Research Article
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Gentle touch of tomato leaves enriches phyllosphere *Pseudomonas* and suppresses gray mold disease

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Abstract: Plants have evolved adaptive responses to a wide range of mechanical stimuli, such as gentle touch caused by light wind. Although touch-induced responses have been shown to share signaling components with defense pathways, whether the phyllosphere microbiota contributes to touch-triggered disease resistance remains unknown. Herein, we demonstrated that touch-induced resistance against *Botrytis cinerea* in tomato leaves is partially dependent on the phyllosphere microbiome, as surface sterilization significantly diminished the protective effect of touch. Using 16S ribosomal RNA (rRNA) amplicon sequencing, we found that repeated gentle touch markedly restructures the phyllosphere bacterial community. Screening against probiotic databases revealed that the majority of the enriched beneficial taxa belonged to the genus *Pseudomonas*. We further conducted plate confrontation assays to isolate seven *Pseudomonas* strains that exhibited antagonistic activity against *B. cinerea*. A synthetic community reconstituted from these isolates significantly reduced lesion development when applied to tomato leaves prior to *B. cinerea* inoculation. Our findings suggest that mechanical stimulation might enrich beneficial *Pseudomonas* populations in the phyllosphere, revealing a previously unrecognized link between mechanical stimuli and the plant microbiome.

Key words: Mechanical stimulation; Microbiota; Gray mold; Biological control; Beneficial bacteria

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1 Introduction

Tomato (*Solanum lycopersicum*) is globally among the most widely cultivated vegetable crops, with annual production exceeding 180 million tons (Mustafa et al., 2025). However, its growth and yield are severely threatened by gray mold, a disease caused by the necrotrophic fungus *Botrytis cinerea,* causing over $10 billion in economic losses worldwide each year (Hua et al., 2018). Treatment with chemical fungicides remain a widely used approach for disease control; however, this is associated with significant concerns, including environmental pollution, health risks and the development of fungicide resistance (Zhu et al., 2024). Biocontrol via microorganisms has emerged as a promising alternative, offering advantages such as high safety, environmental compatibility, and strong efficacy against plant pathogens (Papadopoulou et al., 2025).

Microbiome as the "second genome of plants" interacts with their hosts throughout their entire growth cycle, profoundly influencing plant health, stress resistance and productivity (Vorholt, 2012; Trivedi et al., 2020; Bai, et al., 2022; Jiang Y et al., 2024). The phyllosphere microbiome represents the largest biological surface on Earth and remains a largely untapped reservoir of microbial function, with sources including soil, seeds and air (Hardoim et al., 2012; Brown et al., 2020; Xu et al., 2022). Accumulating evidence suggests that plants can actively enrich specific beneficial microorganisms in response to environmental pressures such as dense planting, salt stress or pathogen attack (Naylor et al., 2017; Wang and Song, 2022; Zhang et al., 2025). For instance, under dense planting conditions, linalool volatiles released by maize leaves accumulate in the canopy, triggering neighboring plants to secrete benzoxazinoids into the soil, which in turn reshapes the soil microbial community and stimulates the plants to synthesize salicylic acid and enhance their systemic defense capabilities (Guo et al., 2025). Therefore, identifying and characterizing these plant-recruited beneficial microbes holds great promise for the development of novel and effective biocontrol agents.

Plants are constantly exposed to diverse mechanical stimuli in their natural environment (Braam, 2005; Hamant and Haswell, 2017; Hansen et al., 2025). Touch, arising from rain and wind, represents a common example (Braam and Davis, 1990; Van Moerkercke et al., 2019; Kouhen et al., 2023). Such mechanical cues can profoundly influence plant morphology, a phenomenon known as thigmomorphogenesis, often resulting in reduced height, shorter internodes and sturdier stems (Jaffe, 1973; Chehab et al., 2008; Braam and Chehab, 2017). Beyond inducing morphological changes, mechanical stimuli enhance leaf defenses against necrotrophic pathogens and pests (Chehab et al., 2012; Brenya et al., 2020; Matsumura et al., 2022). A notable historical example of the agricultural application of mechanical stimulation is the Japanese practice of "mugifumi," in which a mechanical stimulus is applied to wheat seedlings by rollers to optimize growth and increase defenses (Iida, 2014). Although a range of inter- and intracellular signaling components, including hormones and second messengers, have been implicated in touch-induced responses (Telewski and Jaffe, 1986; Braam, 2005; Chehab et al.,

2008), it remains unknown whether touch influences the composition of the phyllosphere microbiome.

