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Original article

Suppression of maize downy mildew by *Streptomyces hygroscopicus*, *Trichoderma asperellum*, and *Paenibacillus polymyxa*

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Abstract

This study identified the causal agent of maize (*Zea mays* L.) downy mildew in Lampung and evaluated the suppressive effects of three antagonistic microorganisms. The pathogen was identified as *Peronosclerospora maydis* (Racib.) C.G. Shaw based on *cox2* sequence and phylogenetic analyses. *Streptomyces hygroscopicus* (Jensen) Waksman & Henrici, *Trichoderma asperellum* Samuels, Lieckf. & Nirenberg, and *Paenibacillus polymyxa* (Prazmowski) Ash, Priest & Collins were evaluated via a seed germination assay and a greenhouse experiment with soil-drenching and foliar-spraying applications. Microbial treatments increased germination from 66.67% to 90.00–96.67% and prolonged the incubation period from 11.78 to 15.15–18.30 days. At 5 weeks post-treatment, disease severity decreased from 96.88% to 63.13–81.87%, and AUDPC decreased from 239.69 (control) to 120.31–177.81. *Streptomyces hygroscopicus* and *T. asperellum* significantly reduced final disease severity, whereas *P. polymyxa* showed an intermediate response. The application method had no significant effect, indicating that *S. hygroscopicus* and *T. asperellum* are promising biological control agents against maize downy mildew.

Keywords: biological control, disease suppression, foliar spraying, seed germination, soil drenching

Introduction

Downy mildew is a highly destructive maize disease, threatening production in tropical and subtropical regions. In Indonesia, *Peronosclerospora maydis* (Racib.) C.G. Shaw is a principal causal agent, causing yield losses up to 90–100% in susceptible cultivars under warm, humid conditions, particularly at early growth stages (Pakki and Djaenuddin 2019; Habibullah *et al*. 2025). In Sumatra, *P. maydis* predominates as a lineage distinct from the main pathogen in Java (Suharjo *et al*. 2020). Yield losses are worsened by agronomic practices common in Indonesia—asynchronous planting, continuous cultivation, and susceptible hybrids—together with climate variability (Velásquez *et al*. 2018; Hanafiah *et al.* 2025), and by declining metalaxyl efficacy from resistant populations (Adhi *et al*. 2024; Habibullah *et al*. 2025), heightening interest in biological control alternatives. Microbial antagonists can suppress disease across diverse crop systems via

resource competition, antimicrobial production, mycoparasitism, and plant defense activation, though mechanisms vary (Dobrzyński and Naziębło 2024; Yuan *et al*. 2025a).

Among the most promising biological control agents are *Streptomyces*, *Trichoderma*, and *Paenibacillus* species, which suppress pathogens and enhance crop resilience through complementary mechanisms (Aeny *et al*. 2018; Khan *et al*. 2020). However, information on their relative performance against maize downy mildew caused by *P. maydis* remains limited, as most prior studies evaluated individual antagonists separately, preventing direct comparisons and limiting identification of optimal candidates (Yuan *et al*. 2025b).

Because several *Peronosclerospora* species occur in Southeast Asian maize-growing regions and may differ epidemiologically, accurate pathogen identification is important for interpreting disease suppression studies. Thus, this study aimed to (i) confirm the pathogen's identity in Lampung via cox2-based phylogenetic analysis and (ii) evaluate and compare the disease-suppressive effects of *S. hygroscopicus*, *T. asperellum*, and *P. polymyxa* under greenhouse conditions, hypothesizing that all three would reduce disease development relative to the control, with varying efficacy. Seed germination and plant-related variables were also assessed to determine whether lower disease pressure improved host performance.

Materials and methods

Research site and plant material

Experiments were conducted from September 2023 to August 2024 under greenhouse conditions at the Plant Disease Laboratory, Faculty of Agriculture, University of Lampung, and the Food Crop and Horticulture Experiment Station, Lampung Province, Indonesia. Hybrid maize seeds (cv. NK 212), susceptible to downy mildew, were surface-sterilized (70% ethanol for 1 min; 1% sodium hypochlorite for 2 min), rinsed three times with sterile distilled water, and air-dried under sterile conditions prior to use.

Phylogenetic analysis of *Peronosclerospora* isolate

Maize leaves naturally infected with downy mildew were collected in Bandar Lampung, Indonesia. Genomic DNA was extracted from infected tissues, and the mitochondrial cox2 gene was amplified using primers PCOXF and PCOXR (650–700 bp) (Hudspeth *et al*. 2000) via PCR (25 µl reactions; 95°C/3 min; 35 cycles of 95°C/30 s, 52°C/45 s, 72°C/1 min; 72°C/7 min). Products were separated on 1% agarose gel, purified, and sequenced (Genetika Science, Jakarta, Indonesia). Sequences were compared with GenBank entries using BLAST, and phylogenetic analysis was conducted using the Neighbor-Joining method in MEGA v12 (Kumar *et al.* 2024) with the Kimura 2-parameter model and 1,000 bootstrap replicates.

