). After complementary DNA (cDNA) synthesis, End Repair Mix was added to create blunt ends, followed by the addition of an adenine base at the 3' end. PCR enrichment was performed, and DNAclean beads were used to select 200–300 bp fragments. After quantification using a TBS380 Mini-Fluorometer and PicoGreen reagent (USA), the library underwent high-throughput sequencing on an Illumina HiSeq X Ten/NovaSeq 6000 platform (USA) with a paired-end 150 bp (PE150) read length.

Data QC was performed using FASTP software to analyze base distribution, error rates, and quality for each sample (Table S3 in Appendix A). The sequencing quality was assessed with Q20 > 97% and Q30 > 92% for each sample (Table S4 in Appendix A), ensuring high-quality data for further analysis.

2.5. Metabolite extraction and analysis

A 50-mg solid sample of fruit was placed in a 2 mL centrifuge tube, and a grinding bead with a diameter of 6 mm was added. Extraction solution (400 μL of a 4:1 v/v solution of methanol: water) containing 0.02 $mg \cdot mL^{-1}$ of internal standard (*L*-2-chlorophenylalanine) was used for metabolite extraction. The sample solution was ground in a frozen tissue mill for 6 min

(−10 °C, 50 Hz), followed by low-temperature sonication extraction for 30 min (5 °C, 40 kHz). The samples were left at −20 °C for 30 min and then centrifuged for 15 min (4 °C, 13000*g*); next, the supernatant was transferred to an injection vial with an internal cannula for liquid chromatography-mass spectrometry (LC-MS) analysis using a Thermo Fisher UHPLC-Q Exactive HF-X systemt (USA). A 2 μL sample was separated using an HSS T3 column (100 mm × 2.1 mm internal diameter (i.d)., 1.8 μm) and analyzed by mass spectrometry. Mobile phase A was 95% water + 5% acetonitrile (with 0.1% formic acid), and mobile phase B was 47.5% acetonitrile + 47.5% isopropanol + 5% water (with 0.1% formic acid). The separation gradient ranged from 0 to 100% B, with varying flow rates from 0.4 to 0.6 mL·min^{-1}. The column temperature was 40 °C. Mass spectrometry was conducted in positive and negative ion-scanning mode (m/z 70–1050) with ion-spray voltages of 3500 V (positive) and 2800 V (negative), sheath gas at 40 psi (≈276 kPa), and ion source heating at 400 °C. The Mass Spectrometry (MS)1 resolution was 70 000 and the MS2 resolution was 17 500, with a collision energy of 20–40–60 V cycles. Equal volumes of metabolites from all samples were mixed and prepared for QC samples.

Information on mass spectra and metabolites was obtained from public databases, including the Human Metabolome Database (HMDB) and METabolite and TAndem MS Database (METLIN), and MajorBio was used to create a self-built database with metabolite information. After searching the library, the data matrix was uploaded to MajorBio's BioCloud platform for analysis. First, the data matrix was pre-processed by removing missing values and applying the 80/20 rule to retain more than 80% of the non-zero values within at least one set of variables. We then filled in the vacant values (using the smallest value in the original matrix). To reduce errors from sample preparation and instrument instability, we used sum normalization to adjust the mass spectrometry peak intensities and create a normalized data matrix. Variables in the QC samples for which the relative standard deviation (RSD) was > 30% were also removed. We applied a logarithm with a base of 10 to obtain the final data matrix for subsequent analyses.

2.6. Statistical analysis

Microbial community analysis was conducted on the MajorBio Cloud Platform with the following workflow: Raw sequences were processed in mothur v1.48.0 to calculate alpha diversity indices (Sobs and Shannon indices), followed by an analysis of variance (ANOVA) to assess inter-group differences (Tukey's honestly significant difference, $\alpha = 0.05$). Beta diversity was evaluated via principal coordinate analysis (PCoA) based on the Bray–Curtis dissimilarity using the vegan package (v2.6-4) in R (v4.3.1), with the statistical significance of community structure differences determined by PERMANOVA (999 permutations, $p < 0.05$). Differentially abundant bacterial taxa (phylum to genus) were identified using LEfSe with a linear discriminant analysis (LDA) score threshold > 3.5 and $p < 0.05$. The results were visualized via the ggplot2 package (v3.4.4). Co-occurrence networks were constructed from species showing strong correlations (|Spearman's r| > 0.6, $p < 0.05$) using the igraph package (v1.5.1), with node centrality metrics calculated and layouts optimized via the ggraph package (v2.1.0). Functional profiling via Functional Annotation of Prokaryotic Taxa (FAPROTAX) was plotted using the pheatmap package (v1.0.12) for heatmap visualization. All figures were generated and refined entirely within the R environment, and images were stitched and beautified using Adobe Illustrator 2019 (Adobe, USA).

The clean transcriptomic data for all samples exceeded 6.15 Gb, which was in accordance with the reference genome. Differential gene expression analysis was performed using Deseq2 with a threshold of $p < 0.05$ and a fold change of 1.8. Gene function enrichment was conducted using Goatools (GO) and the Kyoto Encyclopedia of Genes and Genomes (KEGG) Orthology-Based Annotation System (KOBAS), with the significance set at p.adjust < 0.05. The metabolomic data underwent pre-processing, including filtering, imputation, normalization, and logarithmic transformation. Significant differential metabolites were selected based on variable importance in projection (VIP) >1 and $p < 0.05$ from the Orthogonal Projections to Latent Structures Discriminant Analysis (OPLS-DA) model. Differential metabolite analysis was performed with ropls (R packages) and pathway enrichment was done using KEGG Compound software and scipy (Python). Pathways with corrected p values < 0.05 were considered significantly enriched. Correlations between the different treatments for the transcriptome, metabolome, wetting process, and soil fertility were determined using a Pearson analysis. Structural equation modeling (SEM) was performed using AMOS v22.0 (IBM, USA) to evaluate the direct and indirect pathways of the wetting processes, microbial communities, soil fertility, and transcriptional regulation of metabolic pathways involved in improving production and quality.

