Microbial inoculation increases maize yield and root biomass across smallholder farming systems in Rwanda

Benjamin Bukombe[1,*]Anna Edlund[2], Peter G. Saavedra[2], Josue W. Mberwa[1], Jack A. Gilbert[2,3,4,5], Francois X. Naramabuye[6], Sirikare Sylvere[7], Paige M. Hansen[2], Janet K. Jansson[2,8], Thomas W. Crowther[9,2]

[1]Oath Africa, Kigali, Rwanda

[2]Oath Biome, San Francisco, USA

[3]Department of Pediatrics, University of California San Diego, La Jolla, CA 92037, United States
[4]Scripps Institution of Oceanography, University of California San Diego, La Jolla, 92037 CA, United States
[5]Center for Microbiome Innovation, University of California San Diego, La Jolla, CA 92037, United States
[6]College of Agriculture, Animal Science and Veterinary Medicine, University of Rwanda, Musanze, Rwanda

[7]Ministry of Agriculture and Animal Resources, Kigali, Rwanda

[8]Pacific Northwest National Lab, Washington, United States

[9]King Abdullah University of Science and Technology (KAUST), Thuwal, Saudi Arabia.

*Corresponding author email: benjamin@oathafrica.com

ORCID:

Benjamin Bukombe: 0000-0001-5135-9783

Anna Edlund: 0000-0002-3394-4804

Paige M. Hansen: 0000-0002-9838-5601

Jack A. Gilbert: 0000-0001-7920-7001

Janet K. Jansson: 0000-0002-5487-4315

Thomas W. Crowther: 0000-0001-5674-8913

Francois X. Naramabuye: 0000-0002-4422-0617

Peer review status:

This preprint was also submitted to the New Phytologist journal for peer review.

Summary

Soil degradation, nutrient depletion, and increasing climate stress constrain food productivity across tropical smallholder farming systems. Microbial inoculants have emerged as a promising strategy to improve soil functions and crop yield, yet field-based data from African smallholder systems remain limited, particularly for multi-strain bacterial consortia. Using a multi-strain consortium in a Randomized Complete Block design experiment, we quantified the effect that soil microbial inoculants have on maize yield and root biomass production across six farmer-managed field sites spanning four agroecological zones in Rwanda. Across all sites, we found that maize grain yield was significantly greater in SLP-treated plots than in untreated controls, and maize response magnitude varied among locations. The average grain yield uplift due to microbial inoculants varied between 59–68% compared to the untreated control fields. Root biomass followed a similar trend, with an increase of 62–74% in root biomass in the treated field compared to the untreated control fields. Altogether, these results suggest that soil microbial inoculants can improve crop yield and biomass productivity under heterogeneous smallholder field conditions and highlight the potential of microbiome-based interventions as complements to existing soil fertility management strategies in tropical African agricultural systems for food security and carbon sequestration.

Keywords: maize, root biomass, microbial inoculants, smallholder agriculture, tropical agroecosystems, Rwanda

Introduction

The sustainability of food production in African Tropical agricultural systems is under increasing pressure from soil degradation and nutrient depletion under a changing climate (Giller *et al.*, 2009; Mutsaers *et al.*, 2017; Moreno-Jiménez *et al.*, 2023; Appiah-Twumasi *et al.*, 2026). These challenges are often amplified by unsustainable land management on steep and unstable hillslopes, which accelerates erosion and reduces key agroecosystem functions (Mutsaers *et al.*, 2017; Doetterl *et al.*, 2021; Summerauer *et al.*, 2021). Conventional soil restoration practices, including compost, animal manure, and combinations of organic and inorganic inputs, can improve soil fertility and enhance crop productivity (Vanlauwe *et al.*, 2001; Mando *et al.*, 2005; Pypers *et al.*, 2011). However, in smallholder farming systems, these practices are frequently constrained by the limited availability of organic inputs, which are frequently diverted for other essential uses such as fuel for heating, cooking, or as forage for livestock (Giller *et al.*, 2009; Sileshi *et al.*, 2025). This is compounded by the high costs of mineral fertilizers, which only lead to soil depletion in subsequent agricultural cycles. Identifying scalable solutions to sustainably enhance soil health and nutrient accessibility in the long-term remains among the most critical challenges for achieving sustainable food production and economic security across the region (Chitakira & Torquebiau, 2010; Ullah *et al.*, 2023; Ngango *et al.*, 2023; Othman *et al.*, 2024). In recent years, a growing body of evidence has highlighted the potential of microbial solutions – including microbial community inoculations – for alleviating the limitations on agricultural productivity. Given the potential to improve local biodiversity at the same time as enhancing carbon capture (Leal Filho *et al.*, 2023; Beattie *et al.*, 2024), and improving yields (Wagg *et al.*, 2014; Delgado-Baquerizo *et al.*, 2016; Erktan *et al.*, 2017; Fierer, 2017; Beattie *et al.*, 2024; Pandey & Saharan, 2025; Romero *et al.*, 2025), microbial inoculants have been identified as a unique opportunity for simultaneously meeting multiple global sustainability goals (Crowther *et al.*, 2024; Mason *et al.*, 2025) (Mason et al., 2023). Indeed, although contemporary laboratory and greenhouse experiments highlighted the potential for introductions of individual microbial taxa to increase plant biomass and yields (Adesemoye *et al.*, 2009; Nie *et al.*, 2015; Worsley *et al.*, 2020; Jiang *et al.*, 2023), the emerging consensus is that mixtures of species including "home-grown" or native taxa consistently provide the strongest positive benefits for productivity, highlighting the importance of diversity for maintaining ecological functioning (Kumar *et al.*, 2016; Jack *et al.*, 2021; Averill *et al.*, 2022; Liu *et al.*, 2023; Crowther *et al.*, 2024). Yet, despite the growth of this academic field, the technical challenges in scaling the production of such complex microbial consortia have limited their application in high relevance agro-economic cropping systems. As such, the efficacy of complex microbial consortia for improving agricultural yields in important cash crops at scale remains unclear, particularly in the context of African smallholder farmers, whose livelihoods are so tightly dependent on such productivity. Existing studies that attempted to understand and assess the impact of microbial inoculation in smallholder fields within African Tropical agroecosystems have often relied on single rhizobia inoculants (Wolde-meskel *et al.*, 2018; Adjei-Nsiah *et al.*, 2019; Belete *et al.*, 2019). However, field trials conducted across sub-Saharan regions revealed inconsistent performance and efficacy of rhizobia-based inoculants, likely due to heterogeneity of pedoclimatic conditions of Tropical agricultural systems (Grönemeyer & Reinhold-Hurek, 2018). As such, there is a need to develop and deploy microbial inoculant candidates tailored to the specific environmental conditions of these smallholder farms, including microbial taxa with strong tolerance and adaptability to tropical stressors (Grönemeyer & Reinhold-Hurek, 2018) and soil geochemical gradients (Msimbira & Smith, 2020; Kidinda *et al.*, 2023).

In this study, we quantify the effects and efficacy of a multi-species microbial inoculum, composed of 22 bacterial taxa (Table S1), on maize grain yield and root biomass in tropical smallholder agroecosystems across Rwanda. We hypothesize that inoculation with beneficial, non-GMO microbes increases maize yield and root biomass relative to untreated controls, due to improved plant-microbiome interaction and nutrient acquisition strategies (Kidinda *et al.*, 2023; Shi *et al.*, 2025). We further hypothesize that the magnitude of maize response to microbial inoculants varies among sites due to differences in local edaphic conditions that can mediate inoculant performance, but the effect size of edaphic variability is likely smaller compared to the effect size of microbial inoculants. To test these hypotheses, we conducted microbial intervention field trials on smallholder farms across four agroecological zones in Rwanda. We evaluated the effects of a multi-strain microbial consortium on maize yield and root biomass production with multiple application rates across six sites spanning distinct soil geoclimatic conditions.

Materials and Methods

Study region and sites description

The study sites are located in Rwanda across four agroecological zones (Eastern Savana, Eastern Plateau, Mayaga-Bugesera, and Central Plateau) with contrasting pedoclimatic conditions (Table 1). We established study sites across four agroecological zones: Nova (Eastern Savanna), Gahengeri (Eastern Plateau), Mayange (Mayaga–Bugesera), and Muyira, Save, and Tumba (Central Plateau). The major differences among agroecological systems are driven by variations in climate (precipitation) (Fig. 1), topography, and soil geochemistry (Table 1). Sites in the Eastern Savanna were geologically developed on granitic parent material, at an altitude that ranges between 1380-1450 m and have a pH ranging from 4 to 5. The Eastern Savanna is characterised by low precipitation. Sites in the central plateau were developed on granitic parent material and are characterised by moderate precipitation. Soils at all sites are depleted in macro- and rock-derived nutrients and have low nutrient holding capacity (Table 1).

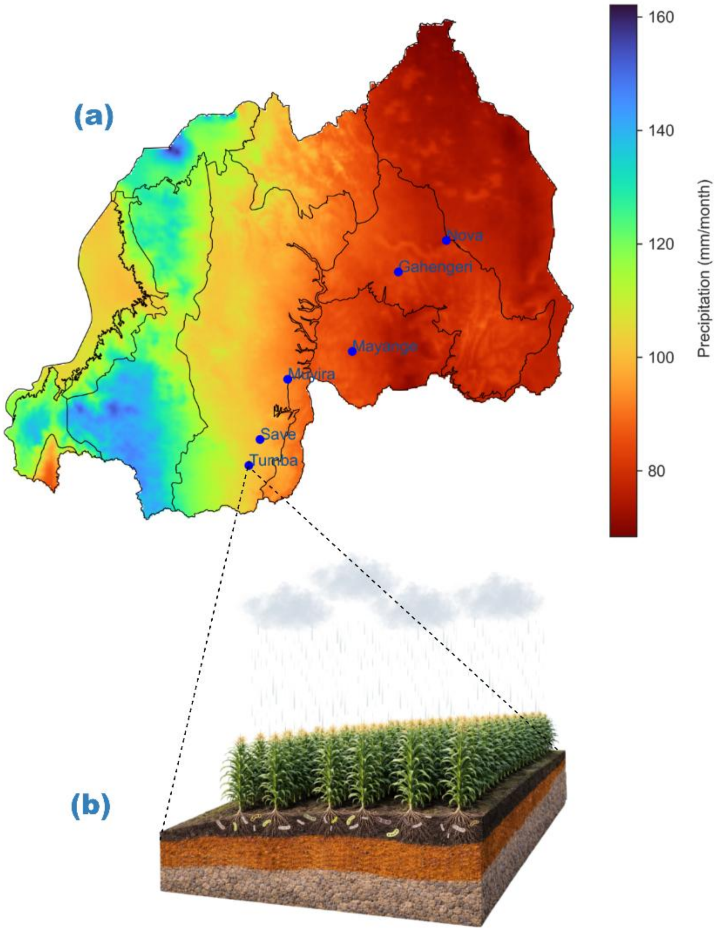

Figure 1. (a) Overview of the study region and location of the study sites in Rwanda across different agroecological zones and climate (i.e., precipitation) patterns. The black lines indicate the boundaries of different agroecological zones. Soil types and topographic data are presented in Table 1. (b) Conceptual figure of the maize experiments setup.