This study aimed to determine whether touch stimulation enhances tomato resistance against gray mold, potentially via reshaping the phyllosphere microbiome, and to identify beneficial microbes that may be recruited to suppress pathogen infection. The findings provide new insights into the mechanisms underlying touch-induced plant defense.

2 Results

2.1 Gentle touch modulates tomato architecture

To mechanically stimulate tomato seedlings, we applied gentle physical touch and slow wind. Physical touch was administered using a wooden stick, while slow wind (4 m/s) was generated with a fan. Stimulations were performed on leaves twice daily for 30 sec each over a period of two weeks. After treatment, both wind and physical touch induced dwarfism in tomato plants (Figs. 1a and b); however, as physical touch had a more pronounced effect, subsequent studies focused primarily on this scenario. Touch also resulted in a reduced leaf size and decreased shoot fresh weight (Figs. 1c–1e). Furthermore, touched plants exhibited darker green leaves, along with significantly elevated chlorophyll and anthocyanin content (Fig. S1). In contrast, touch treatment at the seedling stage did not significantly alter reproductive traits, including flowering time, fruit weight, or fruit number (Figs. 1f–1i). Collectively, these results indicate that gentle mechanical touch applied during the seedling stage can modulate vegetative growth in tomato without compromising yield.

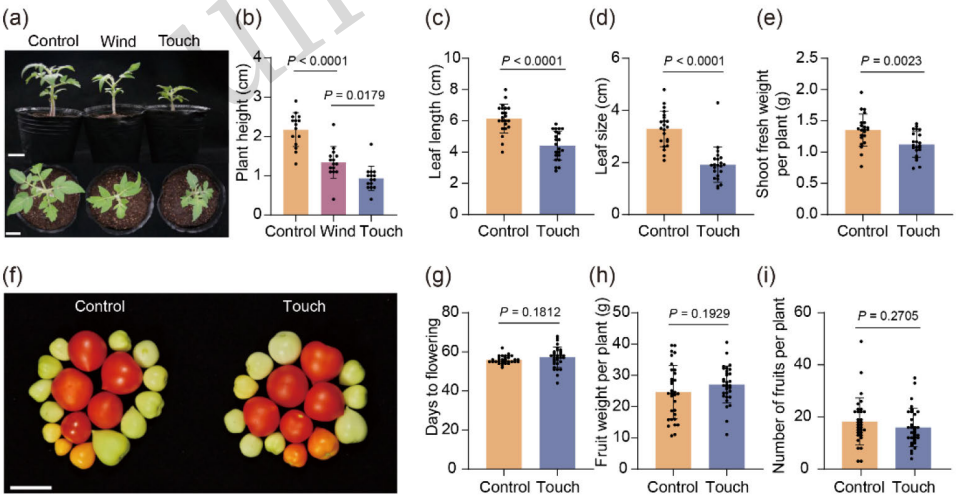

Fig. 1 Gentle touch modulates tomato vegetative growth without compromising yield

(a) Representative images of tomato plants following two weeks of twice-daily wind or physical touch treatment. Treatment was initiated at two weeks post-germination (n = 15 independent plants). Scale bars = 2 cm. **(b–e)** Quantification of plant height (b), leaf length (c), leaf size (d), and shoot fresh weight (e) after touch. Data are shown as mean ± standard deviation (SD) (n = 22 independent plants in b–e). P-values in (b)

were determined by one-way ANOVA; others by unpaired t-tests. **(f–i)** Touch had no significant effect on tomato reproduction. Representative images of tomato fruits are presented in (f). The following key parameters were quantified: days to flowering (g), fruit weight per plant (h), and number of fruits per plant (i). The scale bar in (f) is 2 cm. Data in (g–i) are shown as mean ± SD (n = 32 independent plants). P-values were determined by unpaired t-tests using Welch's correction. The results were consistent among three independent replicates.