3. Results

3.1. Characteristics of soil water content in different wetting processes and effects on tomato yield and quality

The effects of the different wetting processes on crop yield, crop quality, soil water content, and SMFs are shown in Fig. 2. Significant improvements in crop yield and quality were observed for the two planting trials, owing to the different wetting processes (Fig. 2(a)). Under the MW and SW treatments, spring tomato yields increased by 10.44% and 20.68% and autumn yields by 14.16% and 20.35%, respectively, compared with FW. Vitamin C content rose by 13.46% and 17.74% in spring and by 10.01% and 14.93% in autumn. Organic acid content in spring decreased by 22.09% and 29.74%, and that in autumn decreased by 8.58% and 15.57%. Lycopene content increased by 7.15% and 21.22% in spring and by 18.34% and 29.17% in autumn under the MW and SW treatments, respectively, compared with FW.

As shown in Fig. 2(b), slowing down the wetting process resulted in a more even vertical spatial distribution of the average water content of the soil. It reduced the SMFs by 12.82% for MW and 23.17% for SW compared with FW, while conserving the average water content. The Pearson correlation analysis showed that the AQTV (Fig. 2(c)) and SMFs were negatively correlated with crop yield, vitamin C, and lycopene content but positively correlated with organic acid content (Fig. 2(d)).

3.2. Effects of different wetting methods on the microbial community and soil fertility

The 16S rRNA sequencing results showed that the wetting process had a significant effect on the bacterial community in the tomato rhizosphere (Fig. 3). The bacterial community exhibited an increase in alpha diversity as the wetting process gradually slowed, as measured by the Sobs and Shannon indices (Fig. 3(a)). The PCoA grouping showed that the SMFs shaped by different wetting processes caused significant differences in the composition of soil bacteria (Fig. 3(b)). In terms of bacterial phyla, the relative abundance of Myxococcota and Chloroflexi significantly increased, and that of Actinobacteria significantly decreased as the wetting process slowed (Fig. 3(c)). Inter-group significance tests showed that *Streptomyces* was the most abundant genus in all treatments and had the biggest decrease in relative abundance when the wetting process was slowed (Fig. 3(d)). Concurrently, interactions between environmental factors and microbial species in the samples were

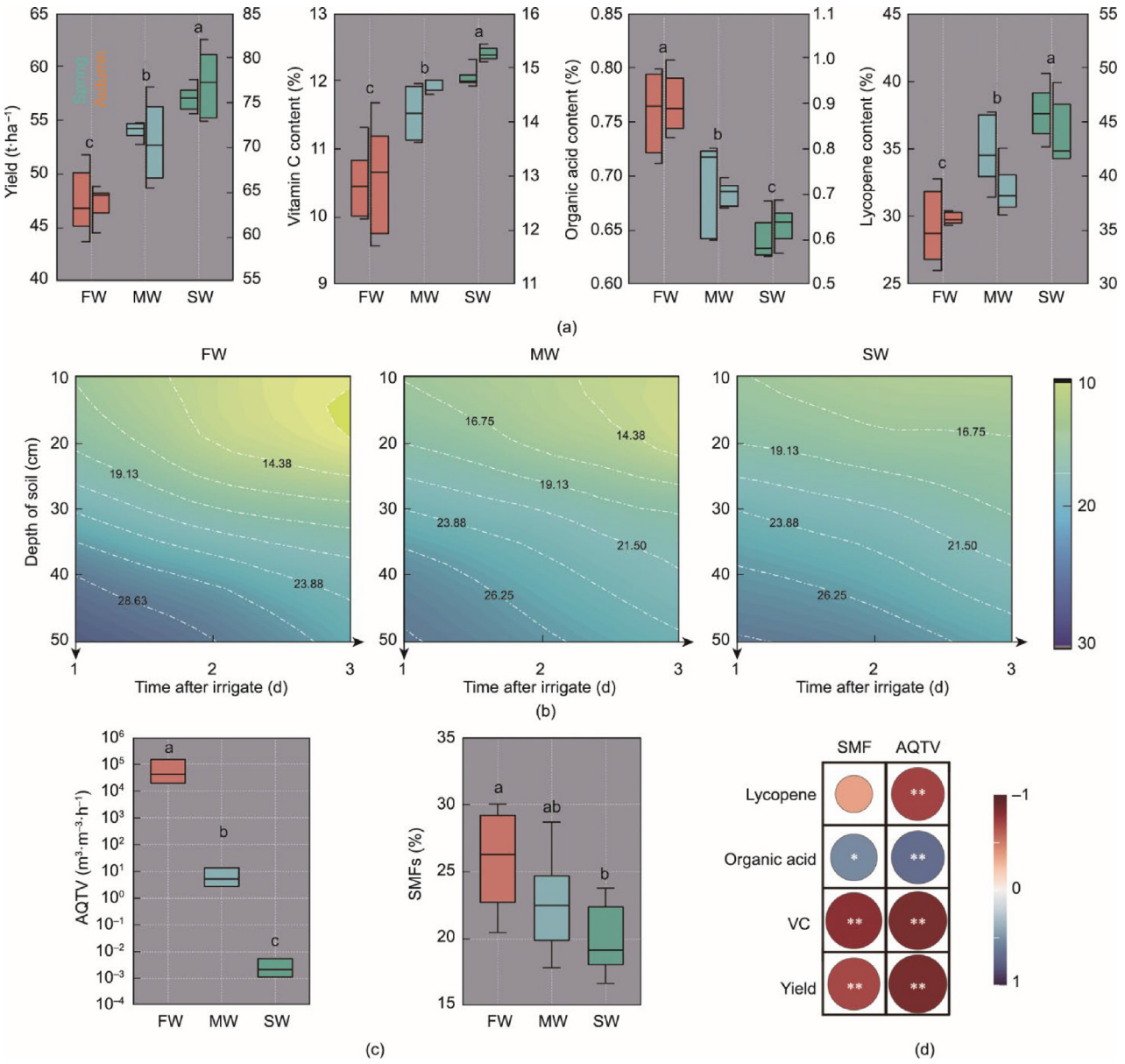

Fig. 2. Effects of different wetting speeds on soil water characteristics and tomato yield and quality. (a) Crop yield and quality under three different treatment conditions. Values are means of six biological replicates ± standard error (SE). (b) Changes in soil moisture content 1–3 d after irrigation under different wetting speeds. Different colors represent soil moisture content (%). (c) AQTV and SMFs under different wetting speeds. Values are means of six biological replicates ± SE. (d) Correlation analysis of the relationships between yield, quality, AQTV and SMF. Red indicates a negative correlation and blue indicates a positive correlation. The darker the color, the stronger the correlation, and vice versa. The size of the circle indicates the degree of correlation. $^{*}p < 0.05$; $^{**}p < 0.01$. Different lowercase letters in (a, c) represent significant differences between respective treatments by ANOVA ($p < 0.05$).