Table 1. Physical and chemical soil properties of the farm sites included in this study before Soil Life Product (SLP) amendment. pH_KCl: soil pH-KCl, SOC: soil organic carbon [%], N: total nitrogen [%], Ca: exchangeable Calcium (cmol.kg^{-1}), Prep: average monthly precipitation [mm], Temp: average monthly temperature [°C], Alt: altitude [m].

Site	pH	SOC	N	Ca	Sand	Silt	Clay	Prec	Temp	Slope	Alt	Soil type
Nova	5.9	2.3	0.16	6.1	61.0	12.0	27.0	77.2	20.2	8.0	1456	Haplic Luvisols
Gahengeri	5.0	3.7	0.01	2.8	65.8	13.0	21.2	81.6	20.5	14.2	1383	Humic Acrisols
Mayange	4.5	3.4	0.04	3.8	78.4	9.2	12.4	81.8	21.1	5.7	1357	Humic Cambisols
Muyira	4.5	3.2	0.05	2.2	79.9	6.9	13.2	93.3	20.5	9.5	1436	Humic Cambisols
Save	5.1	2.8	0.05	8.0	72.6	11.9	15.4	100.6	19.3	8.0	1747	Haplic Ferralsols
Tumba	4.0	3.7	0.03	3.4	66.6	10.8	22.6	102.6	19.5	0.0	1620	Haplic Alisols

Trial design and plots establishment

Six research trials were established between September 2024 and March 2025 in collaboration with the University of Rwanda (UR) and participating smallholder farmers, using a randomized complete block design. Field trials were conducted with the informed consent of participating farmers. The main objective of the trials was to evaluate microbial inoculants under Sub-Saharan small holder farming conditions. We tested a multi-strain microbial consortium with a set of different bacterial strains. The Soil Life Product (SLP) consortium contained bacteria belonging to the genera *Aneurinibacillus, Bacillus, Microbacterium, Paenibacillus, Rhodococcus, and Streptomyces* and is referred to as the SLP. Full species lists and application rates (total cells per hectare; spores and vegetative cells) are presented in Supporting Information Table S1. The trial had four treatments replicated 6 times. Each experimental plot was 5 x 15 m (75 m^2). The tested treatments (T) included T1: Untreated Control; T2: SLP at 50g/Ha; T3: SLP at 150g/Ha, and T4: SLP at 250g/Ha. All treatments received inorganic fertiliser (Diammonium Phosphate (DAP): 18%, 46%) at a rate of 100 kg ha^{-1}, including the control plots. The fertiliser rate and the crop test variety were based on recommendations provided by the Rwanda Agriculture and Animal Resources Board. The test crop across all experiments was a maize variety (RMH1407).

Microbial consortia preparation

The production of the microbial consortia followed previously described methods (PCT Patent Publication WO2025240938, Microbial Consortia Production) (Holloway *et al.*, 2025). In brief, the concentrated SLP was produced using agar growth surface fermentation. The workflow comprised media preparation (liquid media and agar media), seed culture generation, plate-scale biomass production, harvesting biomass from the top of the plates, drying of biomass, grinding dried biomass into a powder, mixing with dextrose sugar to provide an osmoprotectant and a mixing agent, and quality control that included visual inspection of growing bacteria on agar plates at multiple timepoints during incubation in 28 °C, for details see below. All bacterial strains listed in SI Table 1 were cultivated on ISP Medium No. 3 agar (19 g L^{-1}; HiMedia M358). Seed cultures were grown in glucose broth containing glucose (10 g), yeast extract (4 g), peptone (4 g), and calcium chloride dihydrate (0.5 g) in 500 mL of distilled water. Both agar and liquid media were sterilized by autoclaving at 121 °C for 15 min and cooled before inoculation of bacteria.

Working stock cultures preserved in 20% glycerol at −80 °C were retrieved in batches to minimize freeze–thaw cycles. Using a sterile 10 µL loop, frozen stocks were transferred into 3 mL glucose broth in sterile 14 mL culture tubes. Tubes were loosely capped to permit aeration and incubated in a shaking incubator (aniCell NB-206CXXL) at 28 °C and 240 rpm for 36–48 hrs. Turbidity was assessed visually and recorded as growth-positive (T) or no growth (NG); cultures lacking turbidity after 24 hrs of incubation were returned for an additional 24 hrs. For each isolate, one ISP-3 plate labeled "Purity" was inoculated using a sterile swab dipped in the turbid seed culture, streaked for isolation with a sterile loop, and incubated at 28 °C. Seed cultures were advanced only when purity plates showed a single, morphologically consistent colony type; slow-growing isolates were allowed extended incubation when broth turbidity was present. For each qualified isolate, ISP-3 production plates were inoculated under aseptic conditions. A sterile swab dipped in seed culture was used to apply a central streak, followed by uniform surface distribution using a standardized side-to-side "landscaping" pattern with sequential ~60° rotations. Eighty plates were inoculated per isolate and incubated in a walk-in incubator at 28 °C for isolate-specific durations, with periodic inspection for growth and contamination.

At the designated endpoint (visible sporulation on top of colonies), plates were visually inspected and any showing aberrant morphology or suspected contamination were excluded. Under sterile conditions, 50 g sterile dextrose was dispensed onto parchment-lined trays as an osmotic protectant and carrier. Microbial biomass was scraped from agar surfaces using sterile scalpels, transferred onto the dextrose, and homogenized while minimizing agar carryover. Biomass–dextrose mixtures were transferred to sterile trays covered with autoclaved wrap (not contacting the material) and dried on enclosed racks at ambient conditions for ≥7 days until no longer tacky by sterile glove assessment. Grinding was performed in a contained room with enhanced PPE (lab coat, gloves, safety glasses, N95 respirator). The grinder (Vevor Model 1000) was disinfected with 70% ethanol and air-dried before use. Dried material was milled to a homogeneous powder while avoiding excessive repeated grinding to limit heat exposure. The finished product was transferred to 32 oz opaque bags and labeled with batch number and date. To enumerate colony-forming units (CFU) for each strain component, a 0.5 g replicate sample was collected in a sterile 50 mL tube. Negative-control broth tubes and sterility plates were included in each production run to monitor contamination, and cultures failing purity or growth criteria were excluded from downstream processing. Based on the numbers of CFU counts per gram of concentrated material, the final ready-mix was diluted and blended with dextrose and put and carefully sealed in bags (non-transparent).

Microbial inoculants and fertilizer application

The SLP consortium was transported to the field as a wettable powder and was carefully dissolved in water harvested either from rain or collected from nearby streams and lakes before applications. The application was done using a 20 L fermate backsprayer pump (Shixia Holding Co., Ltd., China), and a total of 6 applications were applied on each plot. Ten liters of water containing the assigned SLP product (at application rates specified above) were uniformly sprayed onto each 75 m^2 plot. The SLP consortium was applied 6 times. The first application was conducted at planting (sowing), the second 14 days later, and the remaining four applications were applied at 21-day intervals through maize development, continuing until the end of grain filling of the maize crop. For fertilizer applications, the 100 kg ha^{-1} of DAP was applied in two split doses. 50% was applied at the sowing stage, with the granular fertilizer placed directly in the planting hole together with the seeds. The remaining 50% was applied after 45 days using a broadcast method around the germinated plants.

Soil sampling and nutrient analysis

Baseline soil samples were collected at each site to assess soil physical and chemical properties before the start of the trial. Because of the small size of the farmers' fields in the region, we collected one composite soil sample as follows to analyse major soil properties for each site. Briefly, five soil cores were collected to a depth of 30 cm following a W-shape sampling approach. For each plot, the five cores were homogeneously mixed in a bucket, and 1 kg of composite sample was collected, packed in a zipped plastic bag, and transported to the soil and plant analysis laboratory of the University of Rwanda. Soil samples were air-dried, homogenised, sieved to 2 mm, and subsampled for physical and chemical soil properties (Table 1). Soil texture was analysed using the Bouyoucos hydrometer method (Bouyoucos 1962), with modifications following Beretta et al. (2014). Briefly, 50 g of 2 mm sieved soil were dispersed with 10% sodium hexametaphosphate ($NaPO_3$) and treated with 6% hydrogen peroxide H_2O_2 three times at 60 °C to remove organic carbon. After mixing the soil suspension and transferring it into a clean glass column, hydrometer readings on the density of the suspension were taken after 40 s and 2 hrs to distinguish between the silt and clay fractions, respectively. Soil pH was determined potentiometrically using a glass electrode connected to a portable multiparameter meter (HI9828, Hanna Instruments US Inc., USA), following Black (1965). 20 g of air-dried, 2-mm sieved soil was suspended in 1M KCl at a 1:2.5 soil: solution ratio, stirred for 10 min, and allowed to equilibrate for 30 min before pH measurement. Soil exchangeable calcium was analyzed and quantified by using atomic absorption spectrometry (AAS). Briefly, A soil sample was extracted with an excess of 1 M NH_4OAc (ammonium acetate) solution such that the maximum exchange occurs between the NH_4 and the cations originally occupying exchange sites on the soil surface. The amounts of exchangeable calcium in the extract were then determined by AAS. Total organic carbon is determined by the sulphuric acid and aqueous potassium dichromate ($K_2Cr_2O_7$) mixture. After complete oxidation from the heat of solution and external heating, following Nelson and Sommers (1974). The unused or residual $K_2Cr_2O_7$ (in oxidation) was titrated against ferrous ammonium sulphate. The used $K_2Cr_2O_7$, the difference between added and residual $K_2Cr_2O_7$, gives a measure of organic C content of soil (Nelson & Sommers, 1974).