Source and preparation of antagonistic microorganisms

The antagonistic microorganisms were obtained from the culture collection of the Plant Disease Laboratory, Faculty of Agriculture, University of Lampung: *S. hygroscopicus* strain GGF4 (GenBank accession no. MH170280), *T. asperellum* strain T1 (LC644658), and *P. polymyxa* strain PPL01 (PZ092858). The isolates were propagated on malt extract agar, potato dextrose agar, and yeast potato agar (YPA), respectively, at 27 ± 2°C. Spore suspensions of *S. hygroscopicus* and *T. asperellum* were adjusted to 1×10^6 spores ml^{-1} (hemocytometer; Sinclair and Dhingra 2017), and *P. polymyxa* to ~1×10^6 CFU ml^{-1} via serial dilution plating on YPA.

Seed germination assay

Colonies of *S. hygroscopicus* (14 d), *T. asperellum* (7 d), and *P. polymyxa* (24 h) were cultured at 27 ± 2°C on respective media, and inoculum concentration adjusted as above. Seeds were soaked in 100 ml antagonist suspension or sterile water (control) for 24 h, then placed in rockwool trays in a completely randomized design with four treatments and six replicates (10 seeds each). Germination (radicle ≥2 mm) was recorded at 10 days after sowing.

Greenhouse experiment

The planting medium consisted of a 2:1 (v/v) topsoil-manure mixture. Seeds were soaked 24 h in the respective antagonist suspension or sterile water (control; 20 g seeds/100 ml), and five seeds were sown per polybag. Inoculum was prepared from symptomatic maize leaves incubated overnight in a humid chamber; sporangia from the abaxial leaf surface were suspended in sterile water and adjusted to 1×10^6 sporangia ml^{-1}, then applied as five droplets into the whorl of each seedling 7 days after planting. The corresponding antagonist suspension (or sterile water for controls) was subsequently applied as either a soil drench or foliar spray at 7 DAP and weekly thereafter until 35 DAP.

Observation parameters

Seed germination was assessed at 10 days after sowing. Disease development was assessed weekly from 1 to 5 WPT by recording disease incidence and severity, while the incubation period was determined based on the time to symptom appearance. Disease severity was assessed using a 0–4 scale: 0 = no symptoms; 1 = <10% leaf area affected; 2 = 10–25%; 3 = 26–50%, with distortion and stunting; 4 = >50%, severe stunting, systemic infection, or plant death. Disease severity index (DSI) was calculated as DSI (%) = $[\Sigma(n \times v)/(N \times V)] \times 100$ (Townsend and Heuberger 1943), where n is the number of plants per severity category, v the corresponding rating, N the total plants assessed, and V the highest rating. AUDPC was calculated from sequential severity assessments (Bocianowski *et al.* 2020; Précigout *et al.* 2020). Plant height, leaf number, and shoot/root dry weights were measured at 5 WPT after oven-drying at 70°C to constant weight.

Experimental design and statistical analysis

Statistical analyses were conducted in R software (R Core Team 2024). Seed germination was analyzed via one-way ANOVA. Disease development and plant growth parameters were determined using two-way ANOVA with antagonist treatment and application method as fixed factors. Temporal disease progression was summarized into a single AUDPC variable to prevent pseudoreplication. Significant effects ($p < 0.05$) were further evaluated using Tukey's HSD (emmeans package), with partial η^2 as effect size (effectsize package). Model assumptions were verified using Q–Q plots, Shapiro–Wilk, and Levene's tests.

Results

Phylogenetic analysis of the *Peronosclerospora* isolate

The cox2 sequence of the Lampung isolate was deposited in GenBank (accession no. PZ135412). BLAST showed high similarity to *Peronosclerospora*, particularly *P. maydis*. Neighbor-Joining placed the Lampung isolate (Bulai) in a lineage with *P. maydis* reference sequences (Fig. 1), clustering with voucher KRAM:O-5859(J) from Germany (MW025835.1; 87% bootstrap support), and sister to voucher BRIP 70329 from Australia (OK336447.1; 92%). A separate lineage was comprised of *P. maydis* DM-NR02 from Thailand (LC537879.1) and the strongly supported MT506937.1–*P. sorghi* OR734661.1 subclade from Indonesia (98% and 95%, respectively); other *Peronosclerospora* species occupied separate branches, with *P. maydis* isolate 227171 from Thailand (HM988977.1) on an early-diverging branch.

