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Microbial Synergy Between *Azospirillum brasilense* and *Glomus iranicum* Promotes Root Biomass and Grain Yield in Andean Quinoa Cultivars

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Abstract

Quinoa (*Chenopodium quinoa* Willd.) is a strategic crop for climate-smart agriculture in the Andes, yet yield gains are constrained by soil degradation and low-input systems. We tested whether synergistic bioinoculation with a plant growth-promoting rhizobacterium (*Azospirillum brasilense*) and an arbuscular mycorrhizal fungus (*Glomus iranicum* var. *tenuihypharum*) enhances root function and grain productivity under field conditions. A split-plot RCBD was conducted in Ayacucho, Peru (2735 m a.s.l.) using four cultivars, Blanca de Junín (BJ), INIA 441 Señor del Huerto (SH), INIA 415 Pasankalla (RP) and INIA 420 Negra Collana (NC) and four treatments: uninoculated control, *Azospirillum*, *Glomus* and co-inoculation. Vegetative, root and yield traits were quantified; ANOVA, Tukey/Dunnett contrasts, correlations and PCA were applied. Co-inoculation consistently outperformed single inoculants, increasing root diameter, length, branching, dry weight and volume dry weight, while also enlarging panicle dimensions and raising grain weight per panicle and thousand-seed weight. Grain yield reached 4.94 ± 0.59 t ha^{-1} under co-inoculation, almost triple that of the control (1.71 ± 0.28 t ha^{-1}) and about 1.5 times higher than single inoculations. Genotypic effects were pronounced; BJ and SH combined superior root biomass with higher yield, RP maximized grain size and hectoliter weight, whereas NC responded weakly. Significant genotype × treatment interactions indicated cultivar-dependent microbiome benefits. Correlation and PCA linked root biomass and stem/panicle architecture to yield formation, positioning co-inoculation along trait vectors associated with belowground vigor and productivity. These results demonstrate a robust microbial synergy that translates root gains into yield, supporting co-inoculation as a scalable, low-input strategy for sustainable intensification of quinoa in highland agroecosystems.

Keywords: *Azospirillum brasilense*; *Glomus iranicum*; quinoa; andean highlands; bioinoculantr; root architecture; grain yield; genotype × inoculant interaction

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1. Introduction

Quinoa (*Chenopodium quinoa* Willd.) is an ancient pseudocereal domesticated more than 7000 years ago in the Andean highlands of Peru and Bolivia [1,2]. It has recently gained worldwide attention for its exceptional adaptability to diverse environments and its outstanding nutritional value [3,4]. The crop's capacity to thrive under extreme abiotic stress, including drought, salinity, low temperatures and nutrient-poor soils, makes it one of the most resilient species within the *Amaranthaceae* family and a model for sustainable agriculture in marginal lands [5–7]. This adaptability has enabled quinoa to expand beyond its native range, being cultivated today across all continents, from arid regions of North Africa to saline lowlands in Asia and temperate zones in Europe [8,9]. In parallel, quinoa's nutritional and functional composition has positioned it as a globally relevant superfood. Its seeds contain high-quality proteins (14–18%) and a balanced amino acid profile rich in lysine and methionine, unsaturated fatty acids, dietary fiber, minerals such as iron, zinc and magnesium and numerous antioxidant and anti-inflammatory compounds [10–13]. Importantly, it is gluten-free, offering an alternative source of plant-based proteins for populations with celiac disease or gluten intolerance [14,15].

In Peru, quinoa cultivation has expanded substantially in the last decade, consolidating the country as one of the main global exporters, with a 5.6% production increase between 2020 and 2024, mainly driven by European and North American markets [16]. However, this rapid expansion has occurred in parallel with growing environmental pressures, including soil erosion, loss of organic matter and increasing salinization—especially in highland valleys exposed to erratic rainfall and rising temperatures [17]. The overreliance on synthetic fertilizers to sustain yields has accelerated soil degradation and disrupted microbial community balance, leading to nutrient leaching and contamination of groundwater resources [18,19]. Consequently, there is an urgent need for low-input, environmentally sound alternatives that can maintain productivity while restoring soil health and functional biodiversity in Andean agroecosystems.

Plant growth-promoting microorganisms (PGPMs) have emerged as a cornerstone of sustainable intensification strategies. They include beneficial bacteria and fungi capable of stimulating plant growth, enhancing nutrient acquisition and mitigating abiotic and biotic stress through multiple mechanisms [20,21]. Within this group, plant growth-promoting rhizobacteria (PGPR), particularly *Azospirillum* spp., play a critical role in establishing beneficial plant–microbe interactions. *Azospirillum brasilense* is a diazotrophic bacterium widely studied for its ability to fix atmospheric nitrogen, solubilize phosphorus and other minerals and synthesize phytohormones such as indole-3-acetic acid (IAA), gibberellins and cytokinins that regulate root system architecture and shoot development [22,23]. Its colonization of root surfaces and internal tissues triggers physiological responses that improve nutrient uptake efficiency, water status and photosynthetic capacity, leading to increased biomass and yield in numerous crops including maize, wheat, rice and quinoa [24–26].

Complementarily, arbuscular mycorrhizal fungi (AMF) form obligate symbioses with plant roots, facilitating nutrient and water acquisition through a highly specialized network of hyphae and arbuscules. *Glomus iranicum* var. *tenuihypharum* is an AMF species recognized for its exceptional root colonization efficiency and persistence even under high-input agricultural systems [27,28]. AMF improve phosphorus and zinc uptake, enhance plant water-use efficiency, modulate antioxidant enzyme activity and increase tolerance to salinity and drought stress [29,30]. In quinoa, AMF colonization has been associated with improved growth, nutrient acquisition and grain yield under nutrient-deficient or saline conditions [31]. However, colonization efficiency can vary widely among genotypes and environmental contexts, and in some cases, the association may shift from mutualistic to neutral or parasitic, depending on nutrient availability and soil temperature [32,33].

Recent studies have suggested that combining PGPR and AMF inoculation can produce synergistic effects that surpass the benefits of single inoculants. The dual application of these microorganisms can enhance root biomass, nutrient acquisition and stress resilience by integrating bacterial nitrogen fixation and phytohormone synthesis with fungal nutrient foraging and osmotic regulation [34,35]. Such microbial consortia can improve the plant's adaptive capacity and contribute to soil ecological restoration, especially in degraded Andean soils where the natural abundance of beneficial microorganisms is limited. Nonetheless, the effectiveness of these interactions remains poorly characterized in quinoa cultivated under high-altitude field conditions, where low temperatures, alkaline pH and nutrient imbalances may restrict microbial colonization and activity [7,36,37].

Growing evidence indicates that the synergy between *Azospirillum brasilense* and arbuscular mycorrhizal fungi (AMF) arises from direct mechanistic complementarities rather than simply the additive effect of two beneficial inoculants. PGPR-induced increases in root exudation, rhizosphere metabolism, and lateral root initiation create highly favorable conditions for AMF entry and colonization, while AMF-derived improvements in plant nutritional and water status enhance carbohydrate allocation to the rhizosphere, sustaining larger and more active *Azospirillum* populations. These reciprocal feedbacks reinforce each their synergistic activity, strengthening resource-acquisition pathways and amplifying hormonal and metabolic signals involved in root development—ultimately producing greater biomass and yield than single inoculations [38,39]. Experimental evidence demonstrates that these microorganisms can co-colonize root tissues, altering cell wall architecture and enabling intra- and intercellular coexistence that increases microbial abundance and nitrogenase activity—thereby stimulating root biomass and whole-plant growth [40]. Similar synergistic outcomes have been observed in cherry tomato, where co-inoculation with *A. brasilense* and *Glomus intraradices* increased leaf area, dry biomass, and fruit yield beyond single inoculations [41]. Recent field research in Andean crops further confirms that co-inoculation with *A. brasilense* and *G. iranicum* var. *tenuihypharum* substantially improves root volume, diameter, and branching, resulting in greater nutrient uptake efficiency and grain yield under high-altitude conditions [42]. These mechanistic insights provide a solid biological foundation for hypothesizing synergistic benefits in quinoa grown under Andean field conditions.

Therefore, the present study was designed to evaluate the effects of single and combined inoculation with *Azospirillum brasilense* and *Glomus iranicum* var. *tenuihypharum* on four Andean quinoa cultivars under field conditions in Ayacucho, Peru. We hypothesized that co-inoculation would promote synergistic interactions leading to greater root biomass, improved nutrient uptake and higher grain yield compared with single inoculations or uninoculated controls. By integrating microbiological, physiological and agronomic evaluations, this research aims to provide evidence on the potential of microbial consortia for enhancing the productivity and sustainability of quinoa-based systems in the Andean highlands—thereby contributing to the broader goal of resilient, low-input agriculture in fragile mountain ecosystems.

2. Materials and Methods

2.1. Study Site

The study was conducted at the Canaán Agricultural Experimental Station of the National Institute of Agrarian Innovation (INIA), Andrés Avelino Cáceres Dorregaray District, Huamanga Province, Ayacucho Region, Peru (13°9′49.557″ S; 74°12′6.405″ W; 2735 m a.s.l.) (Figure 1).

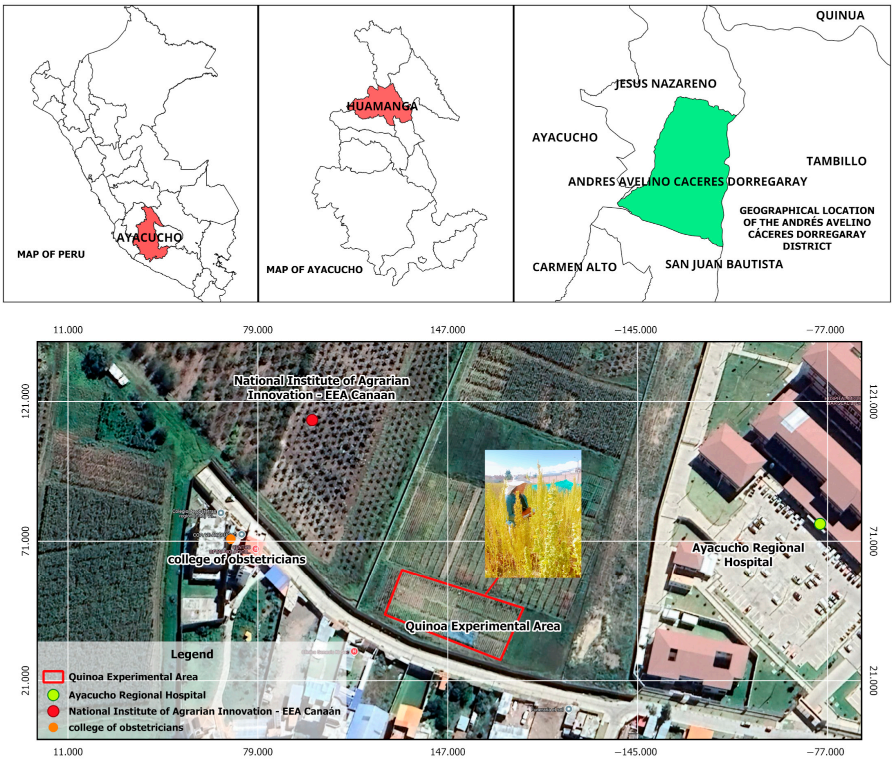


Figure 1. Geographic location of the experimental site. The red-shaded area indicates the department and province, while the green-shaded area represents the district where the experimental site is located. Field trials were conducted on plots managed by Canaán Agrarian Experimental Station the National Institute for Agricultural Innovation (INIA) in the Andrés Avelino Cáceres Dorregaray District, Huamanga Province, Ayacucho, Peru.