2.2 Gentle touch enhances tomato resistance to fungal gray mold

To determine whether mechanical stimulation enhances tomato resistance against fungal gray mold, leaves were subjected to gentle touch treatment for two weeks, then detached and inoculated with *Botrytis cinerea*. By 72 h post-inoculation (hpi), leaves from untouched plants had turned yellowish, whereas those from touched plants remained green (Fig. 2a). Lesion areas caused by *B. cinerea* were significantly smaller in touched leaves compared to untouched leaves at both 72 and 96 hpi (Fig. 2b). Furthermore, the quantification of fungal biomass via quantitative PCR (qPCR) revealed significantly reduced growth of *B. cinerea* in the touched leaves (Fig. 2c). These results suggest that gentle touch treatment of tomato leaves enhances resistance against fungal gray mold.

We next assessed whether gentle leaf touch influenced tomato resistance to a root pathogen. After two weeks of leaf touch treatment, plants were inoculated with *Ralstonia solanacearum*, a soil-borne bacterium that infects through roots and spreads via the xylem, resulting in wilt disease (Shi et al., 2023). Compared with untouched plants, touch-treated plants showed no significant differences in disease index or survival rate (Figs. S2a–S2d). Consistently, gentle touch did not significantly affect root growth, as measured by root length and fresh weight (Fig. S2f–2h). These results suggest that gentle touch of tomato leaves reduces susceptibility to a foliar pathogen but does not alter resistance to a root pathogen.

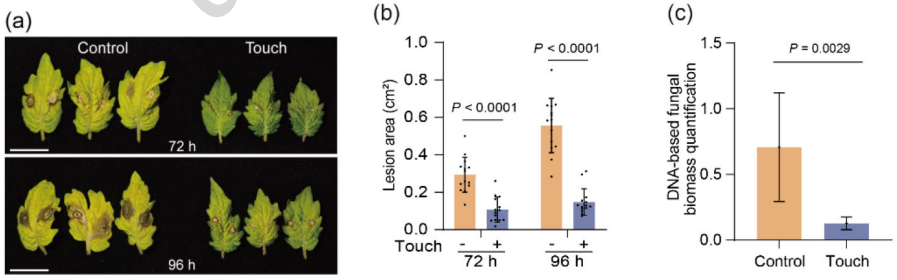

Fig. 2 Touch enhances tomato leaf defense against *Botrytis cinerea*

(a) Representative images of tomato leaves following inoculation with *B. cinerea* (1×10^5 spores/mL), captured at 72 and 96 h post-inoculation (hpi). Scale bar = 2 cm. **(b)** Quantified lesion area. Data are shown as mean ± SD (n = 14 independent leaves). P-values were determined by two-way ANOVA. **(c)** Biomass of *B. cinerea*. Fungal biomass was quantified via qPCR (targeting the *Bc3*) using DNA extracted at 96 hpi, normalized to the tomato *SlACTIN* gene. Data are shown as mean ± SD (n = 3 independent leaves). P-values were determined by unpaired t-test with Welch's correction. The results were consistent among three independent replicates.

2.3 Gentle touch reshapes the phyllosphere microbial community

To investigate the potential involvement of phyllosphere microbes in touch-induced resistance, touch-treated leaves were first surface-sterilized using 75% ethanol and then inoculated with *B. cinerea* (Figs. 3a and 3b). Although touch reduced lesion areas under both sterilized and non-sterilized conditions, the level of reduction was significantly lower in sterilized leaves (45.45%) than in non-sterilized ones (64.91%) (Fig. 3c). These results suggest that the phyllosphere microbial community may contribute to touch-induced resistance. We subsequently compared the phyllosphere bacterial communities of touched and untouched leaves using 16S ribosomal RNA (rRNA) amplicon sequencing. A total of 523 zero-radius operational taxonomic units (zOTUs) were identified using the USEARCH v11 algorithm. While no significant difference was observed in Shannon diversity, the Simpson index indicated a significant decrease in phyllosphere microbial diversity following touch treatment (Fig. 4a). Principal coordinate analysis (PCoA) based on weighted UniFrac distances revealed distinct clustering between touched and untouched leaves (Fig. 4b). Together, these findings indicate that gentle touch reshapes the composition of the phyllosphere microbiota.