determined using a two-factor covariance network analysis (Fig. 3(d); Table S5 in Appendix A). The findings indicated that 63% of the differentiated genera were associated with SMFs, with the relative abundance of the majority of these genera exhibiting a notable negative correlation with SMFs. Conversely, only 37% of the differentiated genera were linked to water content, and the relative abundance of the majority of these genera demonstrated an increase with the average water content. In particular, the increase in abundance of *Gemmatimonas* was significantly correlated with both a decrease in SMFs and an increase in mean water content. FAPROTAX was used to predict ecologically relevant functions on the basis of differential genera (Fig. 3(f)). As the wetting process slowed, changes in differential genera led to a notable decrease in chemoheterotrophy and aerobic chemoheterotrophy, while significantly increasing nitrate reduction, nitrite respiration, nitrate respiration, and aromatic compound degradation (Fig. S3 in Appendix A).

Slowing the wetting process increased soil fertility, as shown in Fig. 3(e). Compared with the FW treatment, the MW and SW treatments raised the total OC by 15.3% and 28.4%, the OM by 4.8% and 12.8%, the TN by 22.9% and 55.3%, and the AN by 6.4% and 10.6%, respectively. AP content increased by 10.1% and 23.8% in MW and SW, respectively, while TP content increased by 8.7% in MW but decreased by 17.9% in SW compared with that in FW.

3.3. Joint analysis of the transcriptome and metabolome in tomato yield and quality under different wetting processes

Combined transcriptional and metabolomic analyses identified 1458, 1302, and 1754 differentially expressed genes, along with