Key meteorological parameters were recorded by the INIA-Canaán automatic weather station, which is jointly managed by National Meteorology and Hydrology Service of Peru (SENAMHI) and the Regional Government of Ayacucho. The study site exhibited a typical Andean highland pattern, with maximum temperatures averaging 24.23–26.54 °C and minimum values around 7.13–12.24 °C throughout the growing season. Rainfall was concentrated between December and March, reaching peaks above 194.6 mm in February and March, while evapotranspiration and soil moisture followed complementary seasonal trends (Figure S1).

2.2. Soil Physicochemical Properties

Prior to the establishment of the experiment, a representative composite soil sample was collected at a depth of 20 cm and analyzed at the Soil, Water and Foliar Analysis Laboratory of the Canaán Experimental Station (LABSAF-CANAÁN) to determine its physicochemical characteristics (Table 1). The assessed parameters included soil texture, pH [43] and electrical conductivity [44]. Organic matter content [45] and total nitrogen [46] were also quantified. Cation exchange capacity, as well as available phosphorus [47] and potassium [48] were extracted.

All soil analyses were performed using certified and traceable instruments to ensure analytical rigor. Soil pH and electrical conductivity were measured with a pH meter (WTW INOLAB, model pH 7310, Xylem Analytics Germany Sales GmbH & Co. KG., Weilheim in Oberbayern, Germany) and a conductivity meter of the same brand (model Cond 7310, Xylem Analytics Germany Sales GmbH & Co. KG., Weilheim in Oberbayern, Germany). Organic matter content was determined using a digital burette (BDeco, model DCB5000, Boeckel, Hamburg, Germany). Soil texture was assessed with a hydrometer (THERMCO

ASTM, model 152H, HB Instrument/Gilson Company Inc., Reading, PA, USA) in combination with a mechanical dispenser (Hamilton Beach, model HMD400, Hamilton Company, Reno, NV, USA). Total nitrogen quantification was carried out using a digestion block (BERT, model Heizblock K24, Heizbiac GmbH, Ulm, Germany) and distillation (Wasserdam, model Destillere 52, Grupo WESDOM, Wenzhou, China). Available phosphorus was measured colorimetrically using a spectrophotometer (Thermo Scientific, model Genesys 150, Thermo Fisher Scientific, Rochester, NY, USA). Exchangeable bases and potassium were analyzed by atomic emission spectrometry (Agilent Technologies, model 4210, Santa Clara, CA, USA). Mass measurements were obtained with an analytical balance (Bell, model M214Ai, BEL Engineering S.r.l., Monza, Italy).

Table 1. Soil physicochemical characteristics before planting the quinoa crop.

Parameter	Result
Sand (%)	40
Silt (%)	46
Clay (%)	14
Texture	Franco
pH	7.80
Electrical conductivity (mS m^{-1})	0.13
Organic matter (%)	2.30
N (%)	0.12
P (ppm)	15.79
K (ppm)	380.26
Ca (cmol(+) kg^{-1})	37.63
Mg (cmol(+) kg^{-1})	6.10
K (cmol(+) kg^{-1})	1.99
Na (cmol(+) kg^{-1})	0.46
CEC (cmol(+) kg^{-1})	46.48

2.3. Plant Material

Four quinoa varieties were evaluated in this study and seeds were provided by the National Institute of Agrarian Innovation (INIA). The first, Blanca de Junín (BJ), was developed by the Universidad Nacional del Centro del Perú. The second, INIA 441 Señor del Huerto (SH), was released by the National Institute of Agrarian Innovation (INIA) at the Canaán Experimental Station and originates from the Ayacucho Region. The remaining two varieties, INIA 415 Pasankalla (RP).and INIA 420 Negra Collana (NC), were released by INIA at the Illpa Experimental Station in Puno (Figure 2).

2.4. Experimental Design

The main plots were assigned to the four quinoa varieties, while the subplots corresponded to four treatments: Control, *Azospirillum brasilense* and *Glomus iranicum* var. *tenuihypharum* and the combination of both microorganisms. This design resulted in a total of 48 experimental units. Each unit covered an area of 12.80 m^2 and comprised four rows, each 3.20 m in length, with 0.80 m spacing between rows and accommodating approximately 256 plants per plot (Table 2)

Table 2. Treatment Combination.

Microorganism	Code
Uninoculated (control)	TR1
Azospirillum brasilense	TR2
Glomus iranicum	TR3
Azospirillum brasilense and *Glomus iranicum*	TR4

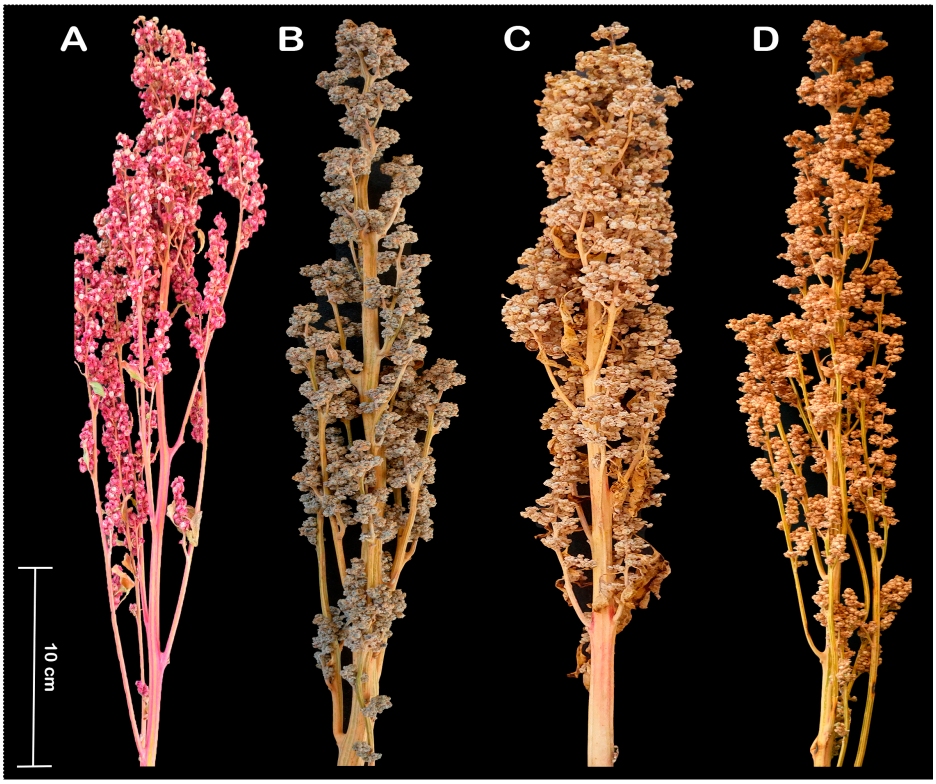


Figure 2. Quinoa genotypes: (**A**) INIA 415 Pasankalla (RP), (**B**) INIA 420 Negra Collana (NC), (**C**) Blanca de Junín (BJ) and (**D**) INIA 441 Señor del Huerto (SH).

2.5. Fertilization and Agronomic Management

The experiment was established on 27 November 2023. Land preparation involved plowing with a disc plow, followed by harrowing and leveling. Rows were spaced at 0.80 m and sowing was carried out in continuous furrows. At sowing, 175 kg ha^{-1} of organic fertilizer (NPK with micronutrients) was applied along the furrow to avoid negative interactions with the microorganisms. A seeding density of 13 kg ha^{-1} was used. Immediately after sowing, irrigation was performed by gravity according to the crop's water requirements. Thinning was conducted to maintain 15–20 plants per linear meter.

To avoid suppressing the activity and establishment of the inoculated microorganisms, synthetic fertilizers were not applied, as mineral NPK sources can negatively affect soil microbial communities by altering pH, reducing organic matter, and decreasing microbial diversity [49,50].

The first phytosanitary treatment was applied as a preventive measure against downy mildew (*Peronospora* spp.) and quinoa moth (*Eurysacca meganocampta*), using metalaxyl and mancozeb (50 g), fipronil (20 mL) and an adherent (40 mL) in a spray volume of 20 L. Harvesting was performed once the panicles reached a grain moisture content of 13–15%, depending on the variety.

2.6. Microbial Seed Inoculation Procedure

The *Azospirillum brasilense* strain Az007 was provided by the FOCAM project "Use of Microorganisms for the Sustainable Organic Production of Quinoa, Maize and Avocado in the Ayacucho Region" of the Universidad Nacional San Cristóbal de Huamanga [51]. The inoculum was prepared in NFb (nitrogen-free medium) liquid medium at a bacterial concentration of 1×10^8 CFU g^{-1}, following the method described by Condori et al. [52]. For each experimental unit, 126 g of quinoa seeds were inoculated as follows: 4 g of solid inoculant (peat), 3 mL of liquid inoculant and 15 mL of adhesive (gum arabic) were thoroughly mixed before adding the seeds. To pelletize the seeds and protect them from direct solar radiation, 50 g of dolomite was incorporated.

The arbuscular mycorrhizal *fungus Glomus iranicum* var. *tenuihypharum* was applied using the commercial biological inoculant MycoUp (agricultural biotechnology company, Coterva Agriscinece, Indianapolis, IN, USA; 120 propalules g^{-1}) was applied at the beginning of the panicle initiation stage. The product was prepared by diluting 384 g in 192 L of water and applied directly to the plant collar.

2.7. Agronomic Measurements

2.7.1. Vegetative Parameters

At physiological maturity, ten randomly selected plants from the two central rows of each experimental unit were evaluated. The following traits were recorded: (i) plant height (PH; cm), measured from the plant collar to the last node bearing the tassel; (ii) panicle length (cm), measured from the supporting node to the tip of the main panicle; both parameters were measured using a measuring tape. (iii) Panicle diameter (cm) was determined at the widest part of the panicle using a ruler. With a digital caliper (DCLA 1205 VINCA, model DCLA-1205, Los Angeles, CA, USA), we further measured: (iv) stem diameter (mm) at the lower third of the stem and (v) central glume length (mm).

2.7.2. Yield Parameters

Ten randomly selected plants from the two central rows of each experimental unit were assessed. The following traits were considered: (i) panicle weight (g panicle^{-1}). Each tassel was then threshed and debris removed to obtain (ii) grain weight (g panicle^{-1}). (iii) Fifty kernels were counted and weighed and the result extrapolated to determine thousand-seed weight (g), using an analytical balance (OHAUS, model AX4202, Newark, NJ, USA). (iv) Grain yield (t ha^{-1}) was estimated from the average grain weight per tassel and plot size and converted to kg ha^{-1}. (v) Grain diameter (mm) was measured with the digital caliper (DCLA 1205 VINCA). (vi) Hectoliter weight (kg hL^{-1}) was determined using a SEEDBURO Filling Hopper balance (model 0201045, Chicago, IL, USA). Finally, the harvest index (HI) was calculated as:

$$\text{HI (\%)} = (\text{Grain yield}/\text{Total weight}) \times 100 \quad (1)$$

2.7.3. Root Development Parameters

Root traits were measured from ten randomly selected plants in the two central rows of each experimental unit. The following parameters were recorded: (i) root dry weight (g plant^{-1}), after drying the samples in paper bags at 105 °C for 24 h; (ii) main root length (cm), measured with a measuring tape; (iii) root diameter (mm), measured at the root collar with a digital caliper (DCLA 1205 VINCA); (iv) number of lateral roots (units); and (v) root volume (VR, $\text{cm}^3\ \text{plant}^{-1}$), determined by water displacement in a 500 mL graduated cylinder, calculated as:

$$VR\ (\text{cm}^3\ \text{plant}^{-1}) = Volumen_{final} - Volumen_{initial} \quad (2)$$