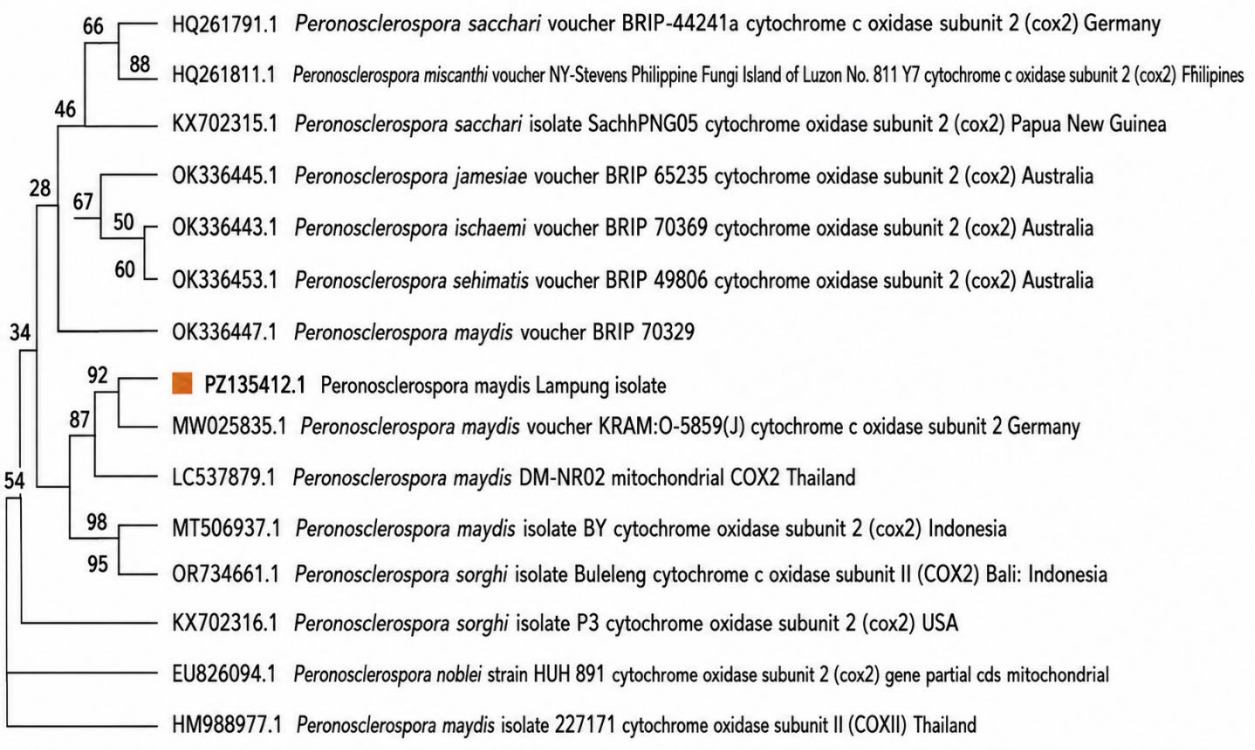

Fig. 1. Phylogenetic tree of *cox2* gene sequences for the *P. maydis* isolate and related reference strains (Neighbor-Joining method, MEGA12, 1,000 bootstrap replicates).

Effects of antagonistic microorganisms on maize seed germination

Treatment significantly affected maize seed germination ($F_{3, 20} = 27.78$, $p < 0.001$, partial $\eta^2 = 0.81$). Germination increased from 66.67 ± 2.11% in the control to 90.00 ± 3.65%, 93.33 ± 2.11%, and 96.67 ± 2.11% with *S. hygroscopicus*, *T. asperellum*, and *P. polymyxa*, respectively (Fig. 2). All microbial treatments differed significantly from the control but not from each other (Tukey's HSD).