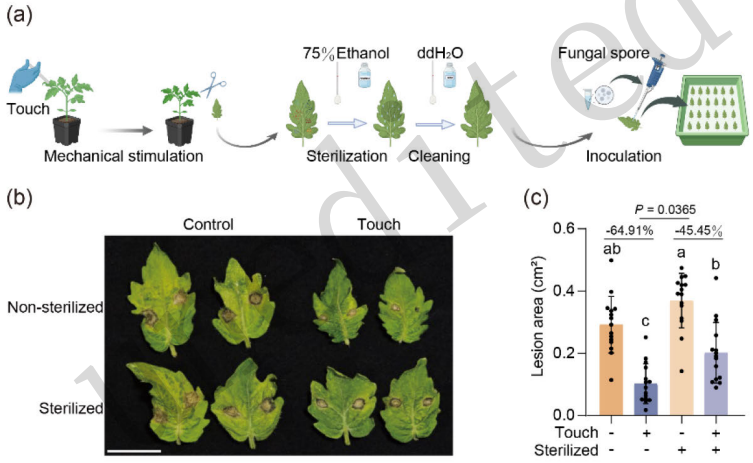

Fig. 3 Microbes contribute to touch-induced leaf defense

(a) Schematic diagram of fungal inoculation after leaf surface sterilization. **(b)** Representative images of leaves at 72 hpi with *B. cinerea* (1×10^5 spores/mL). Prior to inoculation, leaf surface sterilization was performed using 75% ethanol. Scale bar = 2 cm. **(c)** Quantification of lesion area. Data are shown as mean ± SD (n = 15 independent leaves). P-values were determined by unpaired t-test. Different letters indicate significant differences between treatments ($P \leq 0.05$, one-way ANOVA). The results were consistent among three independent replicates.

Analysis at the phylum level revealed a clear shift in community composition. Although Proteobacteria remained dominant in both the control and touch-treated leaves (accounting for 91.77% and 92.78% relative abundance, respectively), touch treatment specifically enriched Actinobacteria while reducing the abundance of Actinomycetes (Fig. 4c). At the genus level, the abundance of *Pseudomonas*, *Pseudonocardia*, *Stenotrophomonas*, *Brevundimonas*, *Streptomyces*, and *Actinoallomurus* increased

after touch treatment (Fig. 4d). Among the 523 zOTUs, 168 exhibited significant abundance changes after touch treatment, with 121 showing significant increases (Fig. 4e). Nearly half (49.4%) of these increased zOTUs belonged to the Proteobacteria phylum (Fig. S3). We subsequently performed BLAST alignment of the 16S rRNA sequences from these 168 zOTUs to obtain their species-level taxonomic assignments. Screening these species against probiotic databases (Winnenburg et al., 2007; Webster et al., 2020) revealed that 22 zOTUs matched known plant-beneficial bacterial species (Table S1), with the majority of those showing increased abundance belonging to the genus *Pseudomonas* (Fig. 4f). Collectively, these findings suggest that gentle touch may promote the enrichment of specific beneficial bacteria in the phyllosphere.