Maize yield and root biomass measurement

At harvest, all maize plants within each plot were harvested, excluding the border row, and the harvested plant material was recorded. Because we focus on grain (commodity) yield, cobs were shelled in the field, and grain was measured immediately. A two kg grain subsample from each experimental site was placed in paper bags and transported to the University of Rwanda. Grain subsamples were oven-dried at 70 °C for 48-72 hrs until a constant dry weight was recorded. Grain dry matter yield per plot was calculated from the fresh field grain weight and the corresponding subsample moisture correction. Root biomass was sampled at harvest following standard protocols (Freschet *et al.*, 2021). Within each plot, maize plants covering 1 m^2 were gently uprooted to minimize loss of fine roots at 5 locations along a diagonal transect. Roots were separated from shoots using scissors (or a machete for thicker stems), placed in paper bags, and transported to the laboratory. Upon arrival, roots were immediately washed and oven-dried for 48-72 hrs at 70°C to constant weight. Dry root biomass was then weighed and recorded. When processing could not be completed on the day of sample collection, samples were stored at 4 °C for 24-48 hrs to minimize biomass decomposition and weight loss

Statistical analyses

Differences in maize grain yield and root biomass among treatments (untreated control, two microbial consortia, and application rates) were evaluated separately for each site and between consortia using the pairwise bootstrap comparisons of treatment means (Efron & Tibshirani, 1994). For this, we ran 10,000 iterations and calculated the difference in average yield between treatments and the application rates, then reported the observed differences in average yield between each pair of treatments along with the associated bootstrap p-values. To evaluate the effects of treatments and application rates across all sites, we fitted a generalised linear mixed-effect model (GLMM) with SLP application rates specified as fixed effects and site as a random factor. Treatment effects on maize yield and root biomass increase were expressed relative to the untreated control by subtracting the control value from each corresponding treatment value at each site separately. To assess the extent to which site-specific soil properties may have on yield and root biomass across all sites, we applied a Bayesian linear mixed-effect model with the intercepts constrained to zero to enable direct comparison of standardised effect sizes between soil property components and the SLP microbial application rates. Because several soil variables were moderately to strongly correlated ($r > 0.5$), which is expected due to the interrelationship between soil properties, we performed principal component analysis (PCA) (Jolliffe, 2002), PCA was used to transform correlated soil variables into a reduced set of orthogonal components (PCs) that capture the major source of variation. The PCs were selected based on the proportion of variance explained by each PC. The resulting components were interpreted and grouped based on domain knowledge. To include SLP application rates as predictors, categorical SLP treatment variables were one-hot encoded, assigning binary indicators (0/1) to represent the presence or absence of each SLP application rate for each observed yield or root biomass. All data processing, statistical analyses, and visualisations were conducted using the Python computing ecosystem (Waskom, 2021; Capretto *et al.*, 2022).

Results

Response of maize yield to soil microbial inoculants

Across all six field sites, maize grain yield was consistently higher in plots treated with the Soil Life Product (SLP) microbial inoculant than in untreated control plots, although the magnitude of response varied among locations (Fig. 2; Table S2). Across all sites, bootstrap pairwise comparisons confirmed that yields in SLP-treated plots were significantly higher than those in untreated controls ($P < 0.05$; Table S2). At the Nova site, mean grain yield reached 4.1 t ha^{-1} in SLP treated plots and was significantly greater than in untreated control (Fig. 2a) Similar responses were observed for the Gahengeri site, where maize yield significantly increased from 0.8 t ha^{-1} in control plots to 1.3-2.5 t ha^{-1} in SLP-treated plots (Fig. 2b). At the Mayange site, control yield averaged 0.75 t ha$^{-1,}$ whereas SLP-treated plots produced significantly higher yield, 1.0 t ha^{-1} to 1.35 t ha^{-1} (Fig. 2c). At the Muyira site, maize yield significantly increased from 1.3 t ha^{-1} in controls to 2.2 to 2.4 t ha^{-1} in treated plots (Fig. 2d). Similarly, yield at the Save site significantly increased from 1.8 t ha^{-1} in untreated controls to 3.0-3.6 t ha^{-1} in treated plots (Fig. 2e). At the Tumba site, control yield averaged 1.0 t ha^{-1}, whereas treated plots were significantly greater at 2.0 to 2.6 t ha^{-1} (Fig. 2f).

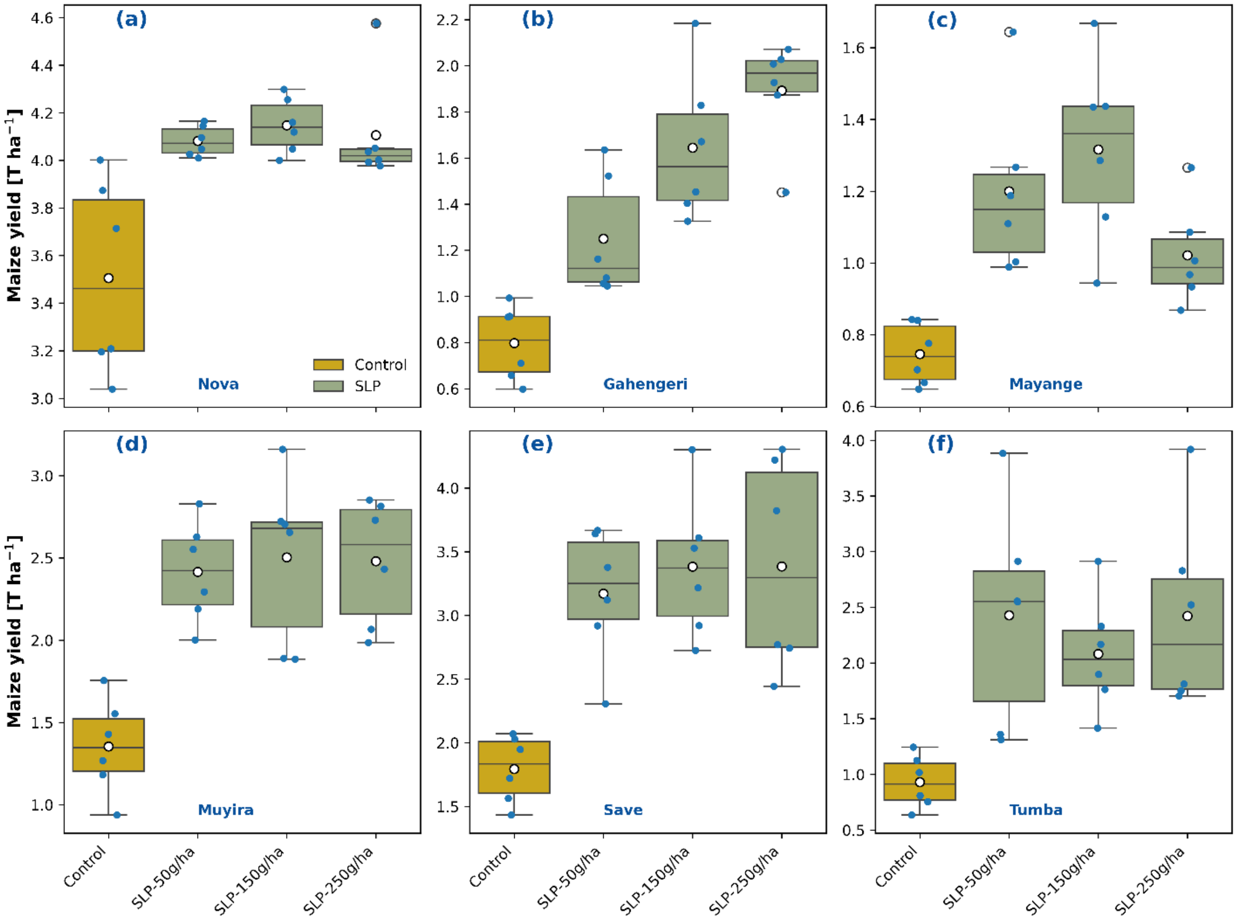

Figure 2. Maize grain yield (dry matter) for the Soil Life Product (SLP) consortium and their application rates at each of the six sites investigated in this study. (a) Nova; (b) Gahengeri; © Mayange; (d) Muyira; (e) Save; (f) Tumba. Each boxplot shows the five descriptive statistics (min, 25th percentile, median, 75th percentile, and maximum maize yield). The white dot in the middle of the boxplot indicates the average maize yield for each application rate. Control: untreated control plots, SLP-50g/ha: 50 g of product was added to replicate plots, SLP-150g/ha: 150 g of product was added to replicate plots, SLP-250g/ha: 250 g of product was added to replicate plots.

Root biomass across treatments and sites

Root biomass followed patterns similar to those observed for grain yield, with consistently higher values in SLP-treated plots than in untreated controls across all sites (Fig. 3, Table S3). At Nova, mean root biomass was 0.75 t ha^{-1} in control plots and increased to 0.86-0.94 t ha^{-1} in SLP-treated plots (Fig. 3a). At Gahengeri, root biomass averaged 0.39 t ha^{-1} in control plots and increased to 0.79-1.27 t ha^{-1} in treated plots (Fig. 3b). At Mayange, root biomass averaged at 0.25 t ha^{-1} in control plots to 0.49 to 0.64 t ha^{-1} in SLP-treated plots with statistically significant differences among treatment rates (Bootstrap difference in average, $P < 0.05$, Fig. 3c). At Muyira, root biomass increased from 0.6 t ha^{-1} in controls to 0.87-0.91 t ha^{-1} in treated plots across all three application rates (Fig. 3d). Similar patterns were observed at the at Save site, root biomass averaged 0.54 t ha^{-1} in control plots and increased to 0.72-0.76 t ha^{-1} in SLP-treated plots (Fig. 3e). At

Tumba, root biomass increased from 0.31 t ha^{-1} in the untreated control plots to 0.56 to 0.59 t ha^{-1} following inoculation (Fig. 3f). Across sites, bootstrap comparisons confirmed significantly lower root biomass in untreated controls than in SLP-treated plots ($P < 0.05$; Table Although numerical differences among SLP application rates were observed at some sites, these differences were not statistically significant or consistent across locations. Across all observations, maize grain yield and root biomass were positively correlated (Fig. S1), suggesting that plots with greater belowground biomass tended to produce higher grain yields.