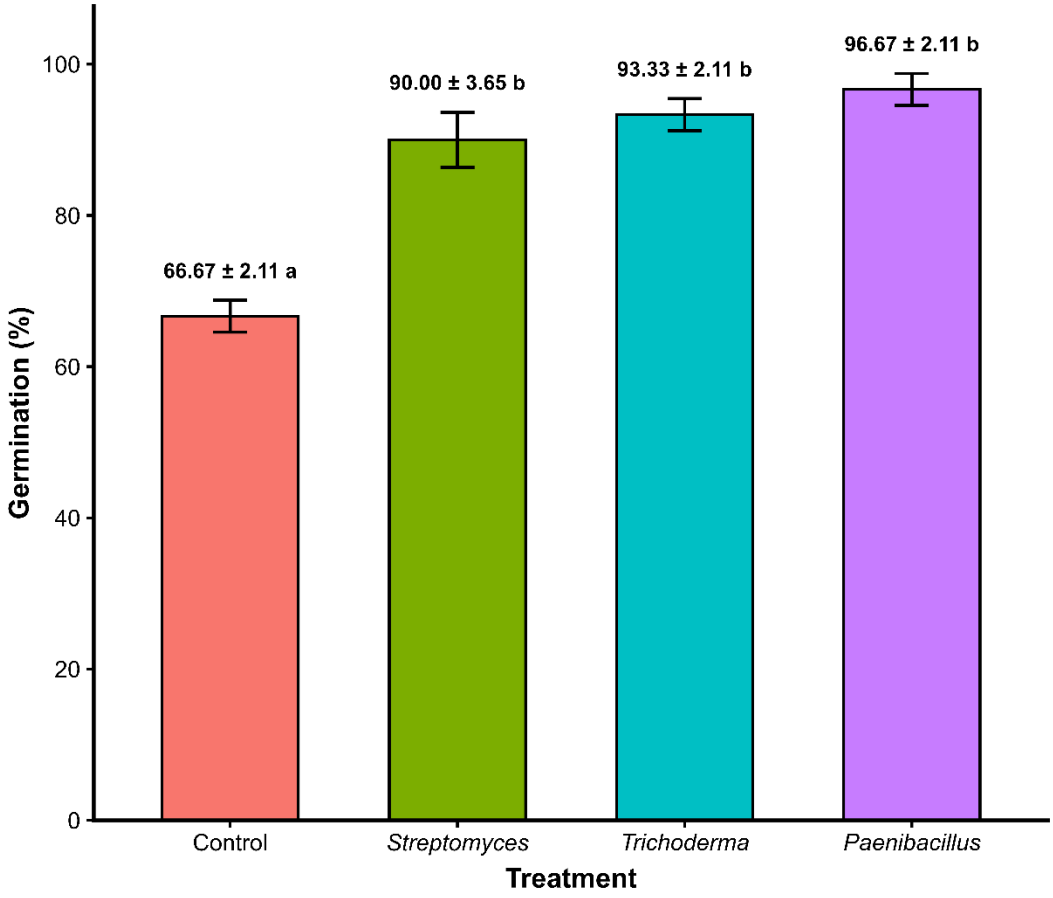

Fig. 2. Germination percentage of maize seeds after treatment with antagonistic microorganisms. Values are mean ± SE (n = 6). Means with the same letter do not differ significantly (Tukey's HSD, $p \leq 0.05$).

Effects of antagonistic microorganisms on maize downy mildew development

Symptom development. Typical symptoms appeared approximately 7 days after inoculation with *P. maydis*, initially as pale chlorotic streaks parallel to the leaf veins. These areas expanded as the disease progressed, and infected leaves produced white conidial masses characteristic of maize downy mildew.

Incubation period. Antagonistic microorganisms significantly affected the incubation period ($F_{3, 24} = 11.84$, $p < 0.001$, partial $\eta^2 = 0.60$), whereas application method and its interaction were not significant ($p > 0.05$). All microbial treatments significantly prolonged the incubation period compared with the control (11.78 ± 0.29 days), with no significant differences between them (Fig. 3). Data were therefore pooled across application methods.

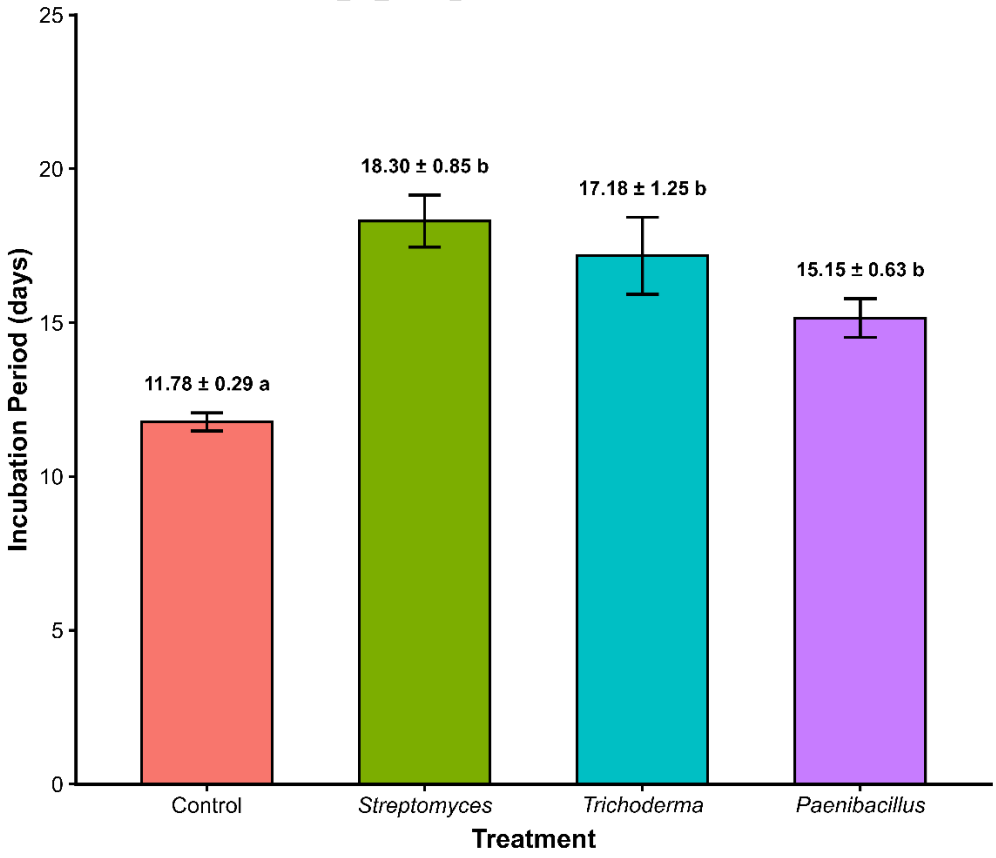

Fig. 3. Effect of antagonistic microorganisms on the incubation period of maize downy mildew (estimated marginal means pooled across application methods). Bars indicate mean ± SE (n = 8). Means with different letters differ significantly (Tukey's HSD, $p \leq 0.05$).

Disease incidence and severity. At 3 weeks post-treatment (WPT), antagonistic microorganisms significantly affected disease incidence ($F_{3, 24} = 7.09$, $p = 0.0014$, partial $\eta^2 = 0.47$) and severity ($F_{3, 24} = 10.16$, $p < 0.001$, partial $\eta^2 = 0.56$). Neither application method nor its interaction with antagonistic microorganisms was significant (Table 1).