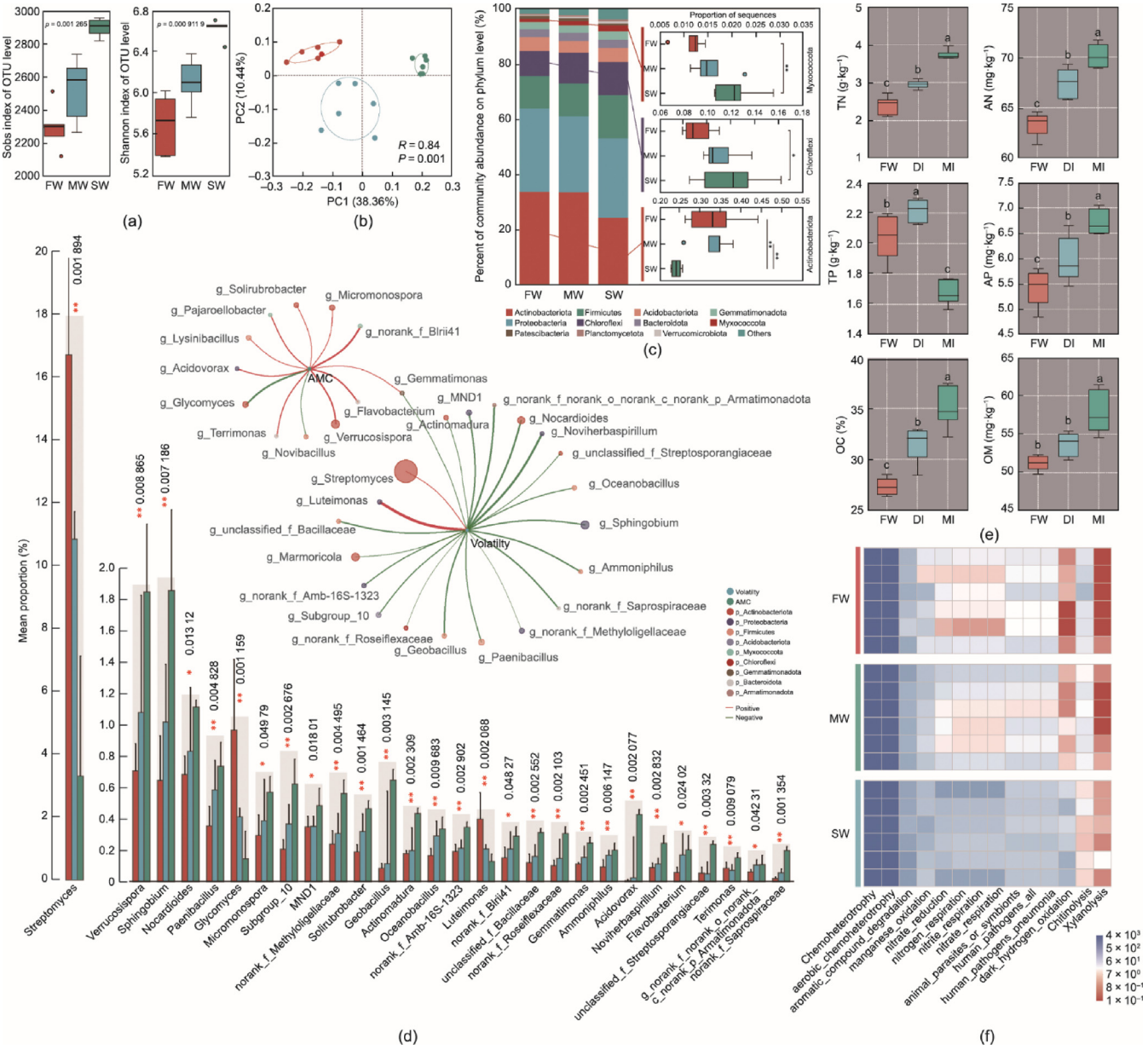

Fig. 3. Bacterial community diversity and structural composition. (a) Alpha-diversity of the bacterial community. (b) Beta-diversity of the bacterial community plotted using PCoA, where each point in the diagram represents a sample and the distance between points ($n = 6$) indicates the degree of difference. Samples from the same treatment are represented by the same color and dotted lines represent the clustering of points for each treatment. (c) Relative abundances of bacteria at the phylum level. (d) Bacterial communities showing significant differences under treatment conditions. Asterisks denote significant differences between treatments as determined by ANOVA. The significance levels are defined as follows: $^{*}p < 0.05$; $^{**}p < 0.01$. (e) Soil nutrient concentrations under different treatment conditions. Values represent the mean ± SE ($n = 6$). (f) Effects of different wetting processes on functions of the bacterial community as predicted using FAPROTAX. OTU: operational taxonomic unit. Different lowercase letters in (e) represent significant differences between respective treatments by ANOVA ($p < 0.05$).

848, 426, and 788 differentially expressed metabolites in the SW versus FW, SW versus MW, and MW versus FW groups, respectively (Figs. S4 and S5 in Appendix A). The fold changes in the pathway metabolites and genes associated with corresponding quality indicators were mapped according to the KEGG pathways (Fig. 4). With the slowing of the wetting process in the SW treatment, the expression of the *GME* gene encoding the rate-limiting enzyme guanosine diphosphate (GDP)-D-mannose 3',5'-epimerase (GME) involved in ascorbic acid biosynthesis was upregulated. The ascorbic acid generated in tomato fruit is rapidly oxidized to dehydroascorbic acid (DHA), which has a weaker reducing ability. The gene expression results showed two patterns for the expression of the *DHAR* gene encoding dehydroascorbate reductase dehydrogenase (DHAR) and that of the gene encoding ascorbate peroxidase: SW > MW > FW and FW > MW > SW, respectively (Fig. 4(a)). The response of these two enzymes may effectively delay the degradation of ascorbic acid. In the tricarboxylic acid (TCA) cycle, the SW treatment significantly inhibited the expression of the *IDH1* gene encoding isocitrate dehydrogenase 1 (IDH1) (Fig. 4(b)), which catalyzes the generation of oxoglutaric acid from citric acid. In contrast, the SW treatment inhibited expression of the *SDBH* gene encoding serum dopamine-beta-hydroxylase (SDBH) activity, which catalyzes the generation of fumaric acid from succinic acid, resulting in a decrease in the amount of organic acids produced. The trends in lycopene content were similar to those of ascorbic acid in the different treatments