2.8. Statistical Analysis

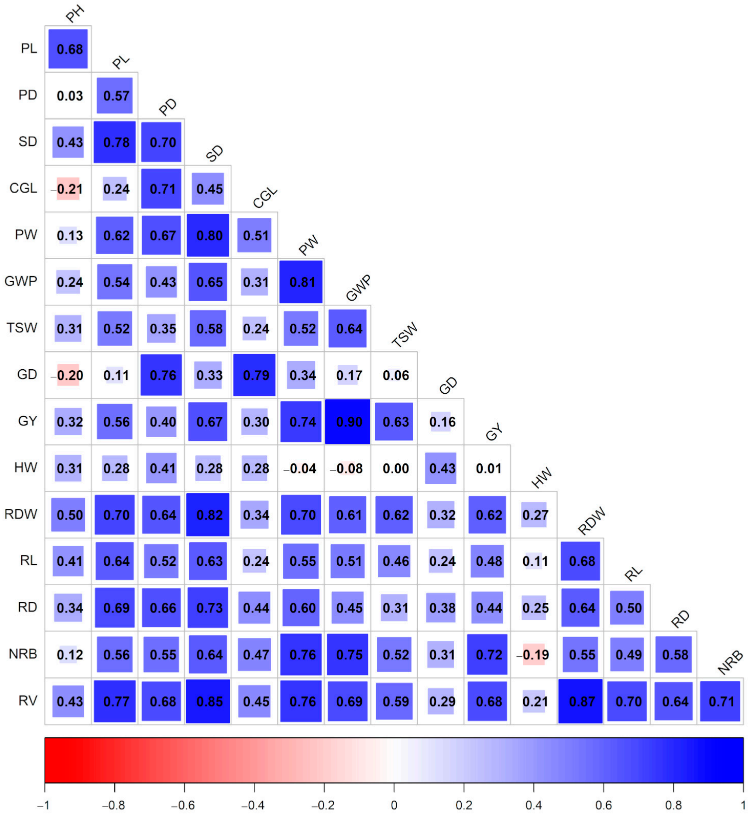
Prior to performing the analysis of variance (ANOVA), the assumptions of homogeneity of variances (homoscedasticity) and data normality were verified. The statistical analysis was carried out according to a split-plot arrangement within a randomized complete block design (RCBD). ANOVA was used to evaluate the effects of treatments, genotypes and their interactions. Mean comparisons were performed using Tukey's test ($p < 0.05$) to detect differences among genotypes, whereas Dunnett's test ($p < 0.05$) was applied to compare each inoculation treatment against the uninoculated control. All statistical analyses were conducted using RStudio software (version 4.5, R Core Team, Vienna, Austria) [53].

For graphical representation, only variables or factors showing statistically significant effects ($p < 0.05$) were plotted. Interaction plots were presented exclusively for traits where the genotype × treatment interaction was significant in the mixed model.

3. Results

3.1. Correlation Analysis

The correlation matrix revealed strong and significant associations among several agronomic and root-related traits of quinoa (Figure 3). Panicule diameter (PD) exhibited a strong positive correlation with stem diameter (SD, $r = 0.70$) and grain diameter (GD, $r = 0.76$). Similarly, SD was positively associated with panicle weight (PW, $r = 0.80$) and all root traits such as RDW ($r = 0.82$) and RV ($r = 0.85$), indicating that thicker stems favored panicle development and root expansion.



	PH	PL	PD	SD	CGL	PW	GWP	TSW	GD	GY	HW	RDW	RL	RD	NRB
PL	0.68														
PD	0.03	0.57													
SD	0.43	0.78	0.70												
CGL	−0.21	0.24	0.71	0.45											
PW	0.13	0.62	0.67	0.80	0.51										
GWP	0.24	0.54	0.43	0.65	0.31	0.81									
TSW	0.31	0.52	0.35	0.58	0.24	0.52	0.64								
GD	−0.20	0.11	0.76	0.33	0.79	0.34	0.17	0.06							
GY	0.32	0.56	0.40	0.67	0.30	0.74	0.90	0.63	0.16						
HW	0.31	0.28	0.41	0.28	0.28	−0.04	−0.08	0.00	0.43	0.01					
RDW	0.50	0.70	0.64	0.82	0.34	0.70	0.61	0.62	0.32	0.62	0.27				
RL	0.41	0.64	0.52	0.63	0.24	0.55	0.51	0.46	0.24	0.48	0.11	0.68			
RD	0.34	0.69	0.66	0.73	0.44	0.60	0.45	0.31	0.38	0.44	0.25	0.64	0.50		
NRB	0.12	0.56	0.55	0.64	0.47	0.76	0.75	0.52	0.31	0.72	−0.19	0.55	0.49	0.58	
RV	0.43	0.77	0.68	0.85	0.45	0.76	0.69	0.59	0.29	0.68	0.21	0.87	0.70	0.64	0.71

Figure 3. Correlation matrix among agronomic and physiological traits in quinoa. PH, plant height; PL, panicle length; PD, panicle diameter; SD, stem diameter; CGL, central glomerule length; PW, panicle weight; GWP, grain weight per panicle; TSW, thousand-seed weight; GD, grain diameter; GY, grain yield; HW, hectoliter weight; RDW, root dry weight; RL, root length; RD, root diameter; NRB, number of root branches; RV, root volume. The color intensity inside square represents the strength of Pearson's correlation coefficients (r), with blue indicating positive and red negative associations.

Grain yield (GY) showed the closest relationships with grain weight per panicle (GWP, $r = 0.90$) and panicle weight (PW, $r = 0.74$), highlighting these variables as primary yield determinants. Thousand seed weight (TSW) was moderately correlated with GY ($r = 0.63$), reinforcing its contribution to yield formation. In contrast, Plant Height (PH) exhibited little negative or positve associations with most agronomic traits, including grain diameter (GD, $r = -0.20$) and central glomerule length (CGL, $r = -0.21$).

Root traits were highly interrelated: Root volume (RV) showed strong positive correlations with all root parameters, particularly with RDW (r = 0.87) and number of root branches (NRB, r = 0.71). Additionally, RV was positively associated with vegetative traits such as panicule length (PL, r = 0.77) and stem diameter (SD, r = 0.85), as well as with yield-related traits, especially panicle weight (PW, r = 0.76).

3.2. Response of Vegetative Parameters

3.2.1. Genotypic Effects

Significant differences among genotypes were observed for all vegetative traits (Table S1). The tallest plants were recorded in SH (106.0 ± 2.81 cm) and BJ (103.0 ± 3.24 cm), clearly exceeding RP (72.10 ± 3.34 cm) and NC (62.50 ± 2.71 cm) (Figure 4A). A contrasting trend was observed for central glomerule length (mm), where RP showed the largest mean (11.77 ± 0.85 mm), while BJ (8.57 ± 0.59 mm) and NC (7.98 ± 0.23 mm) occupied an intermediate range and SH (6.72 ± 0.51 mm) presented the shortest glomerules (Figure 4B). In terms of panicle length (PL), BJ (63.40 ± 2.66 cm) and SH (62.50 ± 4.09 cm) formed the upper tier, RP (54.40 ± 1.98 cm) was intermediate and NC (44.80 ± 2.55 cm) showed the smallest values (Figure 4C). For panicle diameter (PD), RP displayed the largest mean (11.79 ± 0.75 cm), while BJ (8.33 ± 0.66 cm) and SH (7.29 ± 0.83 cm) were lower but still clearly above NC (5.55 ± 0.53 cm). Thus, NC consistently trailed the other three genotypes for this trait (Figure 4D). Finally, stem diameter (SD) also varied significantly among genotypes: BJ (6.76 ± 0.26 mm) and RP (6.25 ± 0.29 mm) exhibited thicker stems compared with SH (6.10 ± 0.35 mm) and NC (5.09 ± 0.36 mm) had the thinnest (Figure 4E). Together, these results indicate that BJ and SH stand out for plant stature and panicle development, BJ additionally excels in stem thickness and RP shows superior glomerule elongation, while NC consistently displays the smallest vegetative dimensions (Table S2).

3.2.2. Treatment Effects

The ANOVA revealed significant differences among treatments for most vegetative traits of quinoa, with the co-inoculation of *Azospirillum brasilense* and *Glomus iranicum* var. *tenuihypharum* (TR4) showing the most consistent and pronounced improvements (Table S1). Although plant height did not differ significantly among treatments, a slight upward trend was evident in inoculated plants, particularly in TR2 (89.00 ± 7.41 cm), TR3 (87.10 ± 6.11 cm), TR4 (87.60 ± 7.05 cm) with co-inoculation, compared with the control TR1 (80.50 ± 4.87 cm) (Figure 5A). In contrast, central glomerule length (CGL) exhibited a marked response to microbial inoculation. The co-inoculated treatment (TR4) achieved the highest mean (10.50 ± 0.85 mm), significantly exceeding the control ($p < 0.0001$), while single inoculations with *A. brasilense* (TR2) and *G. iranicum* (TR3) also promoted substantial increases with 9.14 ± 0.83 mm and 8.77 ± 0.54 mm, respectively (Figure 5B).

A similar pattern was observed for panicle length (PL), where TR4 (64.01 ± 3.90 cm) outperformed all other treatments, followed by TR2 (58.10 ± 3.28 cm) and TR3 (56.20 ± 3.05 cm), with highly significant differences relative to the control ($p < 0.01$) (Figure 5C). The panicle diameter (PD) also increased markedly under inoculation, rising from 5.56 ± 0.78 cm (TR1) to 8.86 ± 0.72 cm (TR2), 8.25 ± 0.96 cm (TR3) and 10.30 ± 0.86 cm (TR4) (Figure 5D). Likewise, stem diameter (SD) exhibited a clear positive response, reaching 6.07 ± 0.30 cm (TR2), 6.28 ± 0.25 cm (TR3) and 6.91 ± 0.37 cm (TR4) compared with 4.49 ± 0.26 cm in the control (Figure 5E). Overall, these results indicate that both single and dual inoculations significantly enhanced the vegetative development of quinoa (Table S3).

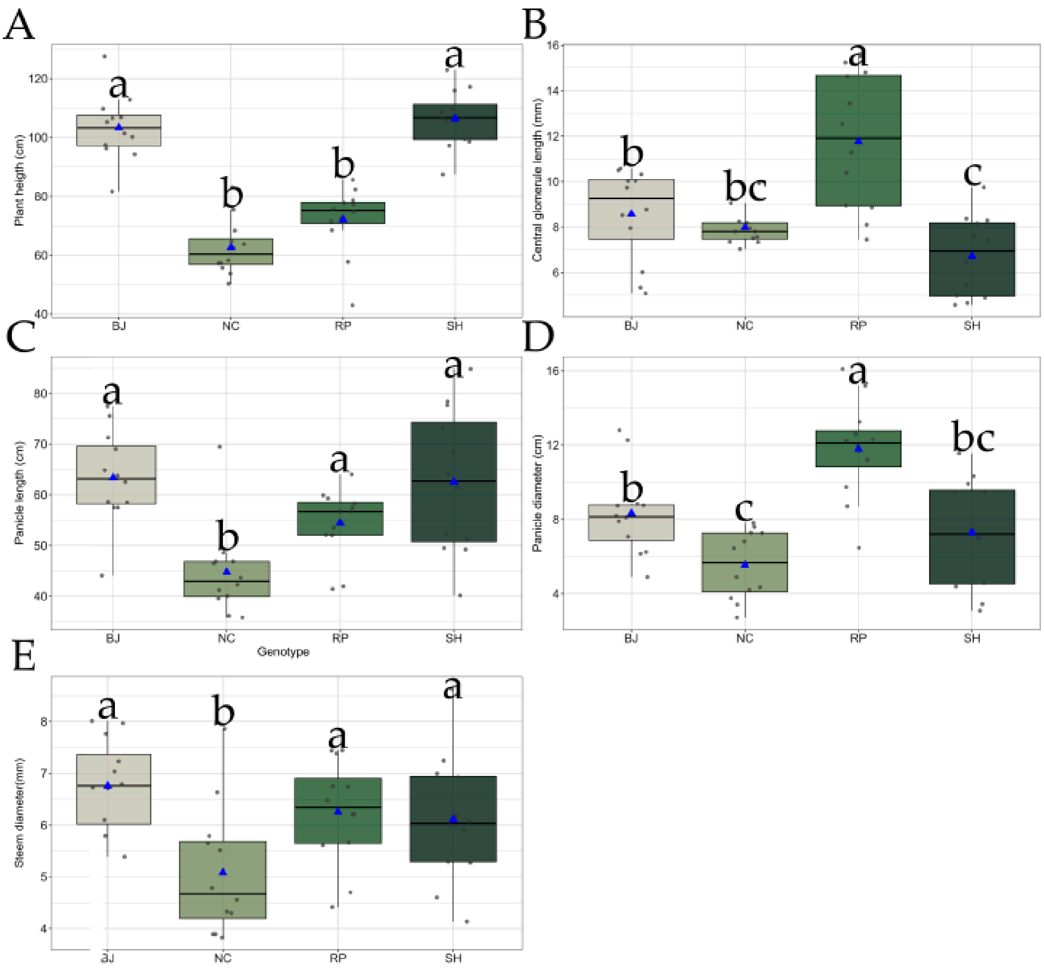


Figure 4. Vegetative traits of quinoa by genotype (BJ, NC, RP, SH). Panels show: (**A**) Plant height (cm), (**B**) Central glomerule length (mm), (**C**) Panicle length (cm), (**D**) Panicle diameter (cm) and (**E**) Stem diameter (mm). Boxplots display the interquartile range (box), median (horizontal line), experimental unit (gray points) and the mean (triangle), while distinct letters indicate significant differences between means analyzed by Tukey's HSD (α = 0.05).