Table 1. Disease incidence and disease severity of maize downy mildew at 3 and 5 weeks post-treatment (WPT) with antagonistic microorganisms.

Treatment	Disease Incidence (%)		Disease Severity (%)	
	3 WPT	5 WPT	3 WPT	5 WPT
Control	97.5 ± 2.50 a	97.5 ± 2.50 a	67.50 ± 2.99 a	96.88 ± 2.49 a
P. polymyxa	65.0 ± 7.32 b	87.5 ± 6.48 ab	44.38 ± 4.38 b	81.87 ± 6.33 ab
T. asperellum	52.5 ± 11.30 b	80.0 ± 6.55 ab	35.00 ± 7.79 b	70.00 ± 6.88 b
S. hygroscopicus	57.5 ± 5.90 b	72.5 ± 3.66 b	31.25 ± 2.63 b	63.13 ± 3.26 b

Notes: Values are mean ± SE (n = 8 pots). Means with the same letter within a column do not differ significantly (Tukey's HSD, $p \leq 0.05$).

At 3 WPT, all microbial treatments significantly reduced disease incidence and severity compared with the control, with no significant differences between them. At 5 WPT, antagonistic microorganisms remained significant for incidence ($F_{3, 24} = 4.13$, $p = 0.017$, partial $\eta^2 = 0.34$) and severity ($F_{3, 24} = 8.13$, $p < 0.001$, partial $\eta^2 = 0.50$), whereas application method and its interaction remained non-significant. *Trichoderma asperellum* and *S. hygroscopicus* significantly reduced final severity, but only *S. hygroscopicus* significantly reduced final incidence, while the effects of *P. polymyxa* were intermediate and did not differ from the control.

Area Under Disease Progress Curve (AUDPC).

The control had the highest AUDPC (239.69 ± 7.57), whereas *S. hygroscopicus* had the lowest (120.31 ± 8.73), followed by *T. asperellum* (135.00 ± 20.17) and *P. polymyxa* (177.81 ± 14.22; Fig. 4). *S. hygroscopicus* differed significantly from the control and *P. polymyxa*, while *T. asperellum* did not differ from either antagonist.

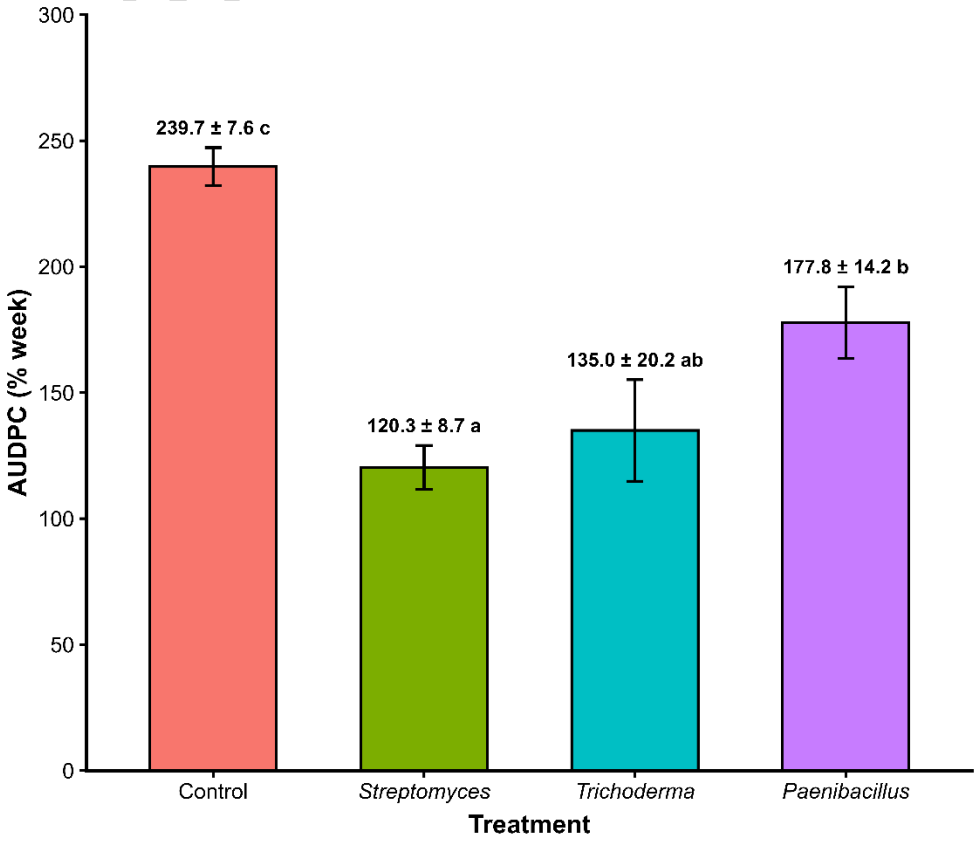

Fig. 4. AUDPC of maize downy mildew under different antagonistic microorganism treatments. Values are mean ± SE (n = 8). Means with the same letter do not differ significantly (Tukey's HSD, $p \leq 0.05$).