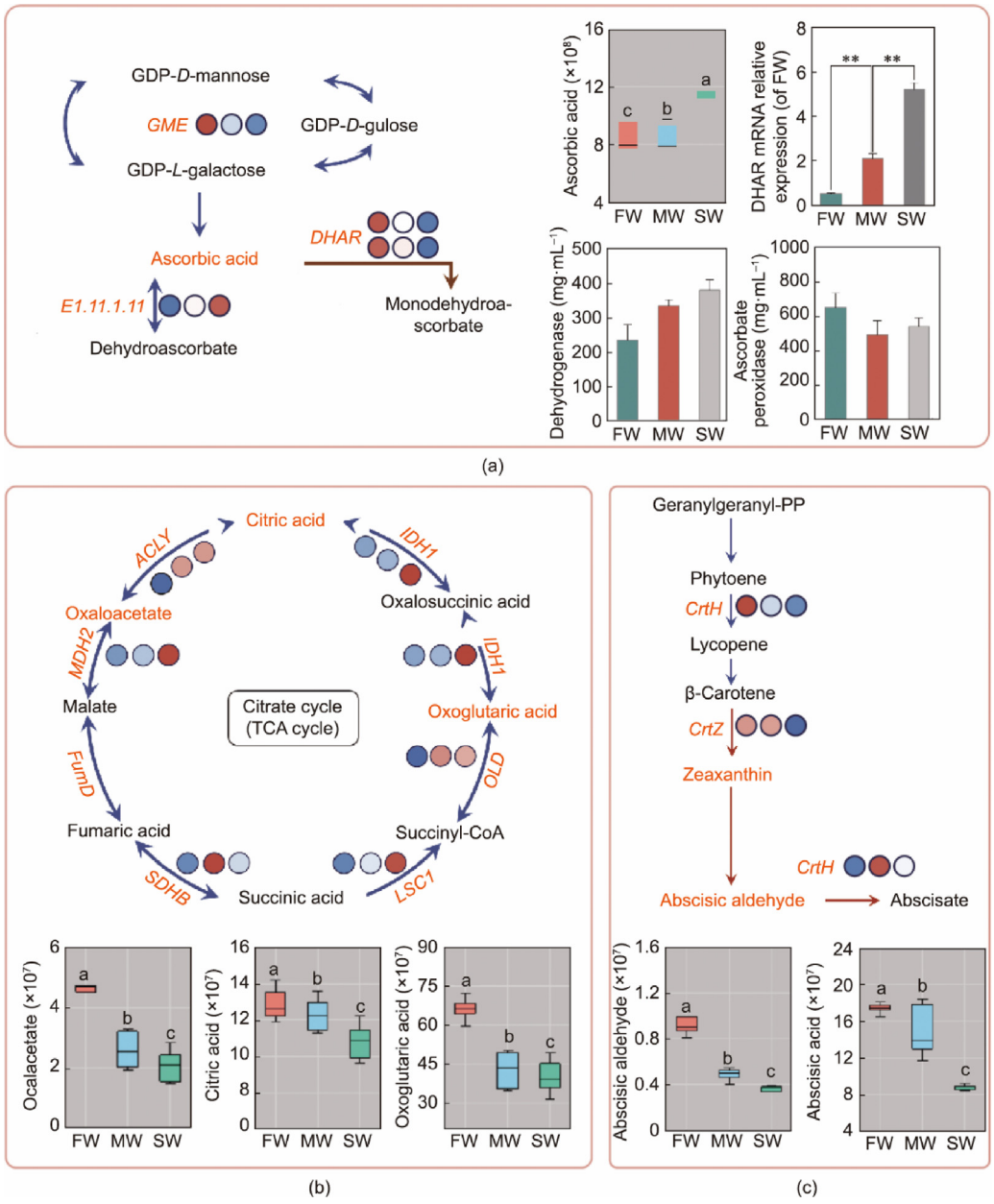

Fig. 4. Joint analysis of changes in the transcriptome and metabolome associated with tomato quality under different wetting treatments. (a) The folding pathway of ascorbate transcriptome and metabolome KEGG is represented. The box plot on the right shows the content comparison of metabolome, and the bar chart shows the content comparison of key enzymes in the qPCR and pathway process of differentially expressed genes (DEGs) respectively. The list of qPCR test methods and primers is shown in Table S6 in Appendix A. (b, c) represent the organic acid TCA cycle) and lycopene transcription combined with metabolome KEGG folding pathways, respectively. The selection of significant differentially expressed metabolites was determined based on the variable weight values (VIP) obtained from the OPLS-DA model and the *p*-value of the student's *t*-test. Metabolites with a VIP > 1 and $p < 0.05$ were identified as significant differentially expressed metabolites, different lowercase letters represent significant differences between respective treatments by ANOVA ($p < 0.05$).

(Fig. 4(c)). SW treatment resulted in upregulated expression of *crtB* and *crtH*, which encode enzymes in the lycopene biosynthesis pathway, improving the efficiency of lycopene synthesis from phytoene. Meanwhile, the MW treatment inhibited the expression of related genes encoding enzymes catalyzing reactions downstream in the lycopene metabolic pathway. The transcriptomic results showed that *AAO3*, which encodes abscisic acid (ABA)—aldehyde oxidase, had expression levels in the order FW > SW > MW. Similarly, the metabolomic results showed that abscisic aldehyde, a precursor of ABA synthesis in tomato fruit, followed the same pattern.

3.4. Mechanisms of the effects of different wetting processes on yield and quality

The correlation heat map of the relationships among yield, bacterial community, soil fertility and AQTV showed that the soil wetting process was significantly correlated with bacterial diversity, dominant bacterial phyla, and key differential genera (Fig. 5). SMF exhibited a pronounced negative correlation with keystone bacteria. Soil fertility demonstrated a statistically significant positive correlation with alpha diversity and the majority of keystone bacteria, while exhibiting a negative correlation with the relative

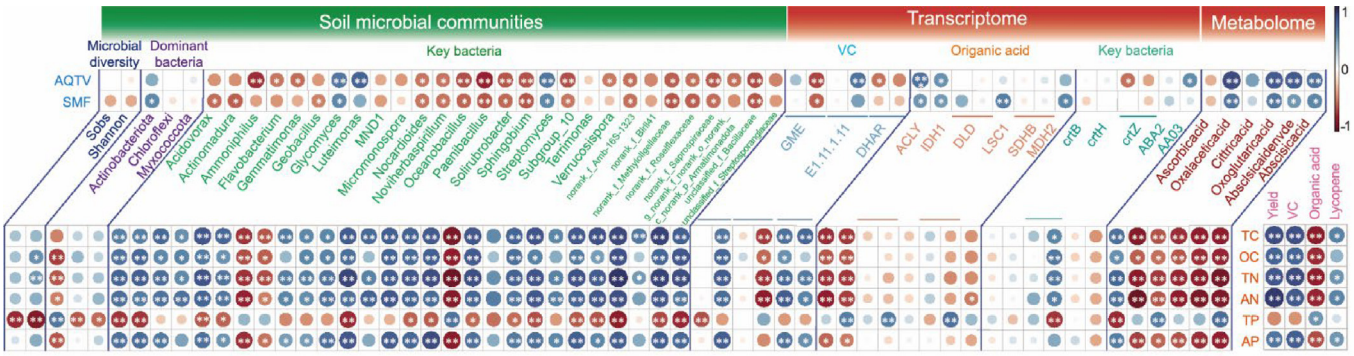

Fig. 5. Correlation analysis of the relationships among yield, bacterial community, soil fertility and AQTV. The red color indicates a negative correlation and the blue color indicates a positive correlation. The darker the color, the stronger the correlation, and vice versa. The size of the circle indicates the degree of correlation, i.e., the greater the size, the stronger the correlation. The correlation heatmap displays the Pearson correlation coefficients between the various variables. VC: vitamin C. $^{*}p < 0.05$, $^{**}p < 0.01$.

abundance of Actinobacteria. Increases in carbon, nitrogen, and phosphorus in the soil boosted yields and the content of lycopene and vitamin C, while decreasing the accumulation of organic acids. Among the factors investigated, soil fertility and SMF were found to be significantly correlated with the differentially transcribed genes and differential metabolites involved in transcriptional metabolic processes, respectively.

Based on the correlations stated above, an SEM was constructed to elucidate the working mechanisms of the effects of different wetting processes on crop yield and quality. It revealed that stable soil moisture directly increases microbial community diversity and soil fertility, which in turn activates the transcriptional pathways associated with nutrient assimilation and antioxidant biosynthesis. Notably, slowing the wetting process affected the ability of the bacterial community to promote soil fertility by decreasing the degree of SMF (Fig. 6). In addition, improvements in soil fertility ultimately promoted crop yield and quality by influencing the transcriptional regulation of metabolic pathways. Moreover, reduced SMFs directly affected the transcriptional regulation of metabolism, further increasing lycopene biosynthesis and fruit yield.