3.2.3. Genotype by Treatment for Glomerule Central Length (mm)

The analysis of variance (ANOVA) revealed significant effects ($p = 0.003$) for central glomerule length (CGL) among genotypes, treatments and their interaction (Table S1). The genotype × treatment interaction indicated that the response to treatments varied depending on the genetic background. In BJ, the highest mean glomerule length was recorded under TR4 (10.0 ± 0.17 mm), followed by TR2 (9.68 ± 0.86 mm), both significantly higher than the control TR1 (5.48 ± 0.28 mm) according to the Dunnett test ($p < 0.001$). In RP, glomerule length increased markedly from 8.14 ± 0.40 mm (TR1) to 15.2 ± 0.20 mm (TR4), representing nearly a twofold increase over the control ($p < 0.0001$). Similarly, in SH, a gradual increase was also observed, ranging from 4.85 ± 0.95 mm (TR1) to 8.49 ± 0.68 mm (TR4), showing a significant difference in improvement under co-ioculation ($p = 0.0017$).

In contrast, NC exhibited minimal variation among treatments, with values ranging between 7.67 ± 0.34 mm and 8.48 ± 0.73 mm, showing no significant differences ($p > 0.05$). Overall, treatments TR2, TR3 and particularly TR4 promoted greater central glomerule elongation in most genotypes, highlighting a differential physiological response among the evaluated materials (Figure 6 and Table S4).

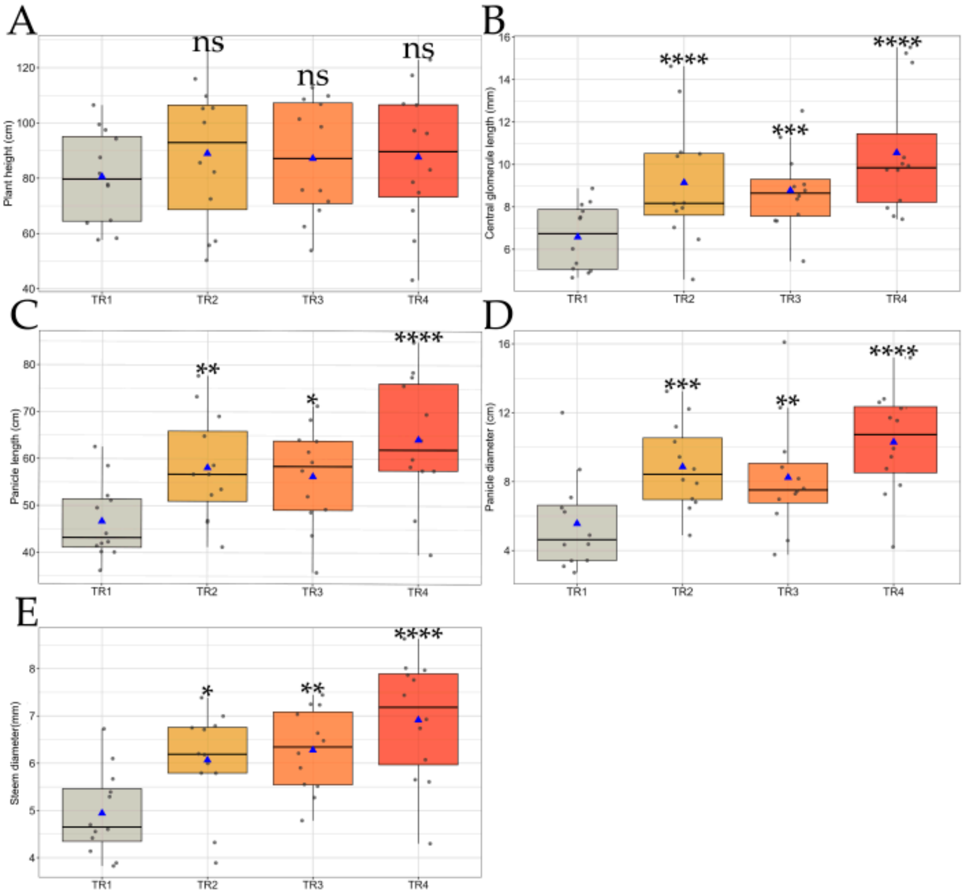


Figure 5. Effect of microbial inoculation on quinoa growth traits under field conditions. Treatments correspond to TR1 = Control, TR2 = *Azospirillum brasilense*, TR3 = *Glomus iranicum* var. *tenuihypharu* and TR4 = combined inoculation (*Azospirillum brasilense* + *Glomus iranicum* var. *tenuihypharum*). Panels show (**A**) Plant height (cm), (**B**) Central glomerule length (mm), (**C**) Panicle length (cm), (**D**) Panicle diameter (cm) and (**E**) Stem diameter (mm). Boxplots display the distribution of values per treatment; dots represent individual experimental units, median (horizontal line), and blue triangles indicate mean values. Significance levels were determined using Dunnett's test compared with the control: $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***), $p < 0.0001$ (****) and ns = not significant.

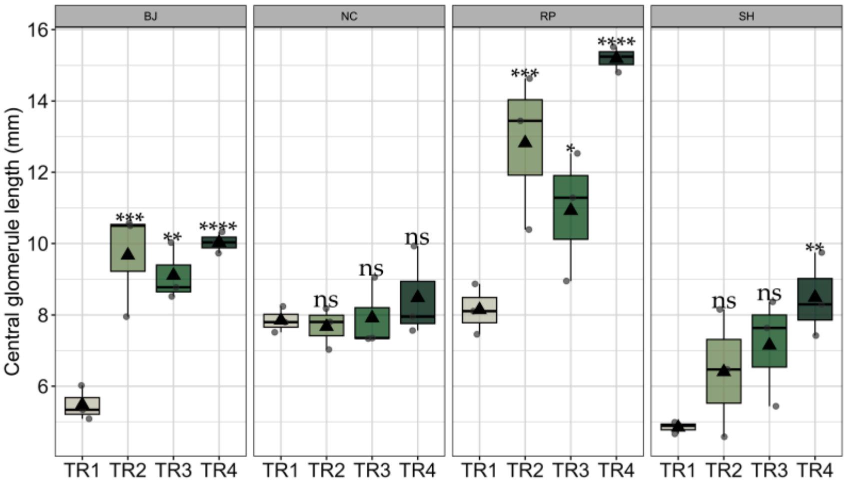


Figure 6. Central glomerule length (mm) by genotype (BJ, NC, RP, SH) across treatments: TR1 = control, TR2 = *Azospirillum brasilense*, TR3 = *Glomus iranicum* var. *tenuihypharum*, TR4 = co-inoculation. Boxplots show the interquartile range (box), median (horizontal line), mean (triangle) and experimental units (gray points). Significance levels were determined using Dunnett's test compared with the control: $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***), $p < 0.0001$ (****) and ns = not significant.

3.3. Response of Yield Parameters

3.3.1. Genotype Effects

The genotypic contrasts for yield-related traits revealed distinct but trait-specific patterns (Table S1). Although panicle weight (g panicle^{-1}) showed no significant differences among genotypes according to Tukey's HSD ($\alpha = 0.05$), the mean values suggested a mild gradient. RP exhibited the highest mean (28.10 ± 3.05 g), closely followed by BJ (26.9 ± 3.10 g), whereas NC (23.4 ± 3.15 g) and SH (23.4 ± 3.71 g) displayed similar, slightly lower values (Figure 7A). By contrast, grain weight per panicle (g) varied significantly across genotype ($p < 0.05$). BJ ranked first (10.85 ± 1.40 g), with NC (8.62 ± 1.21 g) and RP (8.25 ± 1.10 g) forming an intermediate tier and SH (7.88 ± 1.07 g) presenting the lowest mean recorded the lowest performance (Figure 7B).