Early seedling establishment

Microbial treatments produced more uniform emergence and greater shoot development than the control (Fig. 5). These observations are descriptive because seedling

growth at 10 days post-treatment was not statistically quantified. Later measurements of plant height, leaf number, and shoot and root dry weights provided the basis for treatment comparisons.

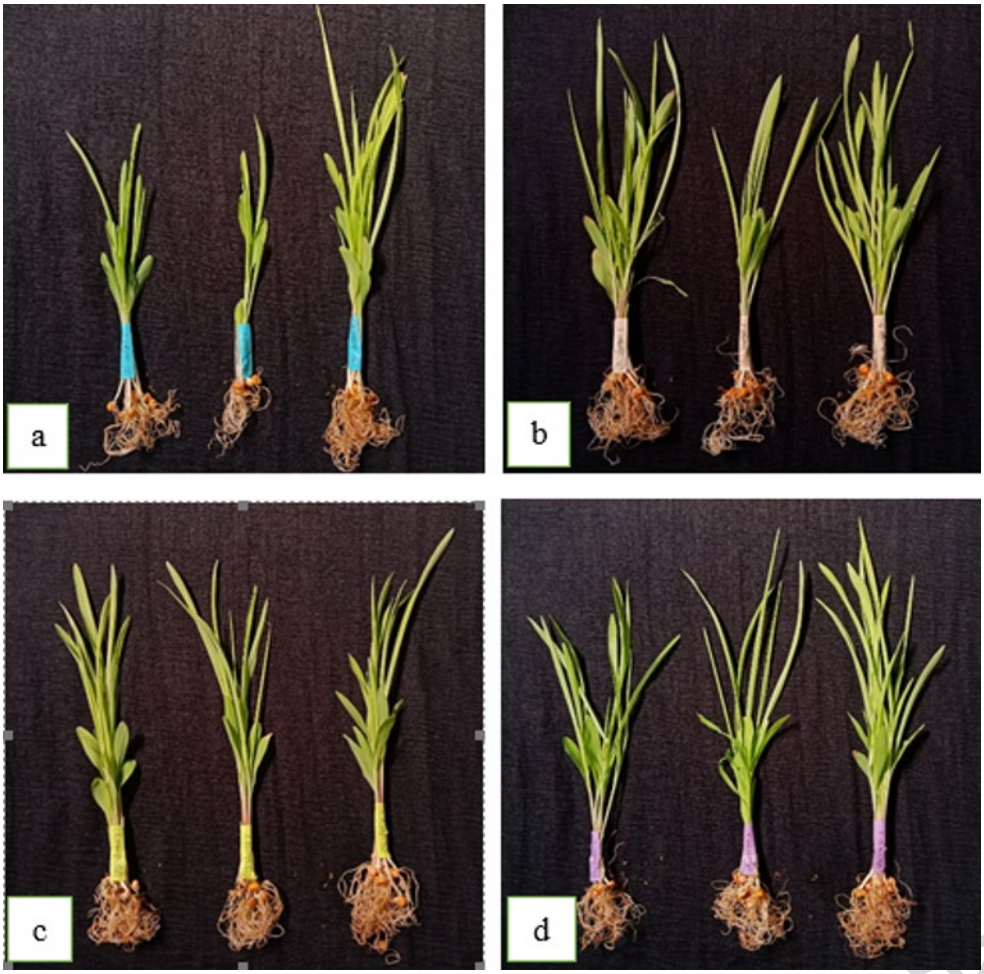

Fig. 5. Representative growth of maize seedlings 10 days after treatment: (a) control, (b) *S. hygroscopicus*, (c) *T. asperellum*, and (d) *P. polymyxa*

Associated host performance under disease pressure

At 5 WPT, antagonistic microorganisms significantly affected plant height ($F_{3, 24}$ = 3.43, p = 0.033, partial η^2 = 0.30), leaf number ($F_{3, 24}$ = 15.62, p < 0.001, partial η^2 = 0.66), shoot dry weight ($F_{3, 24}$ = 7.17, p = 0.0013, partial η^2 = 0.47), and root dry weight ($F_{3, 24}$ = 4.78, p = 0.0094, partial η^2 = 0.37). Application method and its interaction with microbial treatment were non-significant (p > 0.05). Microbial treatments improved growth and

biomass compared with the control (Table 2). *Trichoderma asperellum* produced the greatest plant height (109.81 ± 0.83 cm) and leaf number (9.65 ± 0.13), whereas *S. hygroscopicus* and *P. polymyxa* produced intermediate values. All microbial treatments significantly increased shoot and root dry weights with no differences between them.

Table 2. Growth and biomass of maize at 5 weeks post-treatment (WPT) with antagonistic microorganisms under downy mildew pressure.