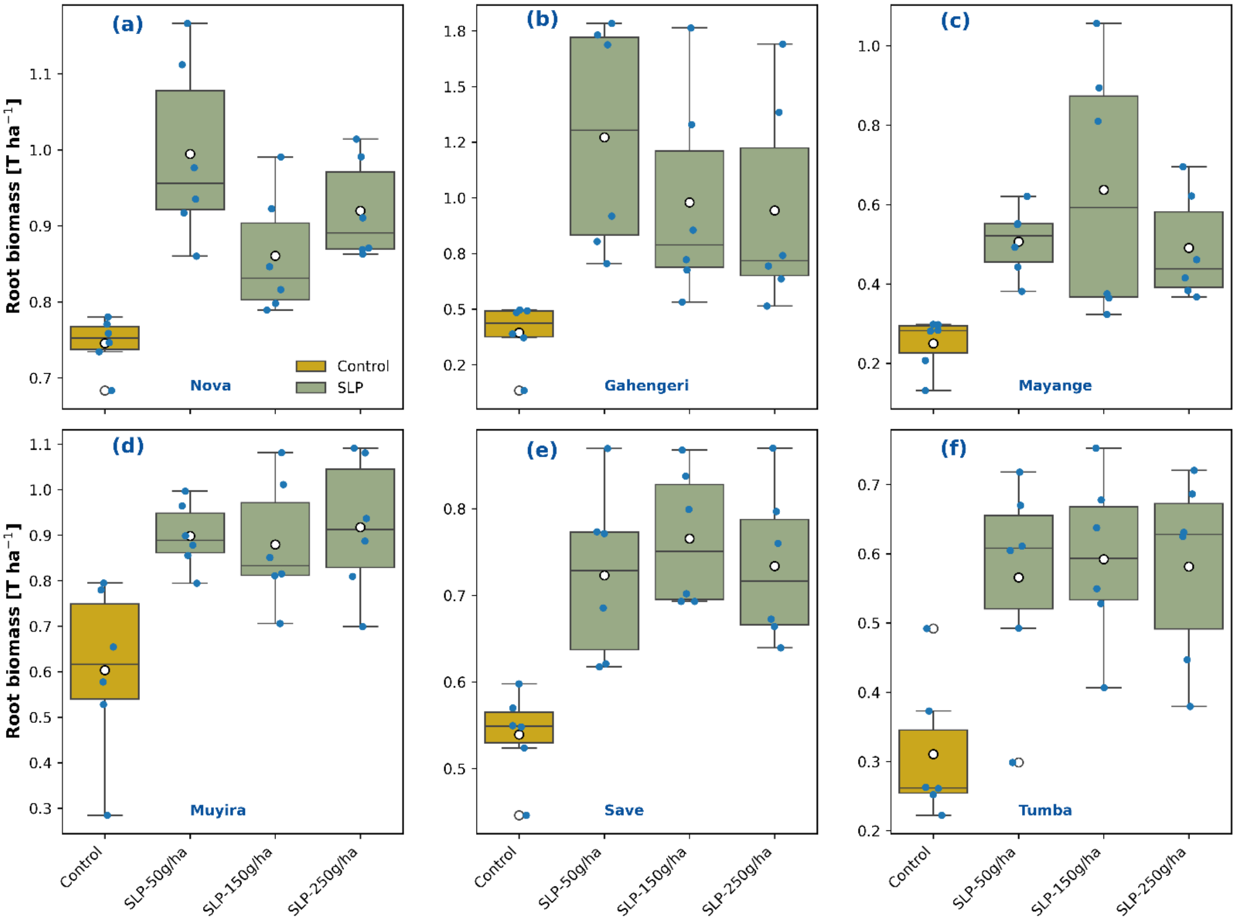

Figure 3. Maize root biomass for the Soil Life Product (SLP) consortium and the application rates at each of the six sites. (a) Nova; (b) Gahengeri; © Mayange; (d) Muyira; (e) Save; (f) Tumba. Each boxplot shows the five descriptive statistics (min, 25th percentile, median, 75th percentile, and maximum maize yield). The white dot in the middle of the boxplot indicates the average root biomass for each application rate. Control: untreated control plots, SLP-50g/ha: 50 g of product was added to replicate plots, SLP-150g/ha: 150 g of product was added to replicate plots, SLP-250g/ha: 250 g of product was added to replicate plots.

Effects of microbial inoculants on yield and root biomass across all sites

Across all sites, mixed-effects modeling showed lower average grain yield in untreated controls (1.52 ± 0.43 t ha^{-1}) than in all treated groups (Fig.4a). For the SLP, the observed average yield was 2.42 ± 0.43 t ha^{-1}, 2.51 ± 0.42 t ha^{-1}, and 2.55 ± 0.42 t ha^{-1}, for 50g ha^{-1}, 150g ha^{-1}, and 250g ha^{-1} application rate, respectively ($P < 0.0001$). The analysis shows that the differences between treated and untreated control plots across all investigated sites resulted in 59.3%, 65.3%, and 67.7% average maize yield uplift for 50g ha^{-1}, 150g ha^{-1}, and 250g ha^{-1} application rates, respectively (Fig. 4a). The average root biomass across all sites followed the yield trends. The average root biomass was significantly lower in untreated controls (0.47 ± 0.07 t ha^{-1}) than in SLP-treated groups (p-value<0.05) (Fig. 4b). For the SLP-treated sites the average root biomass was 0.82 ± 0.07, 0.79 ± 0.07, and 0.76 ± 0.07t ha^{-1} for 50g ha^{-1}, 150g ha^{-1}, and 250g ha^{-1} application rate, respectively (Fig. 4b). Overall, microbial inoculants resulted in 74%, 66%, and 61% average root biomass increase over untreated control for 50g ha^{-1}, 100g ha^{-1}, and 250g ha^{-1} application rates, respectively (Fig. 4b). Despite the overall positive treatment effects, no statistically significant differences were observed among the three SLP application rates at the cross-site level for either maize yield or root biomass (Fig. 4). In addition, root biomass was positively correlated with maize grain yield across all observations, and this trend was consistent across data percentiles (Fig. S1).

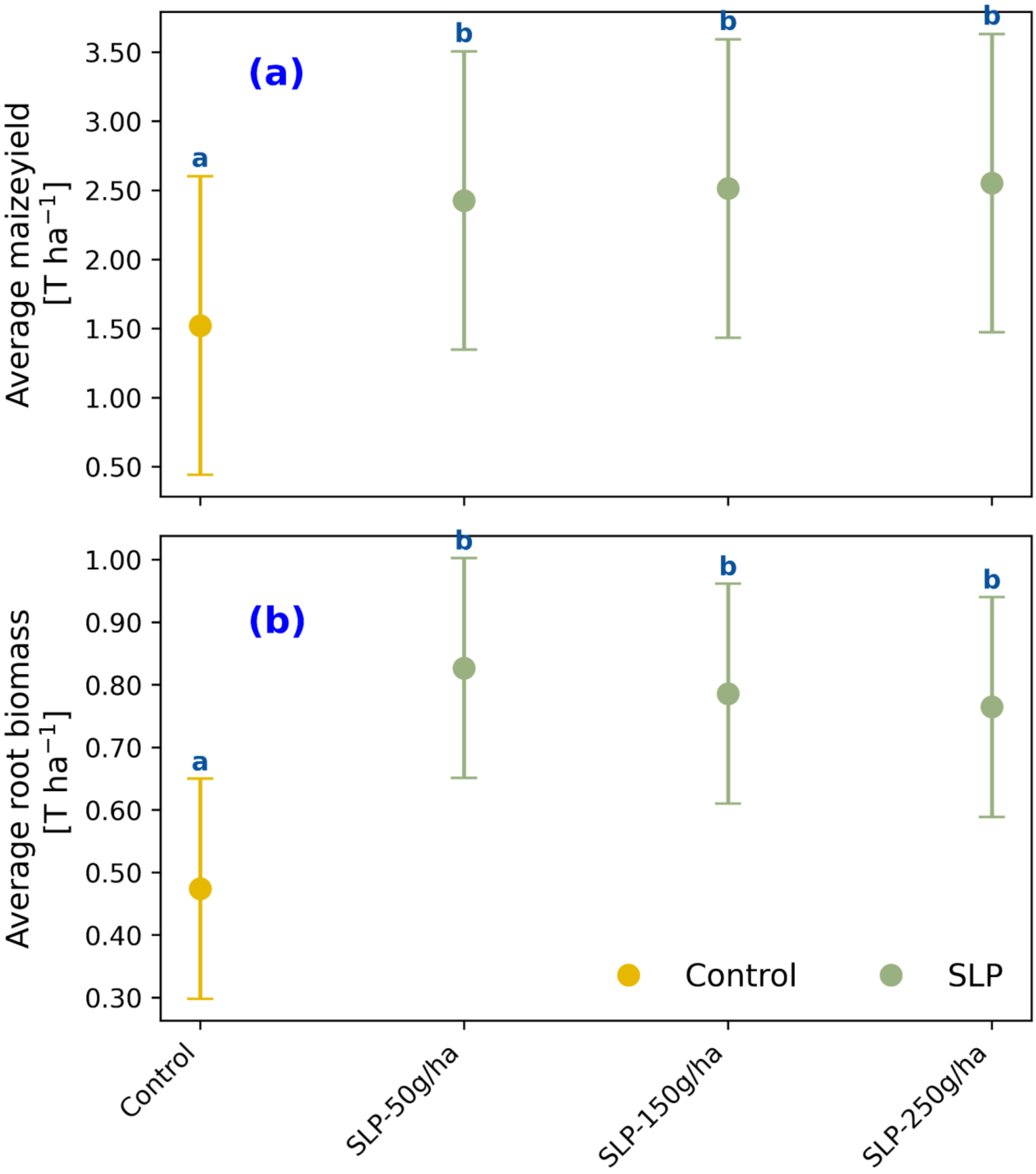

Figure 4. Average (mean ± se) across all investigated sites (a) maize yield and (b) root biomass following the mixed effect model analysis, for untreated control and different application rates of the Soil Life Product (SLP) consortium. Control: untreated control, SLP-50g ha^{-1}: 50 g of product was added to replicate plots, SLP-150g ha^{-1}: 150 g of product was added to replicate plots, SLP-250g ha^{-1}: 250 g of product was added to replicate plots.