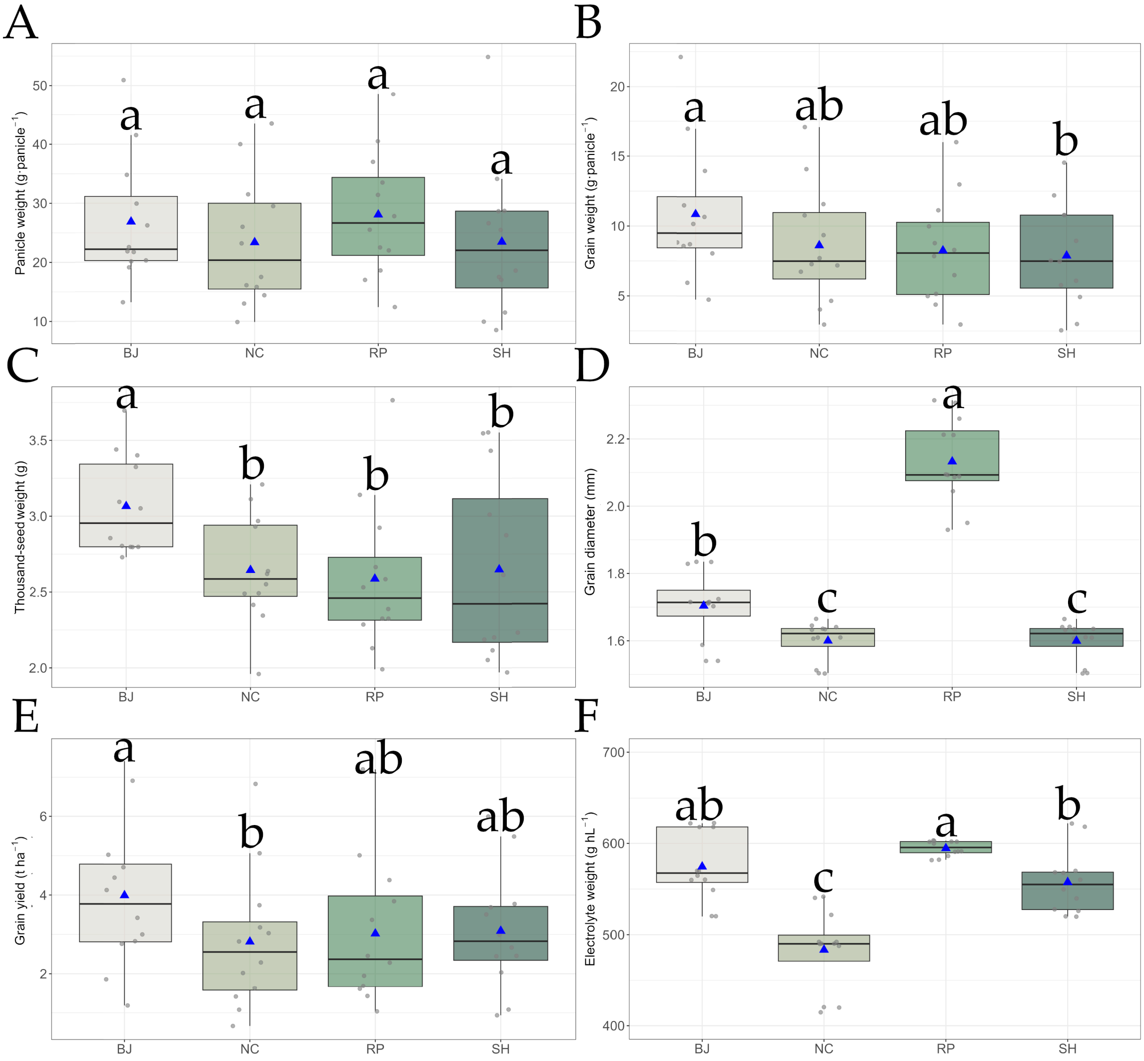


Figure 7. Yield traits of quinoa by genotype (BJ, NC, RP, SH). (**A**) Panicle weight (g panicle^{-1}), (**B**) Grain weight (g panicle^{-1}), (**C**) Thousand-seed weight (g), (**D**) Grain diameter (mm), (**E**) Grain yield (t ha^{-1}) and (**F**) Hectoliter weight (g hL^{-1}). Boxplots display the interquartile range (box), median (horizontal line), experimental unit (gray points) and the mean (triangle). while distinct letters indicate significant differences between means analyzed by Tukey's HSD ($\alpha = 0.05$).

Marked genotypic differentiation also appeared for thousand-seed weight (g). BJ displayed the heaviest seeds (3.07 ± 0.09 g), whereas SH (2.65 ± 0.17 g), NC (2.64 ± 0.10 g) and RP (2.59 ± 0.14 g) were statistically lower and mutually similar (Figure 7C). Interestingly, this pattern was inverted for grain diameter (mm): RP achieved the largest grains (2.13 ± 0.03 mm), while BJ (1.70 ± 0.02 mm), NC (1.60 ± 0.01 mm) and SH (1.60 ± 0.01 mm) exhibited smaller and comparable dimensions (Figure 7D). In terms of grain yield (t ha^{-1}), BJ stood out with the highest productivity (3.99 ± 0.55 t ha^{-1}), followed by SH (3.09 ± 0.44 t ha^{-1}) and RP (3.02 ± 0.53 t ha^{-1}), while NC (2.81 ± 0.51 t ha^{-1}) yielded roughly 30% less than BJ (Figure 7E). Finally, Hectoliter weight favored RP (595 ± 2.41 kg hL^{-1}), followed by BJ (574 ± 10.80 kg hL^{-1}) and SH (558 ± 10.00 kg hL^{-1}); NC (483 ± 12.7 kg hL^{-1}) exhibited the lowest bulk density (Figure 7F). Collectively, BJ and RP emerged as the most productive genotypes, combining superior grain yield and seed quality attributes, while SH performed moderately and NC consistently lagged behind (Table S2).

3.3.2. Treatment Effects

Analysis of variance revealed highly significant treatment effects across most yield-related traits ($p < 0.001$), highlighting the strong influence of microbial inoculation (Table S1). Among treatments, the co-inoculation of *Azospirillum brasilense* and *Glomus iranicum* var. *tenuihypharum* (TR4) consistently outperformed both single inoculations and the uninoculated control. Under TR4, plants achieved the highest values for panicle weight (35.30 ± 3.62 g $plant^{-1}$), grain weight per panicle (13.20 ± 1.30 g $plant^{-1}$), grain diameter (1.82 ± 0.06 mm), thousand-seed weight (3.27 ± 0.11 g) and grain yield (4.94 ± 0.59 t ha^{-1}). These improvements represent a 190% increase in yield relative to the control (1.71 ± 0.28 t ha^{-1}**)**, confirming a strong synergistic interaction between the bacterial and fungal inoculants. The only exception was the hectoliter weight, which slightly decreased (545.0 ± 13.1 g hL^{-1}) compared with the control (570.0 ± 10.3 g hL^{-1}), suggesting that grain density was unaffected by the yield gains driven by co-inoculation.

Single inoculations produced intermediate but trait-specific responses. The application of *A. brasilense* alone (TR2) significantly enhanced panicle weight (25.50 ± 1.98 g), grain weight per panicle (8.33 ± 0.53 g), thousand-seed weight (2.76 ± 0.08 g) and grain diameter (1.82 ± 0.08 mm), resulting in a 75% yield increase (2.98 ± 0.31 t ha^{-1}) compared with the control. However, the hectoliter weight (552 ± 24.10 g hL^{-1}) did not differ significantly from the control. The fungal inoculation (*G. iranicum* var. *tenuihypharum*, TR3) also improved grain diameter (1.75 ± 0.05 mm), panicle weight (26.80 ± 2.26 g), grain per panicle (9.28 ± 0.79 g) and grain yield (3.27 ± 0.32 t ha^{-1}), corresponding to a 91% increase over the control. Interestingly, TR3 (540.00 ± 10.50 g hL^{-1}) reduced hectoliter weight compared with the control (Figure 8A–F; Table S3).

3.3.3. Genotypes by Treatment for Grain Diameter and Hectoliter Weight

Additionally, significant differences ($p < 0.001$) were detected in grain diameter among genotypes, treatments and their interaction, indicating genotype-dependent responses to the applied treatments (Table S1). Mean grain diameter ranged from 1.51 to 2.29 mm, with the highest values observed in the genotype RP and the lowest in NC and SH. In BJ, a gradual increase for BJ was observed from 1.56 ± 0.01 mm (TR1) to 1.83 ± 0.00 mm (TR4), with all treatments showing significant differences compared with the control ($p < 0.001$). Similarly, in NC, TR2–TR4 produced slightly higher diameters (1.64–1.65 mm) than TR1 (1.51 mm), although the magnitude of the response was smaller. The RP genotype exhibited the greatest variability, reaching 2.29 ± 0.01 mm under TR2, which represented an increase of more than 10% compared with the control (1.99 ± 0.05 mm). In SH, grain diameter also increased significantly from 1.51 ± 0.00 mm (TR1) to 1.65 ± 0.00 mm (TR4) ($p < 0.001$). Collectively, treatments TR2–TR4 promoted thicker grains across most genotypes, with TR4 consistently showing the highest response (Figure 9 and Table S5).

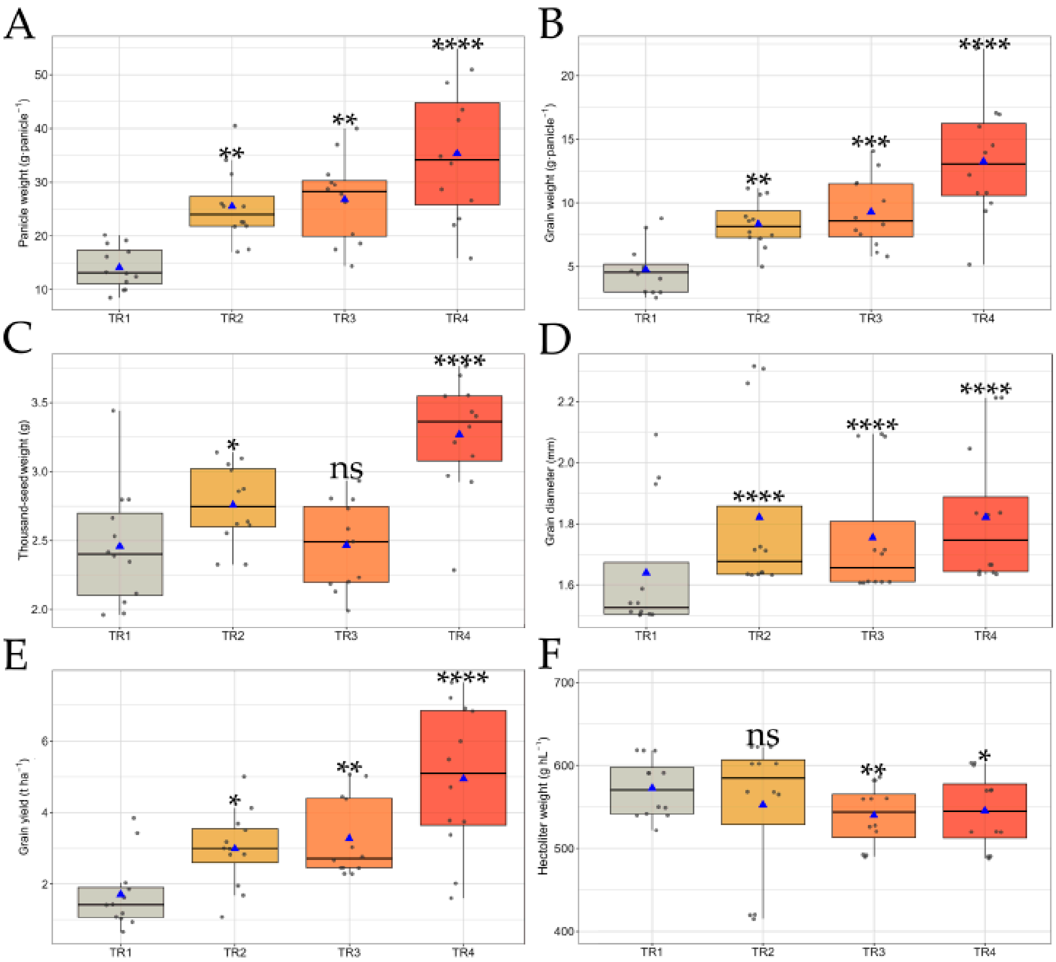


Figure 8. Effect of microbial inoculation on quinoa growth traits under field conditions. Treatments correspond to TR1 = Control, TR2 = *Azospirillum brasilense*, TR3 = *Glomus iranicum* var. *tenuihypharum* and TR4 = combined inoculation (*Azospirillum brasilense* + *Glomus iranicum* var. *tenuihypharum*). Panels show (**A**) panicle weight (g panicle^{-1}), (**B**) grain weight (g panicle^{-1}), (**C**) thousand-seed weight (g), (**D**) grain diameter (mm), (**E**) Grain yield (t ha^{-1}) and (**F**) hectoliter weight (g hL^{-1}). Boxplots display the distribution of values per treatment; dots represent individual experimental units, median (horizontal line), and blue triangles indicate mean values. Significance levels were determined using Dunnett's test compared with the control: $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***), $p < 0.0001$ (****) and ns = not significant.

Significant effects ($p < 0.001$) were detected for genotype, treatment and their interaction, indicating that the response of hectoliter weight depended on the genetic background (Table S1). Mean values ranged from 418.33 to 603.00 g·hL^{-1}, with BJ and RP showing the highest averages, whereas NC exhibited the lowest values across treatments. In BJ, hectoliter weight decreased notably from 595.00 ± 23.0 g·hL^{-1} (TR1) to 546.67 ± 13.30 g·hL^{-1} (TR3) and 553.33 ± 16.70 g·hL^{-1} (TR4). Conversely, NC presented a sharp reduction under TR2 (418.33 ± 1.67 g·hL^{-1}) compared to TR1 (534.67 ± 6.36 g·hL^{-1}), representing a decrease of nearly 22% ($p < 0.001$). In RP, values remained relatively stable across treatments (583.33–602.00 g·hL^{-1}), with no significant differences from the control ($p > 0.05$). For SH, hectoliter weight showed a declining trend from 569.33 ± 24.5 g·hL^{-1} (TR1) to 536.67 ± 16.7 g·hL^{-1} (TR4), although differences were not statistically significant ($p > 0.05$). Overall, the interaction pattern indicates that NC and BJ were more sensitive to treatment effects, while RP maintained higher weight stability (Figure 10 and Table S6).