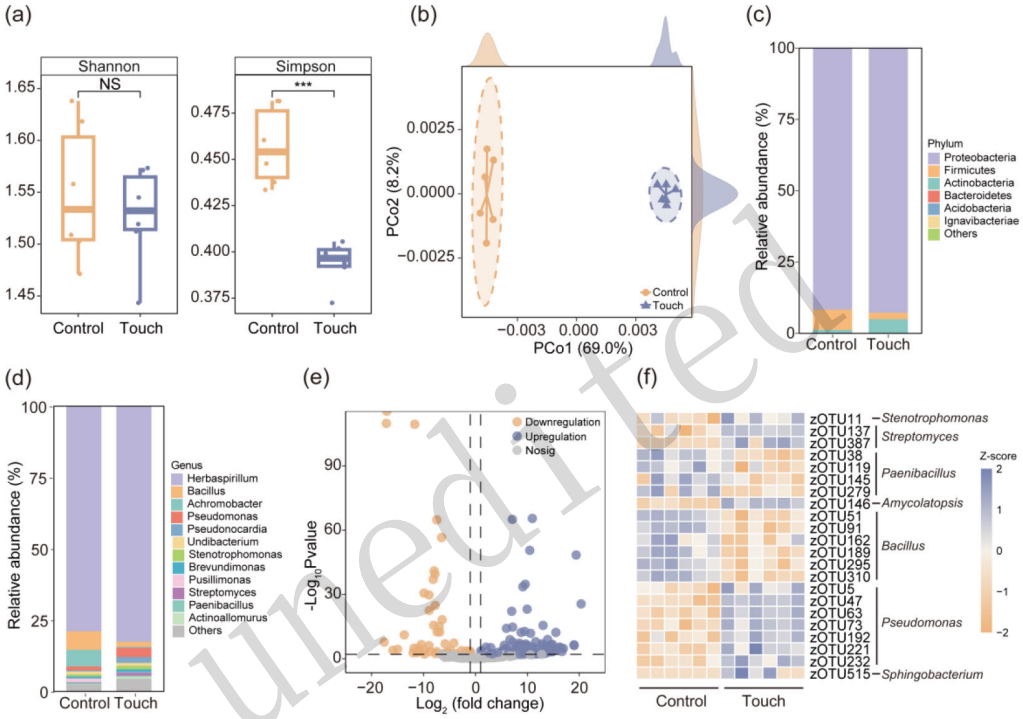

Fig. 4 Touch modulates phyllosphere microbial communities

(a) Alpha-diversity analysis assessed by Shannon and Simpson indices. Data are shown as mean ± SD (n = 6 independent biological replicates). Statistical significance was determined using unpaired t-tests with Welch's correction (NS, no significant difference; ***$P \leq 0.001$). **(b)** β-diversity analysis visualized by unconstrained PCoA based on weighted UniFrac dissimilarity. Ellipses cover 69% of data for each group. The community composition differed significantly between groups (PERMANOVA, $P = 0.004$, $R^2 = 0.91$). Relative abundance of the **(c)** six most dominant bacterial phyla and **(d)** 12 most dominant bacterial genera in the tomato phyllosphere. **(e)** Annotated species with differential abundance in touch samples relative to controls. **(f)** Beneficial bacterial taxa that differ in abundance between touch and control samples. Color intensity indicates relative abundance.

2.4 Touch-enriched *Pseudomonas* isolates can antagonize *B. cinerea*

We next recovered 84 bacterial isolates from the phyllosphere of touch-treated leaves, of which 30 demonstrated antagonistic activity against *B. cinerea* in plate confrontation assays. Among these, seven belonged to the genus *Pseudomonas*, while the remaining strains were classified into ten genera including *Bacillus*, *Priestia* and *Pantoea*. Based on 16S rRNA gene phylogenetic analysis, *Pseudomonas* isolates 1, 2 and 4 clustered with strain MG833380; meanwhile, isolates 3, 5, 6, and 7 clustered with strains OQ799019, PP259448, MK342492, and PP213434, respectively, whereas all strains exhibited genetic differences (Fig. 5a). Plate confrontation assays demonstrated that these seven *Pseudomonas* strains suppressed *B. cinerea* growth by 20% to 50% (Figs. 5b and 5c). To further evaluate the biocontrol potential of these strains *in vivo*, a synthetic community (SynCom) comprising all seven *Pseudomonas* strains was constructed and applied to tomato leaves prior to inoculation with *B. cinerea*. Compared to the control, the lesion area induced by *B. cinerea* on the SynCom-treated leaves was significantly reduced (Fig. 5d). These findings support the notion that touch treatment enriches *Pseudomonas* strains with antagonistic activity against *B. cinerea*, leading to a reduction in gray mold symptoms in tomato.