Microbial inoculant control on maize yield and root biomass

Principal Component Analysis (PCA) of baseline soil properties resulted in three principal components (PCs) that together explained 94.8 % of the total variance in the measured soil dataset (Fig. S2). PC1explained 70% of the total variance and was primarily associated with soil chemical properties, PC2 reflected variation in soil texture, particularly clay content, and PC3 captured variation in soil nutrient status, including total nitrogen and exchangeable calcium. Based on dominant variable loadings, we broadly interpret these axes as representing soil chemistry (PC1), texture (PC2), and soil nutrient status (PC3) (Fig. S2). Principal components explaining more than 5% of the variance and with eigenvalue greater than 0.5 were retained. Because these axes were derived from a limited site-level soil dataset without replicated variance estimates, they should be viewed as exploratory summaries rather than definitive representations of the underlying soil drivers. To explore potential relationships between soil conditions and treatment responses, Bayesian modelling was used to incorporate the PCA-derived soil property components together with SLP application rates. Within this exploratory framework, microbial inoculation showed stronger associations with maize yield and root biomass than the aggregated soil property components included in the analysis (Fig. 5). Across sites, the largest estimated yield increase was associated with SLP applied at 250g ha^{-1} (posterior mean increase of 1.09 t ha^{-1}), with yield variation across sites contributing an estimated increase of 0.2–0.5 t ha^{-1}, followed by SLP at 150 g ha^{-1} (0.97 t ha^{-1}), with 94% credible intervals ranging from approximately 0.8 to 1.25 t ha^{-1} (Fig. 5a).

Among the soil property components, soil nutrient status showed a smaller but detectable association with posterior estimates corresponding to an estimated yield increase of 0.2–0.5 t ha^{-1} (Fig. 5a). Soil texture and soil chemistry (i.e., soil pH and SOC; Fig. S2) were not strong predictors of yield variation in the model (Fig. 5a). A similar pattern was observed for root biomass where SLP treatment effects were larger than those associated with the soil property components (Fig. 5b). Among the soil properties, soil chemistry showed the greatest (0.039 t ha^{-1}) contribution to root biomass followed by soil texture (0.035 t ha^{-1}). Soil nutrients did not emerge as an important driver of root biomass across sites (Fig. 5b). Because soil measurements were limited to composite samples and did not capture within-site variability, the relative contributions of soil property components reported here should be interpreted cautiously. Future analyses incorporating replicated soil measurements, additional soil health indicators, and greater site-level replication will be necessary to more robustly quantify the influence of soil physicochemical variability on treatment responses and to better resolve interactions between soil conditions and microbial inoculant performance.

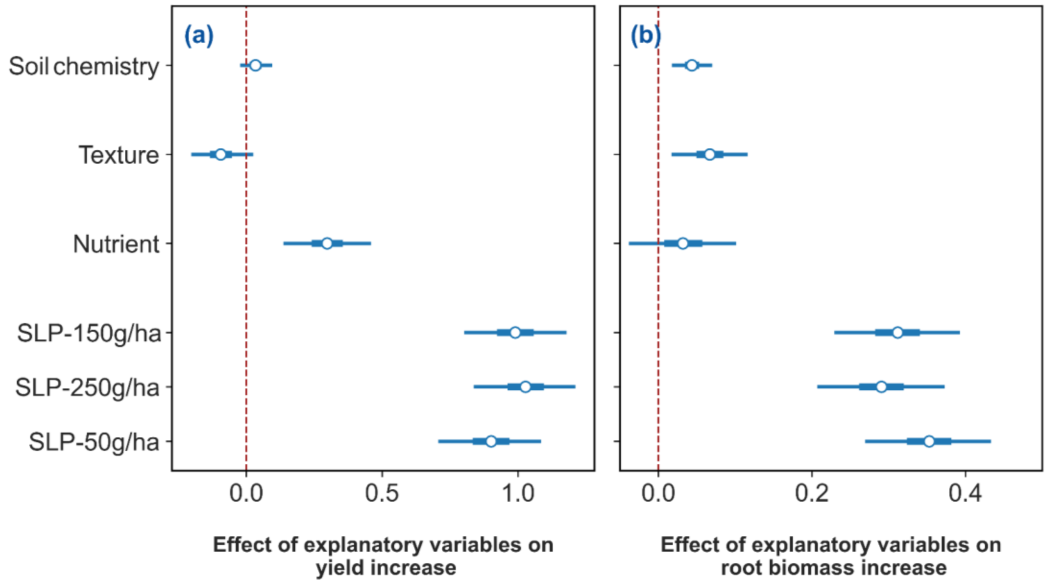

Figure 5. Posterior effect size of each explanatory variable used in the model on (a) maize yield increase and (b) root biomass increase over untreated control plots. The variables include soil properties (soil chemistry, soil texture, and soil nutrients) and the three application rates of the Soil Life Product consortium investigated in this study. The white dot represents the posterior average increase in yield and root biomass. The whiskers represent the 94% HDI, which indicates the Bayesian credible interval of the effect size for each variable. SLP-50g ha^{-1}: 50 g of product was added to replicate plots, SLP-150g ha^{-1}: 150 g of product was added to replicate plots, SLP-250g ha^{-1}: 250 g of product was added to replicate plots.

Discussion

Soil microbial inoculants increase maize yield across heterogeneous field sites

This multi-site field study shows that application of the soil microbial inoculants, Soil Life Product (SLP), consistently resulted in higher maize grain yield compared with untreated controls across contrasting agroecological zones in Rwanda. Yield increase was consistently observed at each of the six sites investigated in this study. However, the magnitude of maize response to microbial inoculants varied among locations (Fig. 2a-f). Across all sites, mixed-effect modelling showed that treated fields produced significantly higher yields than untreated controls. Average yield increased from 1.52 ± 0.43 t ha^{-1} in control plots to 2.42–2.55 t ha^{-1} across SLP application rates, corresponding to yield increases of approximately 59–68% (Fig. 4a). Our findings demonstrate that soil microbial inoculants likely enhanced plant growth and maize grain filling in treated field, particularly by increasing nutrient uptake and use efficiency (Wolde-meskel *et al.*, 2018; Adjei-Nsiah *et al.*, 2019; Belete *et al.*, 2019; Francioli *et al.*, 2025), both vital plant physiological processes in these deeply weathered and nutrient-depleted tropical systems (Moreno-Jiménez *et al.*, 2023; Kidinda *et al.*, 2023). Consistent with our data, a recent study conducted in agricultural lands across a wide gradient of climatic and soil conditions in China revealed a strong relationship between soil microbiome and maize yield, highlighting the potential of soil microbiome in driving agricultural productivity, especially in nutrient-limited tropical systems (Shi *et al.*, 2025). The variation in maize yield observed among the study sites (Fig. 2a-f) indicates that while microbial inoculation produced consistent positive outcomes, treatment performance remained influenced by site-specific environmental conditions (Xue *et al.*, 2018; Han *et al.*, 2024; Lahijanian *et al.*, 2025; Liang *et al.*, 2026). Nevertheless, consistently higher yields observed in the treated fields compared to the control across sites suggest that microbial inoculation can produce a substantial impact under diverse smallholder farming conditions (Fig. 2a-f; Fig. 4a). Across the six investigated sites, microbial application rates did not show up as a strong driver of maize yield. The differences among the three SLP application rates tested in this study were generally small and not statistically significant when analysed across sites (Fig. 4a), suggesting that the presence of the microbial inoculants was a stronger determinant of yield response than the specific dose level. Consistently, similar results were reportedly observed in different meta-analyses and review studies (Li *et al.*, 2024; Kumar *et al.*, 2025). From a practical perspective, these patterns suggest that low application rates are likely sufficient to obtain measurable agronomic benefits under the conditions investigated here. However, the lack of maize yield responsiveness to microbial inoculant application rates is unknown and the subject for future investigation. We acknowledge that several factors that could further explain yield variation in time and space across sites were not considered. For example, multi-seasonal yield records, detailed site-specific climatic and plant physiological data, and characterization of plant and soil microbiome responses to better resolve the durability of treatment effects, were not considered and should be incorporated in future studies. Nevertheless, while such variability likely contributed to differences in response magnitude among sites (Grönemeyer & Reinhold-Hurek, 2018), the consistent yield improvements observed across all locations provide strong evidence that the treatment effect observed on maize yield increase is robust under heterogeneous real-world conditions in the studied agroecological zones in Rwanda (Fig. 4a; Fig. 5a).

Microbial inoculation increases root biomass production

Root biomass followed patterns similar to grain yield, with consistently higher estimated root biomass observed in SLP-treated plots than in untreated controls across all sites. Consistent with yield patterns, differences in root biomass among the three SLP application rates were not statistically significant across the six sites investigated in this study (Fig. 4b). This further supports the observation that the presence of the inoculant, rather than the specific application rate within the tested range, was the dominant driver of response. Across the six locations, average root biomass increased from 0.47 ± 0.07 t ha^{-1} in control plots to approximately 0.76–0.82 t ha^{-1} in treated plots (Fig. 3a-f). This corresponds to an average increase in root biomass of 61–74% relative to untreated controls (Fig. 3a-f, Fig. 4b). We also observed a positive relationship between root biomass and grain yield across heterogeneous sites (Fig. S1), suggesting that enhanced belowground growth may contribute to improving maize grain yield under microbial inoculation. We explain this high root biomass as evidence that multi-strain consortia inoculants accelerated maize root biomass, potentially by improving nutrient acquisition strategies or modulating plant hormone signaling, and that these functional traits are even stronger in resource-limited soils such as the one observed in our study region (Averill *et al.*, 2022; Moreno-Jiménez *et al.*, 2023; Kidinda *et al.*, 2023; Jansson *et al.*, 2023; Li *et al.*, 2024). This relationship between grain yield and root biomass is often used in Earth System Models (ESM) to estimate root carbon input into the soil from grain yield through shoot to root ratios (Bolinder et al., 2007, 2012). By considering that 45% of root biomass is carbon content (IPCC, 2019), we estimated that microbial inoculants contributed to root carbon input into the soil, ranging from 0.34 to 0.37 t ha^{-1}. Furthermore, existing literature shows that the largest proportion of soil organic carbon (SOC) stock is strongly driven by root biomass input into the soil (Kätterer *et al.*, 2011; Menichetti *et al.*, 2015; Bukombe *et al.*, 2026), suggesting that these multi-strain consortia have the potential to enhance atmospheric carbon sequestration and therefore act as a climate regulator (Jansson *et al.*, 2023; Beattie *et al.*, 2024).

Microbial treatment was a stronger driver of response than soil property components across sites

Cross-site statistical analyses further indicated that microbial inoculation was more strongly associated with yield and root biomass responses than the soil property components included in the model (Fig. 5a-b). Principal component analysis suggested that soil chemistry, texture, and nutrient status captured most of the variation in the measured soil dataset. These PCA-derived axes should, however, be interpreted cautiously because they represent a simplified summary of only the soil variables measured in this study, and some overlap among components may arise from covariation among soil properties. Within this framework, the Bayesian regression model indicated that microbial inoculation was more strongly associated with maize yield and root biomass observed in our study sites than the aggregated soil property components derived from the PCA (Fig. 5a-b). Across sites, the largest estimated increases in maize yield were associated with SLP treatments, while soil nutrient status showed a smaller but detectable contribution to yield variation. Soil chemistry and soil texture were not strongly associated with yield variation within this explanatory model (Fig. 5a). Similarly, SLP treatments showed larger estimated contributions to root biomass than soil properties. These results suggest that microbial inoculation was the dominant explanatory factor within this model framework of crop response across the range of soil conditions included in this study. However, the observed variation in treatment response among sites indicates that environmental and edaphic factors still influence microbial performance and should be considered when developing deployment strategies for microbial inoculants. Nevertheless, these results demonstrate that microbial inoculation can provide consistent productivity gains across diverse smallholder farming environments.