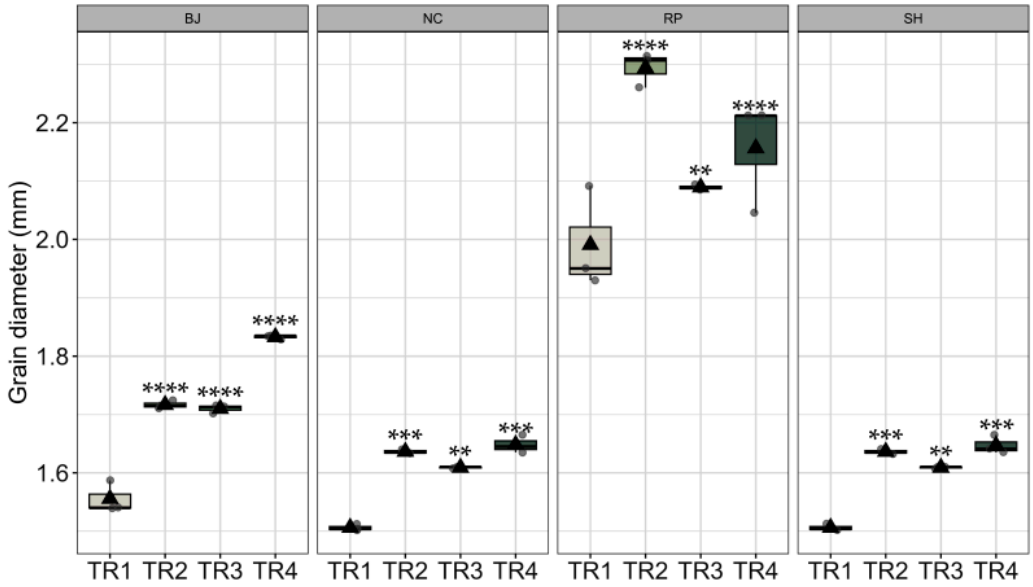


Figure 9. Grain diameter (mm) by genotype (BJ, NC, RP, SH) across treatments: TR1 = control, TR2 = *Azospirillum brasilense*, TR3 = *Glomus iranicum* var. *tenuihypharum*, TR4 = co-inoculation. Boxplots show the interquartile range (box), median (horizontal line), mean (triangle) and experimental units (gray points). Significance levels were determined using Dunnett's test compared with the control: $p < 0.01$ (**), $p < 0.001$ (***), $p < 0.0001$ (****) and ns = not significant.

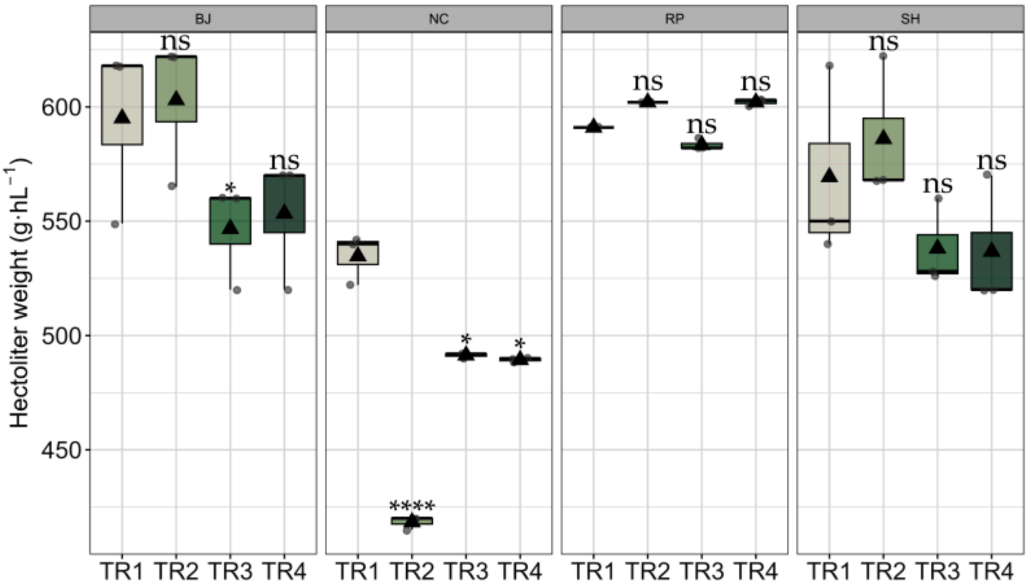


Figure 10. Hectoliter weight (g·hL^{-1}) by genotype (BJ, NC, RP, SH) across treatments: TR1 = control, TR2 = *Azospirillum brasilense*, TR3 = *Glomus iranicum* var. *tenuihypharum*, TR4 = co-inoculation. Boxplots show the interquartile range (box), median (horizontal line), mean (triangle) and experimental units (gray points). Significance levels were determined using Dunnett's test compared with the control: $p < 0.05$ (*), $p < 0.0001$ (****) and ns = not significant.

3.4. Root Parameters

3.4.1. Genotype Effects

Genotypes differed significantly for most root traits (Table S1). Root dry weight was highest in BJ (4.04 ± 0.46 g plant^{-1}), clearly exceeding the intermediate genotypes RP (3.17 ± 0.40 g plant^{-1}) and SH (3.27 ± 0.46 g plant^{-1}), while NC showed the smallest value (1.60 ± 0.21 g plant^{-1}), less than half of BJ. For root length, BJ (20.00 ± 0.37 cm) and SH (19.00 ± 1.07 cm) formed an upper tier with similar means; RP was intermediate

(18.30 ± 0.64 cm) and NC had the shortest roots (16.30 ± 1.28 cm). Root diameter also distinguished the genotypes: RP presented the thickest roots (7.59 ± 0.92 mm), followed closely by BJ (7.47 ± 0.35 mm). SH was intermediate (6.88 ± 0.49 mm) and NC had the thinnest roots (5.17 ± 0.35 mm).

No significant differences were found in the number of root branches, with means ranging narrowly from 14.10 ± 1.38 (BJ) to 12.40 ± 1.60 (SH), while NC and RP each averaged around 14 branches. In contrast, root volume revealed clear separation among genotypes: BJ attained the highest value (7.08 ± 0.85 cm^3 $plant^{-1}$), RP (5.38 ± 0.63 cm^3 $plant^{-1}$) and SH (5.71 ± 0.87 cm^3 $plant^{-1}$) were intermediate and NC recorded the lowest (3.57 ± 0.50 cm^3 $plant^{-1}$). Overall, BJ combines the greatest root biomass and volume with long roots, RP contributes the largest diameters, SH tends to be intermediate to high for length and volume and NC consistently underperforms across root attributes—patterns (Figure 11 and Table S2).

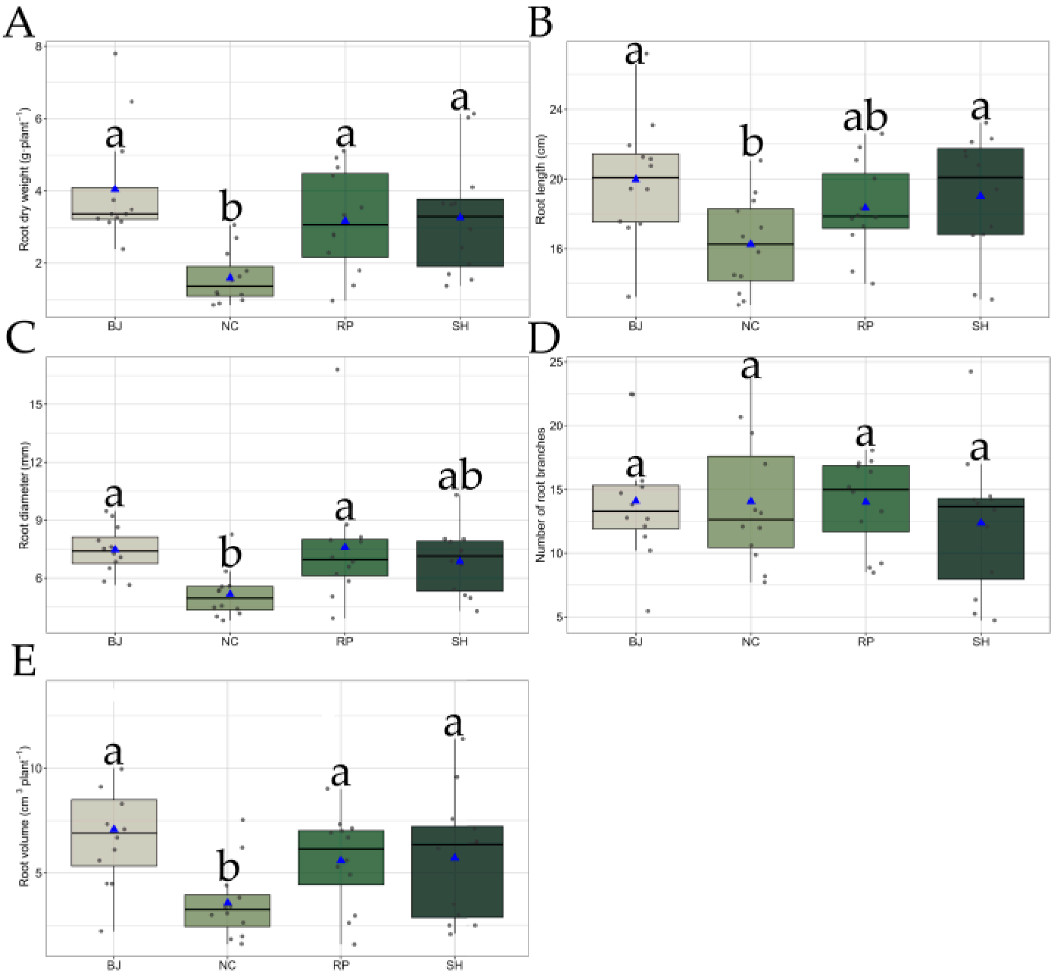


Figure 11. Root traits of quinoa by genotype (BJ, NC, RP, SH). (**A**) Root dry weight (g $plant^{-1}$), (**B**) Root length (cm), (**C**) Root diameter (cm), (**D**) Number of root branches, (**E**) Root volume (cm^3 $plant^{-1}$). Boxplots display the interquartile range (box), median (horizontal line), experimental unit (gray points) and the mean (triangle, while distinct letters indicate significant differences between means analyzed by Tukey's HSD (α = 0.05).

3.4.2. Treatment Effects

Root development responded strongly to microbial inoculation (Table S1). Co-inoculation with *Azospirillum brasilense* and *Glomus iranicum* var. *tenuihypharum* (TR4) delivered the largest and most consistent gains, with highly significant differences versus the control (Dunnett; $p < 0.001$) across all traits. Under Co-inoculation, roots exhibited a diameter 7.78 ± 0.48 mm, length 20.40 ± 0.89 cm, number of branches 18.20 ± 1.28, dry weight 4.24 ± 0.60 g plant^{-1} and volume 8.06 ± 0.85 cm^3 plant $^{-1}$ (Figure 12A–E).