4. Discussion

4.1. Effects of SMFs on rhizosphere soil microbial community

The results showed that SMFs significantly affected the diversity and composition of rhizosphere bacterial communities. Stable soil moisture and oxygen levels promoted microbial diversity and coexistence. Also, according to the network analysis, the number of nodes and connections gradually increased as the SMFs decreased. This finding suggests increased complexity and stability in microbial networks with decreased SMFs, such that microbes can use resources more efficiently, transmit information, and collectively maintain their ecological functions. Reducing the SMFs also reduced the antagonistic relationship among bacteria, which could be one possible reason for the increase in bacterial community diversity (Table S6 in Appendix A). Stable moisture regimes reduce the temporal variability in carbon and nitrogen availability, diminishing "boom/bust" dynamics that favor fast-growing *R*-strategists (e.g., Actinobacteria). Lower resource fluctuation permits the coexistence of *K*-strategists (e.g., Acidovorax and Gemmatimonas), which specialize in degrading complex organic compounds. This aligns with the stress-gradient hypothesis, which posits that environmental stability reduces antagonistic interactions and fosters niche partitioning. Consequently, the microbial communities under SW exhibited greater network complexity, increasing their resilience to perturbations. Further exploration through differential bacteria analysis revealed that, with reductions in SMFs, the greatest decrease in relative abundance was observed for *Streptomyces* (Fig. 3(d)), a bacterial genus capable of secreting multiple antibiotics with strong antagonistic properties in the soil environment. Hence, this considerable decrease in the abundance of *Streptomyces* could have led to an increase in soil bacterial diversity [15].

We also found that different SMFs altered the composition of the soil bacterial communities (Fig. 3(b)). First, the degree of SMF altered the soil microenvironment, which may have changed the community composition. As shown in Fig. S6(a) in Appendix A, SW promoted an increase in the abundance of 30.6% of operational taxonomic units (OTUs), while reducing the abundance of 5.97% of OTUs, in comparison with the FW process. These results were due to the relatively stable soil water content in the SW process, which created a soil microhabitat suitable for the survival and reproduction of more bacterial populations [2]. Furthermore, research has demonstrated that rewetting may result in the lysis of a portion of the microbial biomass due to the rapid increase in water potential [16]. Changes in the microbial community may result from a slowed wetting process, which preserves soil structure and alters oxygen levels. Notably, *Flavobacterium*, an aerobe, showed the greatest increase in abundance, while *Lactococcus*, a facultative anaerobe, showed the greatest decrease. Other studies have reached analogous conclusions, indicating that a reduced wetted soil proportion and emitter flow rate in drip irrigation may increase soil aeration [17]. In our view, sharp SMFs in the FW treatment disrupted the soil structure, altering the pore connectivity and long-term oxygen recovery after irrigation, which impacted the soil oxygen content [18,19]. Reducing SMFs may allow microbes to self-select their environment through diffusive migration [20]. Neutral model analysis showed that, as the fluctuations decreased, bacterial community randomness declined, and species dispersal increased (Fig. S6(b) in Appendix A).

Reducing the magnitude of SMFs during wetting-drying cycles can create a more suitable water environment for microbial activity and functionality in material cycling, thereby improving soil fertility [21]. *Acidovorax*, *Flavobacterium*, *Terrimonas*, and *Solirubrobacter* are extensively involved in OM decomposition and OC conversion [22–24]. *Gemmatimonas* has been found to be extensively involved in phosphate and phosphite metabolism in addition to OM decomposition, while *Paenibacillus* may be involved in processes such as ammonification and nitrification [25,26]. Furthermore, the results of the significance difference test indicated that the abundance of *Flavobacterium*, *Gemmatimonas*, *Terrimonas*, *Paenibacillus*, and *Acidovorax* increased significantly