While treatment responses varied in magnitude among sites, positive yield and root biomass responses were observed everywhere, indicating that microbiome-based interventions may represent a scalable tool for improving crop productivity in heterogeneous agricultural systems. Several limitations should be considered when interpreting these results. The study represents a single growing season across multiple sites, and therefore does not capture potential interannual variability in treatment responses. Future work integrating multi-season field trials with direct measurements of soil carbon pools, plant physiological responses, and soil microbial community dynamics would help clarify the mechanisms underlying the observed yield and root biomass responses.

Conclusions

In conclusion, these results demonstrate that the introduction of biologically diverse microbial inoculation can provide gains in maize yield and root biomass across diverse smallholder farming environments in Rwanda. Although treatment responses varied significantly in magnitude among sites, the direction of these positive responses was consistent across all locations. As such our results suggest a promising avenue for enhancing the sustainability of smallholder farming systems, as microbiome-based interventions may represent a scalable and practical complement to existing soil fertility management strategies in heterogeneous tropical agricultural systems. Given the potential to simultaneously enhance soil biodiversity, carbon sequestration and food production, emerging microbial solutions have remarkable potential to drive progress towards multiple sustainable development goals.

Acknowledgements

The authors would like to thank the following collaborating institutions for the support given to our scientists and this study: The University of Rwanda, the Ministry of Agriculture and Animal Resources, and the Rwanda Agriculture and Animal Resources Development Board (RAB). Special thanks go to the student assistants for their work in the laboratory, and all field helpers who facilitated the field trials at different sites. The authors also thank Martin Voss, Chief Innovation Officer at Oath Biome, for his contributions to the registration of the Soil Life Product in Rwanda and for his advice on the execution of the trial. We are grateful to the microbiology laboratory staff for producing the microbial inoculant. Special thanks are extended to the student assistants for their laboratory work and to all field helpers who supported the field trials across the different sites.

Author contributions

BB, FXN, PGS and AE conceived the study. BB, PGS, FXN, JM, SS performed the experiments. B.B. compiled, analysed, and visualized the data for the manuscript. BB, PMH, and AE wrote the initial draft of the manuscript. All authors interpreted the results and contributed to the writing and editing of the manuscript.

Competing interests

The authors declare potential competing interests as follows: BB, PGS, AE, JM are employees of Oath Inc. JAG, JKJ, TWC, PMH are compensated members of the scientific advisory board of Oath Inc. BB, PGS, AE, JM, JAG, JKJ, TWC are employed by the companies that funded this study. AE is an inventor on patents related to the microbial consortia described in this study (WO2025240938, WO2025097154).

Data Availability

The data that support the findings of this study are available upon request to the corresponding author.

References

Adesemoye AO, Torbert HA, Kloepper JW. **2009**. Plant Growth-Promoting Rhizobacteria Allow Reduced Application Rates of Chemical Fertilizers. *Microbial Ecology* **58**: 921–929.

Adjei-Nsiah S, Kumah JF, Owusu-Bennoah E, Kanampiu F. **2019**. Influence of P Sources and Rhizobium Inoculation on Growth and Yield of Soybean Genotypes on Ferric Lixisols of Northern Guinea Savanna Zone of Ghana. *Communications in Soil Science and Plant Analysis* **50**: 853–868.

Appiah-Twumasi M, Gardebroek C, Ihle R, Ansah IGK. **2026**. Responses of African food systems to climate change: A systematic review of concepts, methods, and evidence. *Agricultural Systems* **233**: 104577.

Averill C, Anthony MA, Baldrian P, Finkbeiner F, van den Hoogen J, Kiers T, Kohout P, Hirt E, Smith GR, Crowther TW. **2022**. Defending Earth's terrestrial microbiome. *Nature Microbiology* **7**: 1717–1725.

Beattie GA, Edlund A, Esiobu N, Gilbert J, Nicolaisen MH, Jansson JK, Jensen P, Keiluweit M, Lennon JT, Martiny J, *et al.* 2024. Soil microbiome interventions for carbon sequestration and climate mitigation. *mSystems* **10**: e01129-24.

Belete S, Bezabih M, Abdulkadir B, Tolera A, Mekonnen K, Wolde-meskel E. **2019**. Inoculation and phosphorus fertilizer improve food-feed traits of grain legumes in mixed crop-livestock systems of Ethiopia. *Agriculture, Ecosystems & Environment* **279**: 58–64.

Bukombe B, Bolinder MA, Börjesson G, Menichetti L, Lang R, Paustian K, Kätterer T. **2026**. Soil carbon accrual in ley rotations compared with cereal monoculture after four decades at four long-term experiments in Sweden. *Agriculture, Ecosystems & Environment* **396**: 110004.

Capretto T, Piho C, Kumar R, Westfall J, Yarkoni T, Martin OA. **2022**. Bambi: A Simple Interface for Fitting Bayesian Linear Models in Python. *Journal of Statistical Software* **103**: 1–29.

Chitakira M, Torquebiau E. **2010**. Barriers and Coping Mechanisms Relating to Agroforestry Adoption by Smallholder Farmers in Zimbabwe. *The Journal of Agricultural Education and Extension* **16**: 147–160.

Crowther TW, Rappuoli R, Corinaldesi C, Danovaro R, Donohue TJ, Huisman J, Stein LY, Timmis JK, Timmis K, Anderson MZ, *et al.* 2024. Scientists' call to action: Microbes, planetary health, and the Sustainable Development Goals. *Cell* **187**: 5195–5216.

Delgado-Baquerizo M, Maestre FT, Reich PB, Jeffries TC, Gaitan JJ, Encinar D, Berdugo M, Campbell CD, Singh BK. **2016**. Microbial diversity drives multifunctionality in terrestrial ecosystems. *Nature Communications* **7**: 10541.

Doetterl S, Asifiwe RK, Baert G, Bamba F, Bauters M, Boeckx P, Bukombe B, Cadisch G, Cooper M, Cizungu LN, *et al.* 2021. Organic matter cycling along geochemical, geomorphic, and disturbance gradients in forest and cropland of the African Tropics – project TropSOC database version 1.0. *Earth System Science Data* **13**: 4133–4153.

Efron B, Tibshirani RJ. **1994**. *An introduction to the bootstrap*. Chapman and Hall/CRC.

Erktan A, Balmot J, Merino-Martín L, Monnier Y, Pailler F, Coq S, Abiven S, Stokes A, Le Bissonnais Y. **2017**. Immediate and long-term effect of tannins on the stabilization of soil aggregates. *Soil Biology and Biochemistry* **105**: 197–205.

Fierer N. **2017**. Embracing the unknown: disentangling the complexities of the soil microbiome. *Nature Reviews Microbiology* **15**: 579–590.

Francioli D, Kampouris ID, Kuhl-Nagel T, Babin D, Sommermann L, Behr JH, Chowdhury SP, Zrenner R, Moradtalab N, Schloter M, *et al.* 2025. Microbial inoculants modulate the rhizosphere microbiome, alleviate plant stress responses, and enhance maize growth at field scale. *Genome Biology* **26**: 148.

Freschet GT, Pagès L, Iversen CM, Comas LH, Rewald B, Roumet C, Klimešová J, Zadworny M, Poorter H, Postma JA, *et al.* 2021. A starting guide to root ecology: strengthening ecological concepts and standardising root classification, sampling, processing and trait measurements. *New Phytologist* **232**: 973–1122.

Giller KE, Witter E, Corbeels M, Tittonell P. **2009**. Conservation agriculture and smallholder farming in Africa: The heretics' view. *Field Crops Research* **114**: 23–34.

Grönemeyer JL, Reinhold-Hurek B. **2018**. Diversity of Bradyrhizobia in Subsahara Africa: A Rich Resource. *Frontiers in Microbiology* **9**.

Han X, Doménech-Pascual A, Pere Casas-Ruiz J, Donhauser J, Jordaan K, Ramond J-B, Priemé A, Romaní AM, Frossard A. **2024**. Soil organic matter properties drive microbial enzyme activities and greenhouse gas fluxes along an elevational gradient. *Geoderma* **449**: 116993.

Holloway JG, Blatezore JC, Edlund AE, Rajangam AS. **2025**. Microbial Consortia Production.

IPCC. **2019**. *2019 Refinement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories — IPCC.*

Jack CN, Petipas RH, Cheeke TE, Rowland JL, Friesen ML. **2021**. Microbial Inoculants: Silver Bullet or Microbial Jurassic Park? *Trends in Microbiology* **29**: 299–308.

Jansson JK, McClure R, Egbert RG. **2023**. Soil microbiome engineering for sustainability in a changing environment. *Nature Biotechnology* **41**: 1716–1728.

Jiang M, Delgado-Baquerizo M, Yuan MM, Ding J, Yergeau E, Zhou J, Crowther TW, Liang Y. **2023**. Home-based microbial solution to boost crop growth in low-fertility soil. *New Phytologist* **239**: 752–765.

Jolliffe IT (Ed.). **2002**. Principal Component Analysis and Factor Analysis. In: Principal Component Analysis. New York, NY: Springer, 150–166.

Kätterer T, Bolinder MA, Andrén O, Kirchmann H, Menichetti L. **2011**. Roots contribute more to refractory soil organic matter than above-ground crop residues, as revealed by a long-term field experiment. *Agriculture, Ecosystems & Environment* **141**: 184–192.

Kidinda LK, Doetterl S, Kalbitz K, Bukombe B, Babin D, Mujinya BB, Vogel C. **2023**. Relationships between geochemical properties and microbial nutrient acquisition in tropical forest and cropland soils. *Applied Soil Ecology* **181**: 104653.

Kumar R, Farda B, Mignini A, Djebaili R, Koolman L, Paul A, Mondal S, Joel JM, Pandit A, Panneerselvam P, *et al.* 2025. Microbial Solutions in Agriculture: Enhancing Soil Health and Resilience Through Bio-Inoculants and Bioremediation. *Bacteria* **4**.