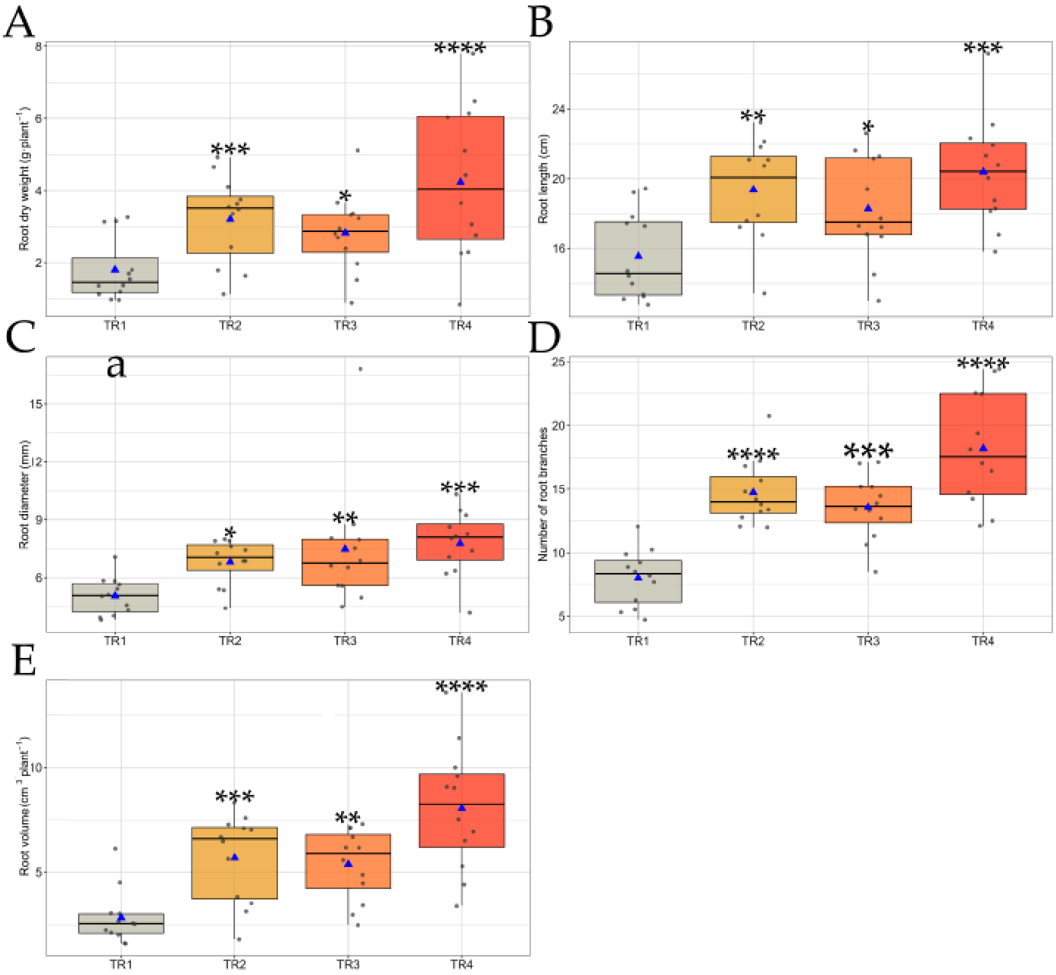


Figure 12. Effect of microbial inoculation on quinoa growth traits under field conditions. Treatments correspond to TR1 = Control, TR2 = *Azospirillum brasilense*, TR3 = *Glomus iranicum* var. *tenuihypharum* and TR4 = combined inoculation (*Azospirillum brasilense* + *Glomus iranicum* var. *tenuihypharum*). Panels show (**A**) Root dry weight (g plant^{-1}), (**B**) Root length (cm), (**C**) Root diameter (cm), (**D**) Number of root branches, (**E**) Root volume (cm^3 plant^{-1}). Boxplots display the distribution of values per treatment; dots represent individual experimental units, median (horizontal line), and blue triangles indicate mean values. Significance levels were determined using Dunnett's test compared with the control: $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***), $p < 0.0001$ (****) and ns = not significant.

Single inoculations produced positive intermediate responses. Inoculation with *A. brasilense* (TR2) significantly enhanced root length (19.40 ± 0.81 cm), number of branches (14.70 ± 0.73), root dry weight (3.21 ± 0.34 g plant^{-1}) and root volume (5.69 ± 0.81 cm^3 plant $^{-1}$); root diameter also increased (6.80 ± 0.33 mm). Inoculation with *G. iranicum* (TR3) significantly improved root diameter (7.48 ± 0.92 mm), number of branches (13.60 ± 0.73) and root volume (5.38 ± 0.48 cm^3 plant $^{-1}$), with additional significant gains for root length (18.30 ± 0.86 cm) and root dry weight (2.83 ± 0.31 g plant^{-1}) (Figure 12A–E).

Overall, the hierarchy of responses across below-ground traits followed the pattern TR4 > TR2 $\gtrsim$ TR3 > TR1, indicating a clear synergy under co-inoculation that enhances both structural attributes (diameter, branching, volume) and biomass accumulation (length, dry weight) of the root system (Table S3).

3.4.3. Genotype by Treatment Root Dry Weight (g·plant^{-1})

Highly significant effects ($p < 0.001$) were observed for genotype, treatment and their interaction, indicating differential root biomass responses among quinoa genotypes under the evaluated conditions (Table S1). Mean root dry weight ranged from 1.10 to 6.46 g·plant^{-1}, with the highest values recorded in BJ and SH and the lowest in NC. In BJ, root dry weight increased markedly from 3.18 ± 0.03 g·plant^{-1} (TR1) to 6.46 ± 0.77 g·plant^{-1} (TR4), with the co-inoculation nearly doubling biomass relative to the control ($p = 0.0002$). The NC genotype exhibited a gradual increase from 1.10 ± 0.62 g·plant^{-1} (TR1) to 2.06 ± 0.64 g·plant^{-1} (TR4), though differences were not statistically significant ($p > 0.05$). In contrast, RP responded strongly to single inoculations: TR2 (4.38 ± 0.42 g·plant^{-1}) and TR3 (3.75 ± 0.69 g·plant^{-1}) both showed significantly higher values than the control. In contrast, SH displayed a consistent increase from 1.54 ± 0.09 g·plant^{-1} (TR1) to 5.28 ± 0.81 g·plant^{-1} (TR4), with TR2 differing significantly from the control (Figure 13). Overall, treatments TR2 and TR4 substantially enhanced root biomass accumulation across most genotypes, particularly in BJ and SH (Table S7).

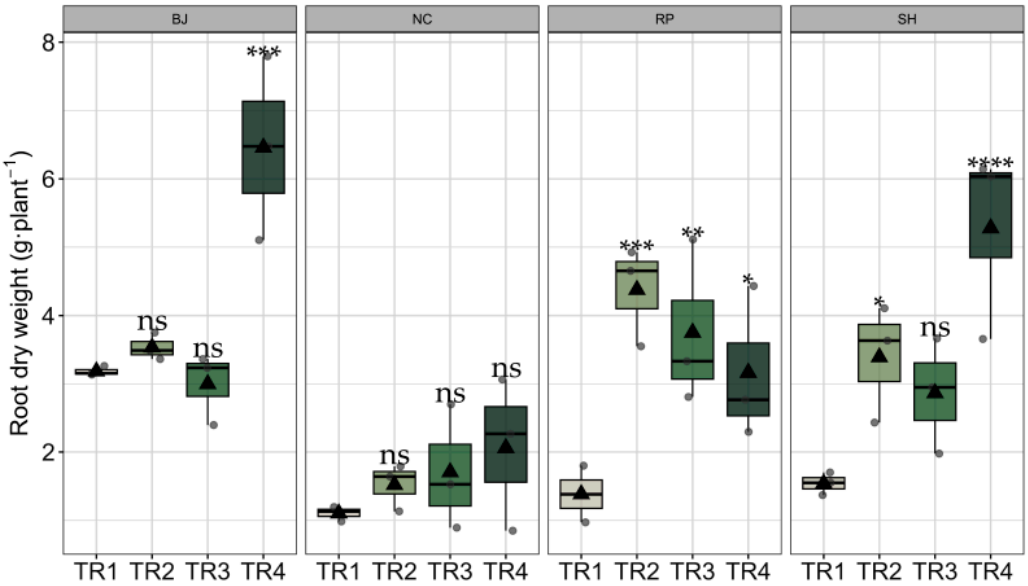


Figure 13. Root dry weight (g·plant^{-1}) by genotype (BJ, NC, RP, SH) across treatments: TR1 = control, TR2 = *Azospirillum brasilense*, TR3 = *Glomus iranicum* var. *tenuihypharum*, TR4 = co-inoculation. Boxplots show the interquartile range (box), median (horizontal line), mean (triangle) and experimental units (gray points). Significance levels were determined using Dunnett's test compared with the control: $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***), $p < 0.0001$ (****) and ns = not significant.

3.5. PCA

Principal Component Analysis (PCA) effectively summarized the multivariate response of quinoa genotypes and yield-related traits under microbial inoculation. The first two principal components Dim-1 (PC1) and Dim-2 (PC2) explained the majority of the total variance (67.8%), separating genotypes according to belowground and aboveground performance.

According to the contribution analysis, the ten variables that contributed most to PC1 were RV, SD, RDW, PW, PL, GWP, NRB, GY, PD and RD, reflecting the dominant influence of belowground biomass and yield-related components on the first axis. Meanwhile, PC2 was mainly explained by GD, CGL, PH, PD and HW, indicating that aboveground growth and reproductive attributes were major contributors to this axis. (Figures S2 and S3).

Genotype RP was positioned on the positive side of PC1, in close association with variables related to grain size and density, indicating superior grain morphology. In contrast, BJ occupied the negative side of PC1, showing strong association with root biomass and panicle weight, typical of vigorous and high-yielding plants. NC and SH were located near the biplot center, reflecting balanced contributions of both root and yield-related components (Figure 14).

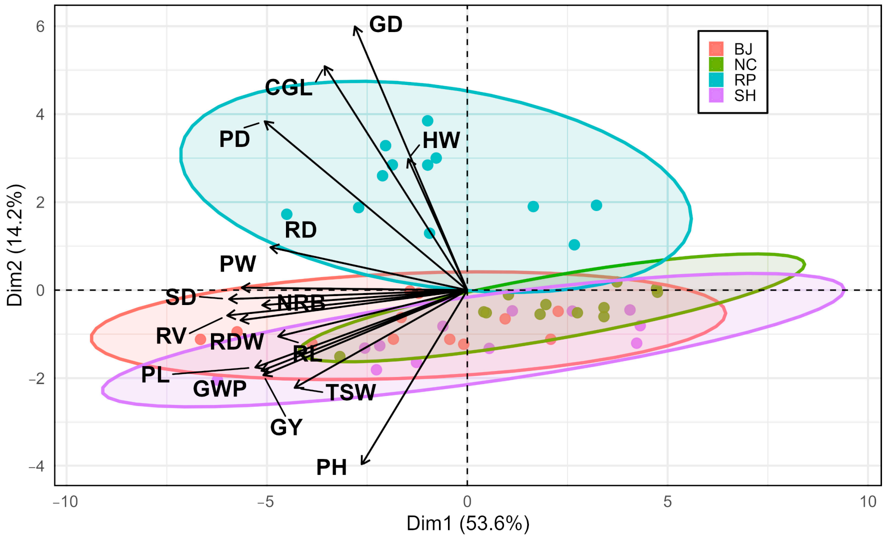


Figure 14. Principal component analysis (PCA) of traits by genotype. Scores are colored by genotype (BJ, NC, RP, SH); shaded ellipses depict the 95% confidence region around each group centroid. Arrows represent standardized variable loadings (vectors point toward increasing values of the trait; arrow length is proportional to the loading magnitude).