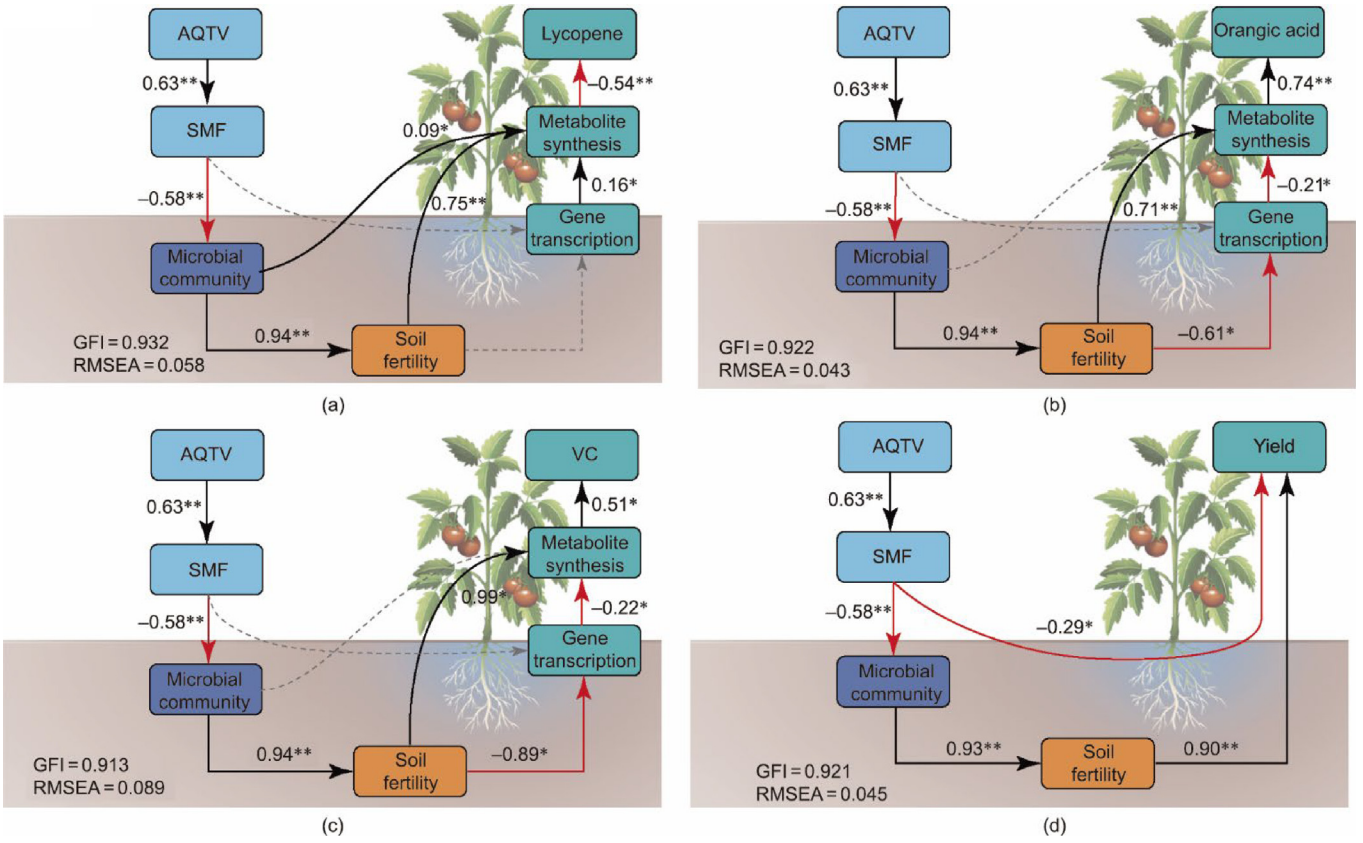

Fig. 6. Mechanisms of the effects of different wetting processes on yield and quality. SEM of the potential relationship among yield, bacterial community, soil fertility, and AQTV. Numbers alongside arrows represent the standardized regression weights; a red line represents a negative relationship and a black line represents a positive relationship. Solid and dashed lines indicate significant and insignificant effects, respectively. goodness-of-fit index (GFI) is an absolute fit index that measures the proportion of variance and covariance in the observed data explained by the model. It ranges from 0 to 1, with values closer to 1 indicating a better fit. While traditionally a cutoff of > 0.90 was considered acceptable, stricter thresholds (e.g., > 0.95) are now commonly recommended for a good fit. Root mean square error of approximation (RMSEA) assesses how well the model fits the population covariance matrix, with a penalty for model complexity. It is sensitive to misspecifications and is one of the most widely reported fit indices. Lower RMSEA values indicate a better fit. A value < 0.05 is considered excellent, <0.08 is acceptable, and >0.10 suggests a poor fit. $^{*}p < 0.05$; $^{**}p < 0.01$.

with the slowing down of the wetting process. While Actinobacteria are recognized for their role in OM decomposition, their dominance under high moisture fluctuations (i.e., FW treatment) may reflect competitive exclusion of other functional taxa. *Streptomyces*, a dominant Actinobacteria genus in our study, produces antimicrobial compounds that suppress microbial diversity, indirectly impairing nutrient cycling efficiency. Conversely, reduced Actinobacteria abundance under SW correlated with increased *Gemmatimonas* and *Flavobacterium*, which increase nitrogen fixation and carbon mineralization, respectively. This finding suggests functional redundancy within the microbiome, where overall community structure and interactions—rather than individual taxa—govern soil fertility outcomes. Such shifts highlight the importance of microbial consortia over single taxa in driving agroecosystem functionality. Furthermore, the results of the co-occurrence network analysis indicated that the abundance of the majority of the differential bacteria increased gradually with the reduction in SMFs. In addition to the increase in the abundance of microbial communities that promote soil fertility accumulation, some deferentially abundant microbes that secrete plant hormones to increase crop yield and quality were found to increase in abundance, such as *Paenibacillus*, which secretes plant hormones such as indole-3-acetic acid (IAA) to promote crop growth [27]. Overall, stable soil moisture increased microbial diversity and improved community composition, reducing antagonism and enhancing nutrient cycling, which ultimately promotes better crop growth and quality.

4.2. Effects of SMFs on transcription and metabolism in fruit quality

The combined analysis of plant transcriptomic and metabolomic results indicates that SMFs significantly affect the biochemical synthesis processes of ascorbic acid, lycopene, and organic acids in the TCA cycle (Fig. 4). The reduction in SMFs allows soil moisture to remain within a more suitable range for a longer duration (Fig. S2). Extensive research has shown that plants produce significant amounts of reactive oxygen species (ROS) after the perception of drought [28]; this induces transcriptional shifts, with ABA acting as the signal molecule [6]. Ascorbic acid and lycopene play important roles in coping with the oxidative stress generated from abiotic stress by scavenging ROS (Fig. S7 in Appendix A) due to their strong antioxidant characteristics [29]. Under the SW treatment, the lower frequency and intensity of oxidative stress may have resulted in minimal consumption of ascorbic acid and lycopene to maintain redox homeostasis, allowing more of these compounds to accumulate—a hypothesis that is supported by the transcriptomic analysis. During the ascorbic acid regeneration cycle, ascorbate peroxidase (APX) uses ascorbic acid as an electron donor [30] to catalyze the conversion of hydrogen peroxide into water, while ascorbic acid is oxidized to DHA. ABA, a downstream product of lycopene degradation, shows reduced content under lower fluctuations, as indicated by metabolomic data (Fig. 4) and SEM (Fig. 6(a)). The SW treatment suppresses ABA-precursor synthesis and inhibits *ABA2* and *AAO3* gene expression, decreasing the catalytic efficiency of the enzymes involved in ABA synthesis.

Consequently, less lycopene is consumed, leading to its increased accumulation.

Regarding organic acids, malic acid and citric acid are the two most abundant acids in the TCA cycle pathway within tomato fruit [31]. In this study, the inhibition of these organic acids' synthesis may be attributed to improved soil fertility under more stable soil moisture conditions, such as increased availability of different forms of nitrogen [32]. Narrower SMF ranges can effectively increase lycopene and ascorbic acid content in tomatoes [32,33], which is supported by this study's findings that SW treatment improves soil fertility. Smaller fluctuations in soil moisture levels increase the contents of major elements in the soil, providing better growth conditions for tomato development—especially during the fruit expansion stage, which demands higher water and fertilizer input. This ensures adequate growth factors, preventing nutrient deficiency and imbalance in redox levels. Under SW treatment, the expression of the genes encoding IDH1, LSC1, and MDH2 is more significantly inhibited (Figs. S8 in Appendix A). The downregulation of *MDH2* gene expression reduces the demand for malate dehydrogenase activity in the malic acid reduction process, leading to a decrease in citric acid concentration within plant cells [34]. Thus, SW treatment affects multiple steps in the TCA cycle, with a tendency to inhibit the synthesis of key enzymes, ultimately reducing the organic acid content in the fruit [35].