Treatment	Plant height	Number of leaves	Shoot dry weight (g)	Root dry weight (g)
Control	104.31 ± 1.85 a	8.65 ± 0.06 a	48.48 ± 1.70 a	6.69 ± 0.25 a
S. hygroscopicus	108.78 ± 1.37 ab	9.15 ± 0.11 b	56.86 ± 1.56 b	8.80 ± 0.43 b
P. polymyxa	109.63 ± 0.89 ab	9.40 ± 0.11 bc	56.57 ± 1.16 b	8.83 ± 0.45 b
T. asperellum	109.81 ± 0.83 b	9.65 ± 0.13 c	57.36 ± 1.58 b	8.79 ± 0.61 b

Notes: Values are mean ± SE (n = 8 independent pots). Means with the same letter within a column do not differ significantly (Tukey's HSD, $p \leq 0.05$).

Discussion

This study demonstrated that antagonistic microorganisms suppressed maize downy mildew under greenhouse conditions. All antagonists prolonged the incubation period, indicating delayed symptom expression and potentially slower disease progression (Précigout *et al*. 2020; Vitale 2023). This response may have reflected interference with early pathogen establishment, consistent with previous reports of microbial inhibition of pathogen penetration and colonization (Mugiastuti *et al*. 2023).

The prolonged incubation period was accompanied by reductions in disease incidence, severity, and AUDPC. Although *S. hygroscopicus* produced the lowest mean AUDPC and severity, most parameters did not differ significantly between antagonists,

indicating comparable suppression that may involve several mechanisms: *Streptomyces* species produce antimicrobial metabolites inhibiting pathogen growth and infection (Viaene *et al*. 2016; Montesdeoca-Flores *et al*. 2023), whereas *Trichoderma* and *Paenibacillus* spp. may act through mycoparasitism, competition, antimicrobial compounds, and induced plant defenses (Guzmán-Guzmán *et al*. 2023; Dobrzyński and Naziębło 2024), though mechanisms were not examined here. Neither application method nor its interaction with an antagonist significantly affected disease development, suggesting that efficacy depended on the antagonist, offering application flexibility pending field validation. Microbial treatments were also associated with higher germination and improved plant performance under disease pressure; however, without pathogen-free antagonist treatments, these responses cannot be interpreted as direct growth-promoting effects (Backer *et al*. 2018; Guzmán-Guzmán *et al*. 2023). Further evaluation across environments and maize cultivars is required to confirm the consistency of these biological control agents. Future studies should examine microbial combinations, pathogen colonization, metabolite production, and host defense responses. Including non-inoculated controls would also clarify potential phytotoxic and growth-promoting effects.

In conclusion, *Peronosclerospora maydis* was confirmed as the causal agent of maize downy mildew in Lampung through *cox2* sequence analysis and phylogenetic placement. Under greenhouse conditions, all antagonists reduced disease development numerically. *Streptomyces hygroscopicus* and *T. asperellum* significantly reduced final disease severity, whereas *P. polymyxa* produced an intermediate response. Field trials, antagonist combinations, and mechanistic studies are required to validate these effects and clarify the mechanisms of disease suppression.

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Data availability

The sequence data generated in this study have been deposited in the NCBI GenBank database. The *Peronosclerospora maydis* isolate is available under accession number PZ135412.

Conflict of interest

The authors declare no conflicts of interest.

References

Adhi S.R., Widiantini F., Yulia E. 2024. Early detection of fungicide resistance through sensitivity testing of various fungicide active ingredients and genetic variation of downy mildew-causing *Peronosclerospora maydis* from maize (corn) production centers in Java, Indonesia. AGRIVITA Journal of Agricultural Science 46 (2): 276–288. DOI: https://doi.org/10.17503/agrivita.v46i2.4276

Aeny T.N., Prasetyo J., Suharjo R., Dirmawati S.R., Efri, Niswati A. 2018. Short communication: Isolation and identification of actinomycetes potential as the antagonist of *Dickeya zeae* pineapple soft rot in Lampung, Indonesia. Biodiversitas 19 (6): 2252–2258. DOI: https://doi.org/10.13057/biodiv/d190610

Backer R., Rokem J.S., Ilangumaran G., Lamont J., Praslickova D., Ricci E., Subramanian S., Smith D.L. 2018. Plant Growth-Promoting Rhizobacteria: Context, Mechanisms of Action, and Roadmap to Commercialization of Biostimulants for Sustainable Agriculture. Frontiers in Plant Science 9: 1473. DOI: https://doi.org/10.3389/fpls.2018.01473

Bocianowski J., Tratwal A., Nowosad K. 2020. Genotype by environment interaction for area under the disease-progress curve (AUDPC) value in spring barley using additive main effects and multiplicative interaction model. Australasian Plant Pathology 49 (4): 525–529. DOI: https://doi.org/10.1007/s13313-020-00723-7

Dobrzyński J., Naziębło A. 2024. *Paenibacillus* as a biocontrol agent for fungal phytopathogens: Is *P. polymyxa* the only one worth attention? Microbial Ecology 87: 134. DOI: https://doi.org/10.1007/s00248-024-02450-8

Guzmán-Guzmán P., Kumar A., de los Santos-Villalobos S., Parra-Cota F.I., Orozco-Mosqueda M.d.C., Fadiji A.E., Hyder S., Babalola O.O., Santoyo G. 2023. *Trichoderma* Species: Our Best Fungal Allies in the Biocontrol of Plant Diseases—A Review. Plants 12 (3): 432. DOI: https://doi.org/10.3390/plants12030432