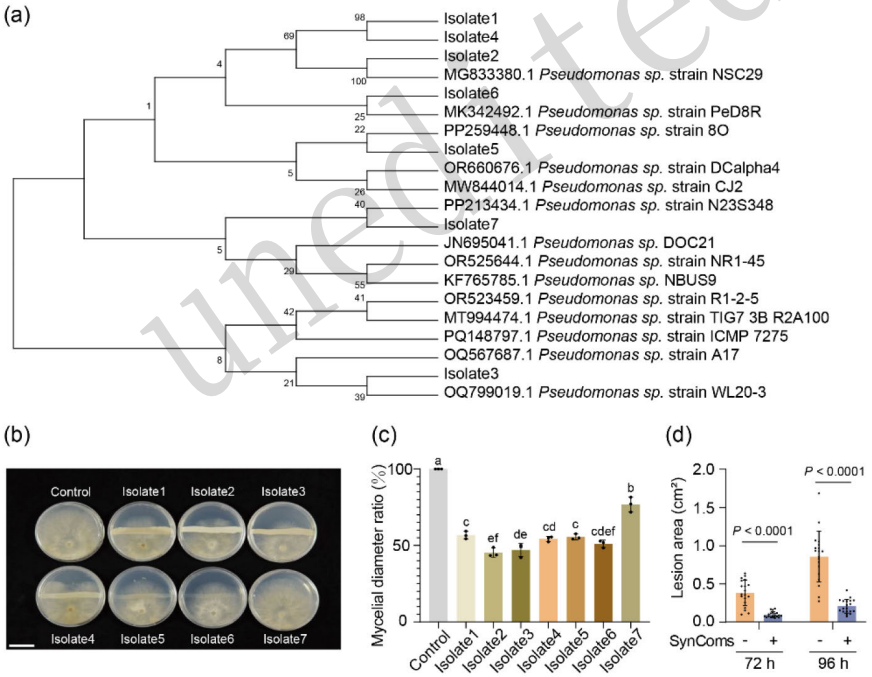

Fig. 5 Touch-enriched *Pseudomonas* isolates antagonize *B. cinerea*

(a) Phylogenetic tree showing genus-level identification of the seven *Pseudomonas* isolates. **(b)** Representative images of the inhibitory effect of *Pseudomonas* isolates against *B. cinerea* in a plate confrontation assay. Scale bar= 2 cm. **(c)** Mycelial diameter ratio, calculated as the *B. cinerea* mycelium diameter in the presence of *Pseudomonas* relative to that in the bacteria-free control. A lower ratio indicates a stronger inhibition by the *Pseudomonas* isolate. Data are presented as mean ± SD (n = 3 independent biological replicates). Different letters indicate significant differences between treatments ($P \leq 0.05$, one-way

ANOVA). **(d)** Leaf lesion area. The synthetic microbial community (SynComs) sprayed on the leaves following *B. cinerea* inoculation and lesion area was measured at 72 and 96 hpi. Data are presented as mean ± SD (n = 19 independent leaves). *P*-values were determined using two-way ANOVA.

3 Discussion

The plant phyllosphere microbiome is increasingly recognized as a key determinant of host health and defense (Sohrabi et al., 2023); however, its potential role in touch-induced plant defense remains largely unexplored. Herein, we not only showed that repetitive gentle touch reshapes the phyllosphere microbial community but also identified seven *Pseudomonas* isolates capable of suppressing *B. cinerea* growth. These findings uncover a new phenomenon whereby mechanical stimuli influence plant-associated microbiomes to enhance plant resistance.

Although we observed significant reshaping of the phyllosphere microbial community in response to touch, the underlying mechanisms were yet to be clarified. Mechanical stimulation is known to elevate endogenous jasmonic acid (JA) levels in both tomato and *Arabidopsis*, a key hormone in defense against necrotrophic pathogens such as *B. cinerea* (Luo et al., 2023; Li et al., 2025; Zhang, 2025). A plausible model, therefore, is that gentle touch activates the JA pathway, which in turn modulates the leaf surface microenvironment, potentially through alterations in secondary metabolites, leading to shifts in phyllosphere microbial community. This hypothesis is supported by evidence that mutations in JA signaling can substantially alter phyllosphere microbial composition (Kniskern et al., 2007). In addition, touch induces changes in anthocyanins and the synthesis of lignin and callose (Porter et al., 2009; Gladala-Kostarz et al., 2020), which may all contribute to alterations in the microbiota. Notably, surface sterilization reduced touch-induced resistance by only about 20% (from 64.91% to 45.45%), suggesting that while phyllosphere microbes contribute to this resistance, intrinsic plant defense mechanisms may play a more dominant role. Nevertheless, our findings confirm a significant contribution of the phyllosphere microbiota to touch-induced resistance. Further investigation is required to elucidate the precise mechanisms by which touch remodels this community.