Kumar P, Pandey P, Dubey RC, Maheshwari DK. **2016**. Bacteria consortium optimization improves nutrient uptake, nodulation, disease suppression and growth of the common bean (*Phaseolus vulgaris*) in both pot and field studies. *Rhizosphere* **2**: 13–23.

Lahijanian S, Schmidt J, Feuerstein U, Polle A. **2025**. Effects of cover crops and microbial inoculants in different farming systems on soil microbial communities and yield of maize. *Biology and Fertility of Soils* **61**: 1165–1182.

Leal Filho W, Nagy GJ, Setti AFF, Sharifi A, Donkor FK, Batista K, Djekic I. **2023**. Handling the impacts of climate change on soil biodiversity. *Science of The Total Environment* **869**: 161671.

Li C, Chen X, Jia Z, Zhai L, Zhang B, Grüters U, Ma S, Qian J, Liu X, Zhang J, *et al.* 2024. Meta-analysis reveals the effects of microbial inoculants on the biomass and diversity of soil microbial communities. *Nature Ecology & Evolution* **8**: 1270–1284.

Liang X, Zhao Y, Song Y, Chai B, Jia T. **2026**. The soil depth determines soil multifunctionality via shaping the soil properties and microbial diversity. *PeerJ* **14**: e20734.

Liu X, Mei S, Salles JF. **2023**. Inoculated microbial consortia perform better than single strains in living soil: A meta-analysis. *Applied Soil Ecology* **190**: 105011.

Mando A, Ouattara B, Sédogo M, Stroosnijder L, Ouattara K, Brussaard L, Vanlauwe B. **2005**. Long-term effect of tillage and manure application on soil organic fractions and crop performance under Sudano-Sahelian conditions. *Soil and Tillage Research* **80**: 95–101.

Mason ARG, Salomon MJ, Lowe AJ, Cavagnaro TR. **2025**. Arbuscular mycorrhizal fungi inoculation and biochar application enhance soil carbon and productivity in wheat and barley. *Science of The Total Environment* **977**: 179230.

Menichetti L, Ekblad A, Kätterer T. **2015**. Contribution of roots and amendments to soil carbon accumulation within the soil profile in a long-term field experiment in Sweden. *Agriculture, Ecosystems & Environment* **200**: 79–87.

Moreno-Jiménez E, Maestre FT, Flagmeier M, Guirado E, Berdugo M, Bastida F, Dacal M, Díaz-Martínez P, Ochoa-Hueso R, Plaza C, *et al.* 2023. Soils in warmer and less developed countries have less micronutrients globally. *Global Change Biology* **29**: 522–532.

Msimbira LA, Smith DL. **2020**. The Roles of Plant Growth Promoting Microbes in Enhancing Plant Tolerance to Acidity and Alkalinity Stresses. *Frontiers in Sustainable Food Systems* **4**.

Mutsaers H, Coyne D, Hauser S, Huising J, Kamara A, Nziguheba G, Pypers P, Taulya G, Asten P van, Vanlauwe B. **2017**. *Soil and Soil Fertility Management Research in Sub-Saharan Africa: Fifty years of shifting visions and chequered achievements*. London: Routledge.

Nelson DW, Sommers LE. **1974**. A Rapid and Accurate Procedure for Estimation of Organic Carbon in Soils.

Ngango J, Musabanganji E, Maniriho A, Nkikabahizi F, Mukamuhire A. **2023**. Examining the adoption of agroforestry in Southern Rwanda: a double hurdle approach. *Forest Science and Technology* **19**: 260–267.

Nie M, Bell C, Wallenstein MD, Pendall E. **2015**. Increased plant productivity and decreased microbial respiratory C loss by plant growth-promoting rhizobacteria under elevated CO2. *Scientific Reports* **5**: 9212.

Othman Z, Shahzad A, Ramalu SAS. **2024**. Environmental, Technical, and Resources Challenges Facing Agroforestry: A Case of Sustainable Land Management in Malaysia. *Journal of Intercultural Communication* **24**: 63–76.

Pandey K, Saharan BS. **2025**. Soil microbiomes: a promising strategy for boosting crop yield and advancing sustainable agriculture. *Discover Agriculture* **3**: 54.

Pypers P, Sanginga J-M, Kasereka B, Walangululu M, Vanlauwe B. **2011**. Increased productivity through integrated soil fertility management in cassava–legume intercropping systems in the highlands of Sud-Kivu, DR Congo. *Field Crops Research* **120**: 76–85.

Romero F, Labouyrie M, Orgiazzi A, Ballabio C, Panagos P, Jones A, Tedersoo L, Bahram M, Eisenhauer N, Sünnemann M, *et al.* **2025**. The soil microbiome as an indicator of ecosystem multifunctionality in European soils. *Nature Communications* **17**: 705.

Shi S, Gong X, Cheng S, Tao D, Chen X, Van Der Heijden MGA, Trivedi P, Baquerizo MD, Liu M. **2025**. Maize growth as a function of cover crop-mediated soil microbiome. *New Phytologist* **248**: 872–885.

Sileshi GW, Stewart ZP, Odhong J, Mhlanga B, Amede T, Aynekulu E, Thierfelder C, Marenya P, Dittmer KM, Aliyu KT, *et al.* **2025**. A review of organic inputs to inform soil health advice for African smallholder farmers: localization matters. *npj Sustainable Agriculture* **3**: 20.

Summerauer L, Baumann P, Ramirez-Lopez L, Barthel M, Bauters M, Bukombe B, Reichenbach M, Boeckx P, Kearsley E, Van Oost K, *et al.* **2021**. The central African soil spectral library: a new soil infrared repository and a geographical prediction analysis. *SOIL* **7**: 693–715.

Ullah A, Mishra AK, Bavorova M. **2023**. Agroforestry Adoption Decision in Green Growth Initiative Programs: Key Lessons from the Billion Trees Afforestation Project (BTAP). *Environmental Management* **71**: 950–964.

Vanlauwe B, Aihou K, Aman S, Iwuafor ENO, Tossah BK, Diels J, Sanginga N, Lyasse O, Merckx R, Deckers J. **2001**. Maize Yield as Affected by Organic Inputs and Urea in the West African Moist Savanna. *Agronomy Journal* **93**: 1191–1199.

Wagg C, Bender SF, Widmer F, van der Heijden MGA. **2014**. Soil biodiversity and soil community composition determine ecosystem multifunctionality. *Proceedings of the National Academy of Sciences* **111**: 5266–5270.

Waskom ML. **2021**. seaborn: statistical data visualization. *Journal of Open Source Software* **6**: 3021.

Wolde-meskel E, van Heerwaarden J, Abdulkadir B, Kassa S, Aliyi I, Degefu T, Wakweya K, Kanampiu F, Giller KE. **2018**. Additive yield response of chickpea (*Cicer arietinum* L.) to rhizobium inoculation and phosphorus fertilizer across smallholder farms in Ethiopia. *Agriculture, Ecosystems & Environment* **261**: 144–152.

Worsley SF, Newitt J, Rassbach J, Batey SFD, Holmes NA, Murrell JC, Wilkinson B, Hutchings MI. **2020**. Streptomyces Endophytes Promote Host Health and Enhance Growth across Plant Species. *Applied and Environmental Microbiology* **86**: e01053-20.

Xue P-P, Carrillo Y, Pino V, Minasny B, McBratney AB. **2018**. Soil Properties Drive Microbial Community Structure in a Large Scale Transect in South Eastern Australia. *Scientific Reports* **8**: 11725.

Supporting Information

Table S1. Taxonomic composition of the Soil Life Product.

ID	Species-Level Taxonomy	ID	Species-Level Taxonomy
1	Aneurinibacillus aneurinilyticus	12	Streptomyces bikiniensis
2	Bacillus licheniformis	13	Streptomyces echinatus
3	Bacillus velezensi	14	Streptomyces globosus
4	Lysinibacillus sphaericus	15	Streptomyces griseoaurantiacus
5	Microbacterium oxydans	16	Streptomyces misionensis
6	Microbacterium paraoxydans	17	Streptomyces murinus
7	Paenibacillus cellulositrophicus	18	Streptomyces musisoli
8	Rhodococcus erythropolis	19	Streptomyces olivaceus
9	Streptomyces achromogenes	20	Streptomyces rochei
10	Streptomyces antibioticus	21	Streptomyces sennicomposti
11	Streptomyces bacillaris	22	Streptomyces toxytricini

Table S2. Analysis of the difference in average maize yield and bootstrap pairwise comparison of treatments and SLP application rates at different farms. Observed-Diff indicates the observed difference between treatment1 and treatment2 by the Bootstrap resampling method.

Site	Treatment1	Treatment2	Observed-Diff	p-value
Nova	Control	SLP-50g/ha	0.58	0.0100
Nova	Control	SLP-150g/ha	0.64	0.0067
Nova	Control	SLP-250g/ha	0.60	0.0157
Nova	SLP-50g/ha	SLP-150g/ha	0.07	0.2124
Nova	SLP-50g/ha	SLP-250g/ha	0.02	0.7403
Nova	SLP-150g/ha	SLP-250g/ha	-0.04	0.6614
Gahengeri	Control	SLP-50g/ha	0.45	0.0099
Gahengeri	Control	SLP-150g/ha	0.85	0.0022
Gahengeri	Control	SLP-250g/ha	1.10	0.0002
Gahengeri	SLP-50g/ha	SLP-150g/ha	0.39	0.0407
Gahengeri	SLP-50g/ha	SLP-250g/ha	0.64	0.0039
Gahengeri	SLP-150g/ha	SLP-250g/ha	0.25	0.1310
Mayange	Control	SLP-50g/ha	0.45	0.0058
Mayange	Control	SLP-150g/ha	0.57	0.0027
Mayange	Control	SLP-250g/ha	0.28	0.0063
Mayange	SLP-50g/ha	SLP-150g/ha	0.12	0.3912
Mayange	SLP-50g/ha	SLP-250g/ha	-0.18	0.1220
Mayange	SLP-150g/ha	SLP-250g/ha	-0.29	0.0325
Muyira	Control	SLP-50g/ha	1.06	0.0007
Muyira	Control	SLP-150g/ha	1.15	0.0029
Muyira	Control	SLP-250g/ha	1.13	0.0012
Muyira	SLP-50g/ha	SLP-150g/ha	0.09	0.7073
Muyira	SLP-50g/ha	SLP-250g/ha	0.06	0.7302
Muyira	SLP-150g/ha	SLP-250g/ha	-0.02	0.9233
Save	Control	SLP-50g/ha	1.38	0.0014
Save	Control	SLP-150g/ha	1.59	0.0018
Save	Control	SLP-250g/ha	1.59	0.0031
Save	SLP-50g/ha	SLP-150g/ha	0.21	0.4679
Save	SLP-50g/ha	SLP-250g/ha	0.21	0.5701
Save	SLP-150g/ha	SLP-250g/ha	0.00	0.9981
Tumba	Control	SLP-50g/ha	1.50	0.0085
Tumba	Control	SLP-150g/ha	1.15	0.0024
Tumba	Control	SLP-250g/ha	1.49	0.0064
Tumba	SLP-50g/ha	SLP-150g/ha	-0.35	0.4077
Tumba	SLP-50g/ha	SLP-250g/ha	-0.01	0.9889
Tumba	SLP-150g/ha	SLP-250g/ha	0.34	0.3793