Habibullah M., Joko T., Wibowo A., Widiastuti A. 2025. Maize induced resistance against downy mildew mediated by benzoic acid increased photosynthesis rate and chlorophyll content. Journal of Tropical Plant Pests and Diseases 25 (2): 255–261. DOI: https://doi.org/10.23960/jhptt.225255-261

Hanafiah D.S., Syamsafitri, Mariati, Hanum C., Muhdi, Rakasiwi G., Abdurrahman M.H., Nur M.A., Sahtika D. 2025. Identification and characterization of corn plants for downy mildew resistance in North Sumatra, Indonesia. Biodiversitas 26 (5): 2130–2138. DOI: https://doi.org/10.13057/biodiv/d260511

Hudspeth D.S.S., Nadler S.A., Hudspeth M.E.S. 2000. A *cox2* molecular phylogeny of the Peronosporomycetes. Mycologia 92 (4): 674–684. DOI: https://doi.org/10.1080/00275514.2000.12061208

Khan M.S., Gao J., Chen X., Zhang M., Yang F., Du Y., Moe T.S., Munir I., Xue J., Zhang X. 2020. Isolation and characterization of plant growth-promoting endophytic bacteria *Paenibacillus polymyxa* SK1 from *Lilium lancifolium*. BioMed Research International 2020: 8650957. DOI: https://doi.org/10.1155/2020/8650957

Kumar S., Stecher G., Suleski M., Sanderford M., Sharma S., Tamura K. 2024. MEGA12: molecular evolutionary genetics analysis version 12 for adaptive and green computing. Molecular Biology and Evolution 41 (11): msae263. DOI: https://doi.org/10.1093/molbev/msae263

Montesdeoca-Flores D.T., Hernández-Bolaños E., León-Barrios M., Hernández-Amador E., Díaz-González S., Abreu-Acosta N., Luis-Jorge, J.C. 2023. Antifungal Activity of *Streptomyces* spp. Extracts *In Vitro* and on Post-Harvest Tomato Fruits against Plant Pathogenic Fungi. Horticulturae 9 (12): 1319. DOI: https://doi.org/10.3390/horticulturae9121319

Mugiastuti E., Manan A., Soesanto L. 2023. Biological control of maize downy mildew with the antagonistic bacterial consortium. Biodiversitas 24 (9): 4644–4650. DOI: https://doi.org/10.13057/biodiv/d240904

Pakki S., Djaenuddin N. 2019. The effectiveness combination of resistant varieties and metalaxyl fungicide in controlling downy mildew disease (*Peronosclerospora maydis*) in maize plant. Journal of Tropical Plant Pests and Diseases 19 (1): 42–51. DOI: https://doi.org/10.23960/j.hptt.11942-51

Précigout P.A., Claessen D., Makowski D., Robert C. 2020. Does the latent period of leaf fungal pathogens reflect their trophic type? A meta-analysis of biotrophs, hemibiotrophs, and necrotrophs. Phytopathology 110 (2): 345–361. DOI: https://doi.org/10.1094/PHYTO-04-19-0144-R

R Core Team. 2024. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from: https://www.R-project.org/

Sinclair J.B., Dhingra O.D. 2017. Basic Plant Pathology Methods. 2nd ed. CRC Press, Boca Raton, FL, USA, 434 pp. DOI: https://doi.org/10.1201/9781315138138

Suharjo R., Swibawa G., Prasetyo J., Fitriana Y., Danaatmadja Y., Budiawan A., Roberts S., Noorhajati N., Amad M., Thines M. 2020. *Peronosclerospora australiensis* is a synonym of *P. maydis*. Mycological Progress 19 (12): 1309–1315. DOI: https://doi.org/10.1007/s11557-020-01628-x

Townsend G.R., Heuberger J.W. 1943. Methods for estimating losses caused by diseases in fungicide experiments. Plant Disease Reporter 27: 340–343

Velásquez A.C., Castroverde C.D.M., He S.Y. 2018. Plant-pathogen warfare under changing climate conditions. Current Biology 28 (10): R619–R634. DOI: https://doi.org/10.1016/j.cub.2018.03.054

Viaene T., Langendries S., Beirinckx S., Maes M., Goormachtig S. 2016. *Streptomyces* as a plant's best friend? FEMS Microbiology Ecology 92 (2): fiw119. DOI: https://doi.org/10.1093/femsec/fiw119

Vitale A. 2023. Epidemiology and Control of Plant Diseases. Plants 12 (4): 793. DOI: https://doi.org/10.3390/plants12040793

Yuan P., Zhu L., Song Z., Wang Y., Chen X. 2025a. From biocontrol to synthesis: innovative progress of *Paenibacillus* in mechanism analysis, gene editing and platform construction. International Journal of Molecular Sciences 26 (22): 10886. DOI: https://doi.org/10.3390/ijms262210886

Yuan P., Song Z., Zhang L., Pan Z., Chen X. 2025b. Exploring the multifunctional role of *Paenibacillus* metabolites in various fields. International Journal of Molecular Sciences 26 (24): 12089. DOI: https://doi.org/10.3390/ijms262412089