Repetitive touch is known to induce visible morphological changes in a variety of plant species (Kouhen et al., 2023). In this study, we found that repetitive gentle touch significantly altered tomato vegetative phenotypes, leading to dwarfism, reduced leaf size, and darker green leaves. These morphological changes are consistent with those previously reported in other plant species (Braam and Chehab, 2017). However, we observed that touch treatment during the tomato seedling stage did not affect flowering time. This contrasts with findings in *Arabidopsis*, where repetitive gentle touch has been shown to delay flowering (Wang et al., 2024). This discrepancy may be attributed to differences in species, touch intensity, or developmental stage at the time of treatment. Alternatively, given the longer growth cycle of tomato, it is plausible that touch-induced responses occur primarily during vegetative growth, with

limited impact on reproductive stages. Furthermore, touch treatment applied to leaves did not enhance resistance against the root pathogen *R. solanacearum*, possibly due to either the non-broad-spectrum nature of the resistance or the weak systemic acquired resistance induced by touch. Alternatively, as xylem lignification serves as the primary defense mechanism against *R. solanacearum* infection (Li et al., 2023), it is possible that mechanical stimulation of the leaves failed to induce an increase in root lignification. This specificity highlights the potential of touch or its associated signaling pathways as a targeted green management strategy in agriculture, pointing to the capability of inducing leaf disease resistance without compromising yield or root growth.

Biocontrol holds great promise as a strategy for managing fungal diseases, with the isolation of new strains being an ongoing endeavor (Zhou et al., 2022; Fan et al., 2024). In this study, seven *Pseudomonas* strains were isolated from leaves subjected to touch treatment, six of which exhibited strong inhibitory activity against *B. cinerea*. 16S rRNA gene sequencing revealed that these isolates clustered with known *Pseudomonas* species; however, isolates 3, 5, 6, and 7 appeared to be potentially novel strains, as they showed sequence divergence from previously characterized strains. Further genome sequencing is required to confirm their taxonomic status as novel species. Among the 30 antagonistic bacterial strains obtained in this study, *Bacillus* was the second most abundant genus. Although 16S rRNA gene sequencing showed a decrease in the total abundance of *Bacillus*, it remains possible that beneficial lineages within this genus did not decline, warranting further investigation. Moreover, although the antifungal mechanisms of *Pseudomonas* and *Bacillus* spp. have been studied extensively, including competition for nutrients and the production of various secondary metabolites such as antibiotics, siderophores, and volatile organic compounds (Köhl J, 2019), these potentially novel strains may possess yet undiscovered mechanisms of action that need further elucidation.

In summary, our study reveals that mechanical stimulation can reshape the phyllosphere microbiota to enrich beneficial *Pseudomonas* populations, thereby enhancing plant resistance to gray mold. Future research should clarify the mechanisms by which touch reshapes the phyllosphere microbiota, particularly the role of JA and other hormone pathways in mediating the recruitment of beneficial microbes. Overall, our findings suggest new possibilities for developing crop disease management strategies based on mechanical stimulation or mimicking its signaling pathways.

Materials and methods

Detailed descriptions of the materials and methods used in this study are provided in the supplementary materials.

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request. The raw FASTQ files generated in this study have been deposited in the NCBI

Sequence Read Archive (SRA) under accession number PRJNA1436826 (https://www.ncbi.nlm.nih.gov/sra/PRJNA1436826).

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Author contributions

Yan LIANG conceived and designed the research. Ying PENG and Xijie GUO performed the majority of the experiments and analyzed the data. Yaxing SU assisted with disease assays. Qinghong LI contributed to tomato growth and maintenance. Chaozheng WANG, Hongkai WANG, and Qianli AN helped with bacterial isolation. Huiquan WANG assisted with the mechanical stimulation treatment. All authors read and approved the final manuscript.

Compliance with ethics guidelines

The authors declare that they have no conflicts of interest.

This article does not contain any studies involving human or animal subjects.

Declaration on the use of generative AI tools

During the preparation of this manuscript, the authors used ChatGPT (OpenAI) to improve the readability and linguistic clarity of the text. The authors reviewed and revised the content as necessary and take full responsibility for the final manuscript.

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Supplementary information

Materials and methods; Figs. S1–S3; Table S1