The key to determining the flavor of tomatoes lies in the combination of sugars and organic acids (e.g., malic acid and citric acid) and their balanced interaction. Metabolomics revealing variations in different types of organic acids may help shape a more ideal sugar-to-acid ratio, providing tomatoes with better sensory properties to consumers [36]. A reduction in SMFs allows the soil in the root zone to remain within a more consistent moisture range for a longer period, while simultaneously increasing soil fertility. These positive effects significantly alter the crop's transcriptional-metabolic biochemical synthesis processes and may show greater advantages in agricultural practices in regions prone to severe drought.

4.3. Prospects for the application of technology to reduce SMFs

Slowing down the wetting process is an effective way to control SMFs within the wetted volume. During infiltration, the soil wetting process affects particle and solute distribution. Pore clogging reduces water-retention capacity, leading to poor water-holding ability and greater moisture fluctuations after irrigation [37,38]. In addition, as the wetting process slows, the wetting front diffuses more gradually, making the shape of the wetted zone less influenced by gravity (Fig. S9 in Appendix A) and thereby avoiding the issue of gravitational water seeping deep beyond the root zone where it is less accessible to crops [39]. This was confirmed by monitoring the soil moisture content at different depths (Fig. S2). Slowing the wetting process increases the average moisture content in the wetting zone by affecting water distribution and infiltration, while reducing the fluctuations ensures greater water availability throughout the crop growth period. Compared with the rapid wetting process in traditional furrow irrigation, SW can achieve overall water savings of up to 35.1% (Fig. S2). This affects subsequent water and fertilizer movement and the composition and migration of microbial communities in the rhizosphere [40,41]; it also influences the rhizosphere microenvironment, shaping plant growth and leading to differences in crop development (Fig. S10 in Appendix A), yield, and quality [42]. Changes in soil water distribution and fluctuations within the wetted soil body alter the composition, abundance, and function of the microbial community, impacting material and energy cycling in the soil–plant system [43,44]. This triggers sensing mechanisms in the plant, which result in changes in the expression of differentially expressed genes (DEGs) [7]. In addition to the pathways described above, the effects of wetting processes on microbial communities can directly affect the transcriptional metabolism of crops (Fig. 6(c); Fig. S11 in Appendix A). It has been found that the differential strain *Paenibacillus* can secrete IAA, which promotes crop growth [27], and ABA [45], which plays an important regulatory role in promoting crop yield and fruit quality in plants. In addition, ABA, as a differential metabolite, significantly affects the lycopene degradation pathway (Fig. 4), which could significantly affect the accumulation of lycopene in fruits.

Slowing the wetting process to reduce SMFs enhances crop yield and quality. By adopting advanced irrigation technologies such as drip irrigation, water and fertilizers can be precisely delivered to the crop root zone. During wetting-drying cycles, reducing the magnitude of SMFs can be a key approach to shape a more favorable root-zone microenvironment. Minimizing SMFs creates a sustainable environment, while drip or micro-irrigation further enhances water conservation and crop performance. Although our greenhouse-controlled experiments provide mechanistic insights, field validation is essential to address environmental variabilities (e.g., rainfall interference and soil texture gradients) that may attenuate the observed effects under open-air conditions. Therefore, in practical engineering applications, it is essential to fully consider soil texture, irrigation rotation systems, and crop root architecture when controlling emitter flow rates. Additionally, a greater proportion of recycled materials should be mixed into the fabrication of capillary wall materials to effectively control the cost of applying this technology in practice. Unlike deficit irrigation, which requires complex management and limits crop adaptability, slowing the wetting process is simpler, requires less expertise, and has broader applicability. SMFs can also be reduced through irrigation, water-retaining agents, and mulching. This study introduces a sustainable method that improves yield and quality, reduces water use, and minimizes environmental impact, making it ideal for regions with limited resources and water scarcity. In the future, further research can be conducted in the following two aspects: ① Systematically decoupling SMFs into amplitude and frequency through sinusoidal irrigation protocols will clarify their distinct impacts on microbial functionality and metabolic trade-offs. ② Quantifying how SMF regimes alter rhizosphere physical metrics could reveal novel pathways linking soil structure to microbiome-mediated yield-quality synergies.

5. Conclusions

This study demonstrated that controlling SMFs can significantly increase crop yield and fruit quality while notably reducing irrigation quotas. Under more stable soil moisture conditions, microbial diversity increases significantly, which further accelerates soil nutrient mineralization and enhances soil fertility. Additionally, stable SMFs have a direct impact on transcription-metabolic processes in the biochemical synthesis pathways that determine fruit quality; the *GME* gene in the ascorbic acid synthesis pathway and the *DHAR* gene in the regeneration cycle pathway are upregulated to promote substance accumulation. SW treatment leads to upregulation of the expression of the enzymes crtB and crtH in the lycopene synthesis pathway, increasing the efficiency of lycopene biosynthesis in plants. At the same time, the reduction of the wetting process inhibits the expression of genes such as *SDBH*, suppressing the synthesis of succinic acid and fumaric acid and thereby reducing organic acid content. This approach challenges conventional irrigation methods and presents a scalable strategy for sustainable agriculture, tackling issues of food security and environmental sustainability. Continued research is necessary to refine these irrigation techniques across different crops, assess

their long-term impacts on soil health, explore precision irrigation technologies, and evaluate their economic feasibility for widespread application. In summary, this method offers a promising path forward for sustainable agriculture in the face of climate change and increasing water scarcity.

CRediT authorship contribution statement

Weijie Chen: Writing – review & editing, Writing – original draft, Visualization, Validation. **Naikun Kuang:** Writing – review & editing, Software, Data curation. **Christoph Martin:** Writing – review & editing. **Akshit Puri:** Writing – original draft. **Bin Liu:** Data curation. **Jing He:** Methodology, Data curation. **Yunpeng Zhou:** Funding acquisition. **Yunkai Li:** Funding acquisition, Conceptualization.

Declaration of competing interest

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

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Data availability

The data that support the findings of this study are available in the Supporting Information of this article. The fastq sequence data with associated metadata for this study have been deposited at the National Center for Biotechnology Information (NCBI) under BioProject PRJNA1298903.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.eng.2025.10.038.

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