Table S3. Analysis of the difference in average root biomass and bootstrap pairwise comparison of treatments and SLP application rates at the different farms. Observed-Diff indicates the observed difference between treatment1 and treatment2 by the Bootstrap resampling method.

site	Treatment1	Treatment2	Observed-Diff	p-Value
Nova	Control	SLP-50g/ha	0.25	0.0034
Nova	Control	SLP-150g/ha	0.11	0.0132
Nova	Control	SLP-250g/ha	0.17	0.0016
Nova	SLP-50g/ha	SLP-150g/ha	-0.13	0.0414
Nova	SLP-50g/ha	SLP-250g/ha	-0.07	0.1735
Nova	SLP-150g/ha	SLP-250g/ha	0.06	0.1622
Gahengeri	Control	SLP-50g/ha	0.88	0.0055
Gahengeri	Control	SLP-150g/ha	0.58	0.019
Gahengeri	Control	SLP-250g/ha	0.55	0.0256
Gahengeri	SLP-50g/ha	SLP-150g/ha	-0.29	0.2963
Gahengeri	SLP-50g/ha	SLP-250g/ha	-0.33	0.243
Gahengeri	SLP-150g/ha	SLP-250g/ha	-0.04	0.8833
Mayange	Control	SLP-50g/ha	0.26	0.0015
Mayange	Control	SLP-150g/ha	0.39	0.0166
Mayange	Control	SLP-250g/ha	0.24	0.0057
Mayange	SLP-50g/ha	SLP-150g/ha	0.13	0.3085
Mayange	SLP-50g/ha	SLP-250g/ha	-0.02	0.7909
Mayange	SLP-150g/ha	SLP-250g/ha	-0.15	0.2896
Muyira	Control	SLP-150g/ha	0.28	0.0203
Muyira	Control	SLP-250g/ha	0.31	0.0137
Muyira	SLP-50g/ha	SLP-150g/ha	-0.02	0.7495
Muyira	SLP-50g/ha	SLP-250g/ha	0.02	0.7615
Muyira	SLP-150g/ha	SLP-250g/ha	0.04	0.6277
Save	Control	SLP-50g/ha	0.18	0.0062
Save	Control	SLP-150g/ha	0.23	0.0015
Save	Control	SLP-250g/ha	0.19	0.0041
Save	SLP-50g/ha	SLP-150g/ha	0.04	0.3914
Save	SLP-50g/ha	SLP-250g/ha	0.01	0.8327
Save	SLP-150g/ha	SLP-250g/ha	-0.03	0.5002
Tumba	Control	SLP-50g/ha	0.26	0.0078
Tumba	Control	SLP-150g/ha	0.28	0.0045
Tumba	Control	SLP-250g/ha	0.27	0.0055
Tumba	SLP-50g/ha	SLP-150g/ha	0.03	0.7221
Tumba	SLP-50g/ha	SLP-250g/ha	0.02	0.8342
Tumba	SLP-150g/ha	SLP-250g/ha	-0.01	0.8785

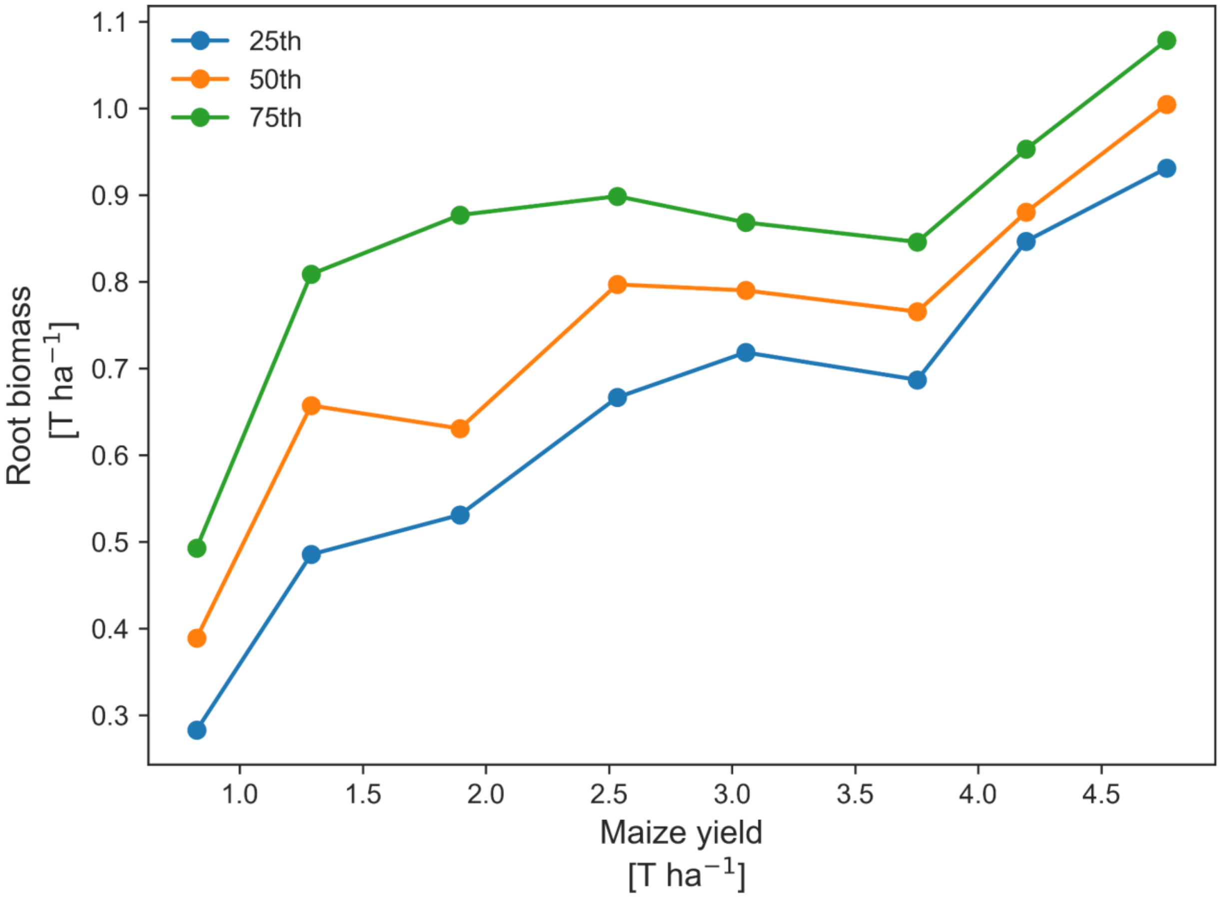

Figure S1. Relationship between the average maize yield and root biomass production across three percentiles (i.e., the 25th, 50th, and 75th).

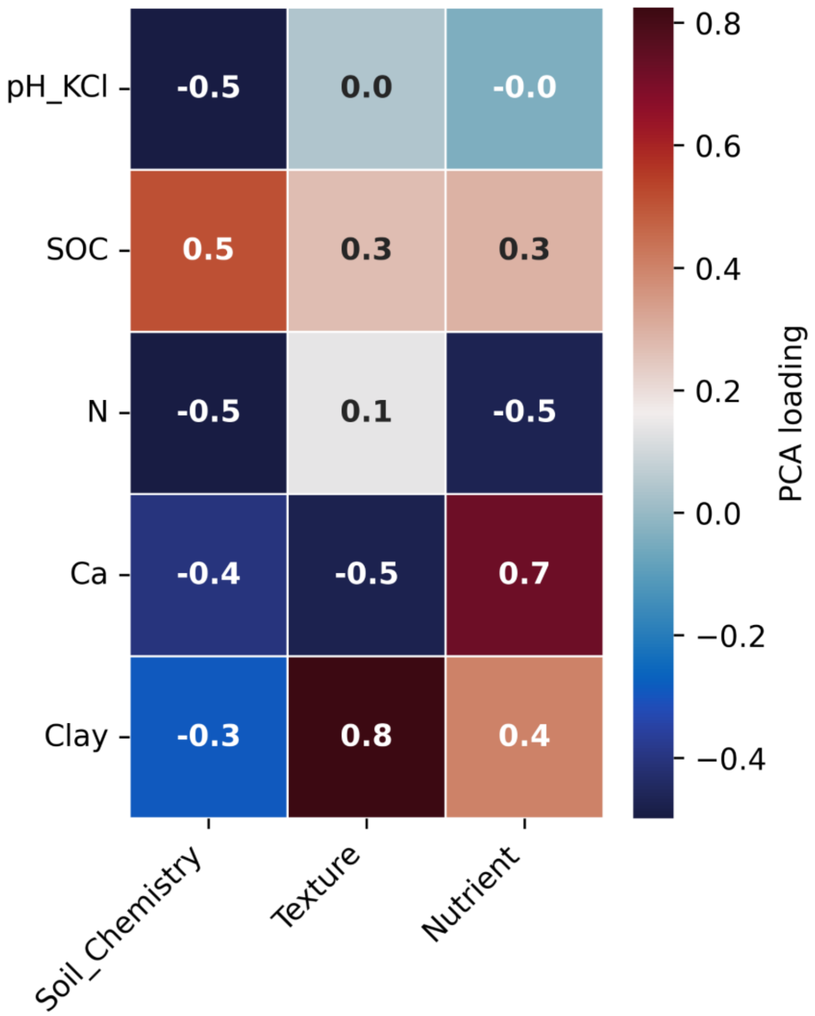

Figure S2. The loadings of the variables included in the analysis related to soil properties before Soil Life Product inoculation. Soil chemistry, soil texture, and soil nutrients are soil predictors representing the three principal components. Loadings indicate the correlation between the newly created Principal Components (PCs) and the original soil properties used for PCA. They reveal the contribution of each variable to each PC.