Similarly, the biplot of treatments demonstrated clear separation patterns among the four treatments. The co-inoculated treatment (TR4) was positioned on the negative side of PC1, closely associated with enhanced root biomass, panicle development, and yield formation, confirming a synergistic effect between *A. brasilense* and *G. iranicum*. The single fungal inoculation (TR3) showed moderate association with grain structure and density traits, whereas the bacterial inoculation (TR2) displayed intermediate responses across yield components. In contrast, the uninoculated control (TR1) clustered on the opposite side of PC1, far from productivity-related variables, reflecting lower vegetative vigor and grain yield (Figure 15).

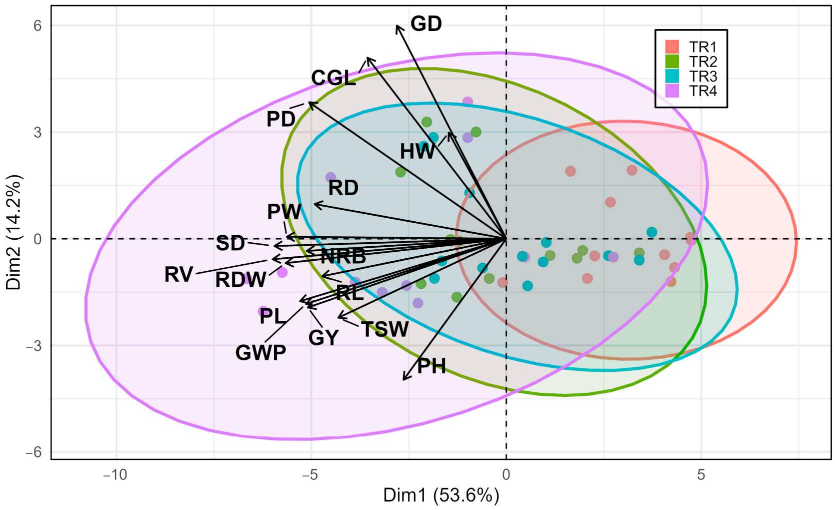


Figure 15. Principal component analysis (PCA) of traits by treatment. Scores are colored by treatment (TR1–TR4); shaded ellipses are 95% confidence regions. Arrows show standardized variable loadings; vectors indicate the direction of increasing trait values and their lengths are proportional to the contribution to the component.

4. Discussion

Our field results demonstrate that co-inoculation with *Azospirillum brasilense* and *Glomus iranicum* var. *tenuihypharum* can substantially improve quinoa growth and productivity. The combined microbial treatment produced marked increases in root development and yield-related traits compared to uninoculated controls, aligning with previous studies in quinoa [37,54–57]. For instance, [58] reported that inoculation with plant growth-promoting rhizobacteria (PGPR) boosted quinoa yield by 40% and [36] observed greater improvement in root biomass with a beneficial *Pseudomonas* strain than in non-inoculated treatments. Likewise, several independent trials have documented significant quinoa yield enhancements due to PGPR application (e.g., increased grain and panicle weight), as seen in both greenhouse and field settings [35,59,60]. Our findings corroborate this positive trend; the treated quinoa plants exhibited larger panicles and greater thousand-seed weight than the controls, thereby reinforcing the evidence that quinoa is highly responsive to biofertilization with beneficial microbes [57,61]. Notably, we observed root system expansion (longer, thicker roots with more branches) under microbial inoculation, which likely underpins the gains in yield. A more robust root system can explore soil resources more effectively and support higher shoot and grain growth [62,63], a relationship also highlighted in correlation analyses of quinoa traits (e.g., root volume correlating strongly with panicle size and yield components). These results underscore that harnessing PGPR and other symbionts is a promising strategy to improve quinoa's agronomic performance in sustainable ways [6,64].

Importantly, the present study provides new insights into the synergy between *A. brasilense* and *G. iranicum* in quinoa. While single inoculations of either microbe did enhance certain growth parameters, the dual inoculation consistently produced the greatest improvements, indicating a complementary or synergistic interaction [65–67]. Co-inoculated plants had the highest root biomass and grain yield, often exceeding the sum effect of each microbe alone [68,69]. This synergism is biologically plausible: *Azospirillum brasilense* is known to fix atmospheric nitrogen and secrete phytohormones (such as indole acetic acid), which stimulate root proliferation and nutrient uptake [70–72]. Meanwhile, *Glomus iranicum* (an arbuscular mycorrhizal fungus, AMF) greatly improves phosphorus acquisition, water uptake and overall nutrient status of the host plant by extending the root's absorptive network [28,73].

Building on this biological complementarity, previous research provides deeper mechanistic evidence that reinforces the synergistic behavior observed in the present field trial. Earlier studies demonstrated that *Azospirillum* and *Glomus* can simultaneously colonize emerging lateral roots, altering cell wall structure and increasing the density of endophytic microbial populations, which enhances nitrogen fixation and root metabolic activity [40]. These synergistic interactions also reshape the plant's secondary metabolism and stress-response signaling. For example, in maize, three-component consortia involving *Azospirillum*, *Pseudomonas*, and *Glomus* induced stronger transcriptional and metabolic responses than individual inoculants [74]. More broadly, PGPR–AMF partnerships enhance plant resilience by increasing metal chelation, solubilizing nutrients, modulating ethylene levels through ACC deaminase activity, and improving water and ion homeostasis under stress [75–78]. Collectively, these mechanisms explain why the combined inoculation in our study produced a more integrated improvement in root development, nutrient acquisition, and yield components, reflecting a well-established synergistic advantage compared to single-microbe applications.

Arbuscular mycorrhizal fungi (AMF), such as *Glomus iranicum* var. *tenuihypharum*, play a mechanistic role far beyond root colonization, functioning as active mediators of phosphorus acquisition and transfer. Extensive extraradical hyphae explore soil microsites inaccessible to roots, mobilizing inorganic phosphorus (Pi) and transporting it toward the root cortex [79]. AMF possess high-affinity phosphate transporters that load Pi into the fungal cytoplasm and deliver it to arbuscules, where it is subsequently released and taken up by plant Pi transporters located in the periarbuscular membrane [80,81]. Additionally, AMF can hydrolyze organic P to release plant-available Pi, particularly in acidic or nutrient-limited soils [82].

Although nitrogen use efficiency (NUE), phosphorus use efficiency (PUE) and plant hormone profiles were not directly quantified in this study, the agronomic responses observed align with well-established mechanisms through which PGPR and AMF modulate plant physiology. PGPR are known to enhance plant growth through multiple plant growth-promoting traits, including nitrogen fixation, hormone synthesis and nutrient solubilization [83–85]. They also influence plant stress physiology via ACC deaminase activity, which regulates ethylene levels and promotes root development and stress resilience [75,81,86]. Complementarily, AMF improve the acquisition of immobile nutrients—particularly phosphorus—through extensive extraradical hyphae, enhancing mineral uptake and rhizosphere enzymatic activity [76,86,87]. They additionally contribute to nitrogen, potassium, magnesium, calcium and sulfur acquisition, especially under stress conditions [88]. The synergistic action of AMF and PGPR has been consistently associated with improved root architecture, biomass accumulation and nutrient-use efficiency across crops [78]. Therefore, although hormonal and nutrient-mobilization measurements were not performed, the positive agronomic responses observed in quinoa are biologically consistent with the documented capacity of these microbial groups to modulate hormone production, enhance nutrient uptake and support plant performance under diverse environmental conditions.

In our quinoa plants, the *A. brasilense* treatment alone promoted root elongation and branching (consistent with auxin-mediated root growth), whereas *G. iranicum* alone mainly enhanced root thickness and access to soil nutrients. When combined, these microbes appear to reinforce each other's benefits: the bacteria-induced increase in root surface and exudation likely facilitated more extensive mycorrhizal colonization and in turn the mycorrhiza-provided nutrients (especially phosphorus) supported greater overall plant growth [35,73]. Indeed, previous work suggests that PGPR can actively *promote* AMF symbiosis [89]. Single AMF or *Rhizobium* treatment dramatically increased shoot biomass by 36–281% and root biomass by 16–36% than non-inoculated control and dual inoculation of *Rhizobium* and *Paraglomus occultum* or *Rhizophagus intraradices* further magnified the positive effect, attributed to mutual reinforcement of the two symbionts. Our results align with these findings, confirming that co-inoculation led to synergistic outcomes in quinoa. The pronounced gains under dual inoculation, nearly two-fold increase in certain panicle traits in some genotypes, highlight that these microbes provided complementary functions to the plant rather than redundantly competing. This aligns with broader agricultural studies, for example, a classic wheat field experiment by [90] showed that a triple inoculation of a nitrogen-fixing bacterium (*Azotobacter*), a phosphate-solubilizing *Bacillus,* and an AMF (*Glomus fasciculatum*) resulted in a two-fold grain yield increase over controls. In our case, *A. brasilense* and *G. iranicum* presumably played analogous roles (biological nitrogen supply plus enhanced phosphorus uptake), yielding a net positive effect on quinoa growth and yield far beyond what either could achieve alone. Such evidence strongly supports the use of microbial consortia as a means to amplify plant productivity through multiple mechanisms acting in concert.

A closer look at plant responses reveals that the effects of co-inoculation extend beyond root morphology and involve deeper physiological adjustments linked to stress resilience. In our field conditions, the synergistic inoculation of *Azospirillum brasilense* and *Glomus iranicum* significantly increased root length, root surface area and root dry biomass of quinoa, indicating that the microbial treatment modified root system architecture toward a more exploratory and highly branched phenotype. Similar relationships between enhanced root foraging capacity, deeper rooting and improved acquisition of water and nutrients have been described for Andean Chenopodium species and cultivated quinoa under water-limited or low-fertility environments [62,63]. Beyond these morphological adjustments, our results are consistent with current knowledge that quinoa stress tolerance relies on a coordinated suite of physiological and biochemical responses, including osmotic adjustment via accumulation of soluble sugars and other compatible solutes, maintenance of photosynthetic pigments and activation of antioxidant pathways that limit reactive oxygen species build-up and membrane damage under drought or salinity stress [91–93]. The observed increases in root biomass and grain yield in co-inoculated plants, therefore, likely reflect both improved physical soil exploration and microbially mediated priming of canonical stress-response pathways, as reported for quinoa and other crops colonized by plant-growth-promoting rhizobacteria and arbuscular mycorrhizal fungi [94–96]. Taken together, these findings support the view that quinoa is a suitable model crop to study how belowground microbial consortia modulate root system architecture and ecophysiological responses to water and nutrient stress in deep soil layers.

It is worth noting that the effect of inoculation varied among quinoa genotypes in our study, which is an important consideration for practical applications. Three of the four tested cultivars responded strongly to the bio-inoculants (showing significant improvements in root and panicle metrics), whereas one variety (NC) exhibited minimal response. This differential response mirrors findings by [17], who reported genotype-dependent efficacy of endophytic bacterial consortia in quinoa. Some quinoa genotypes may inherently benefit more from symbiotic associations, perhaps due to genetic differences in root exudation patterns or immune tolerance to colonization [97,98]. In our results, for example, genotype RP showed an exceptional increase in central glomerule length (nearly 2× the control) under co-inoculation, whereas genotype NC's glomerule length changed little with inoculation (Figure 5). This suggests that plant breeding or selection could play a role in maximizing the advantages of bioinoculants; breeders might target traits that improve colonization efficiency or cooperation with beneficial microbes [98,99]. Conversely, the lack of response in certain genotypes also reminds us that biofertilization is not a one-size-fits-all solution; field evaluations should account for varietal interactions. Understanding why some quinoa varieties do not respond to inoculation, maybe by differences in root architecture or mycorrhizal signaling, could be a fruitful area for future research. On the whole, however, even the least responsive variety in our trial did not suffer any yield penalty from inoculation; it simply did not gain as much, indicating that microbial amendments are generally safe to use across diverse germplasm, with the upside varying by genotype [100].

Our findings also contribute to the ongoing discussion about quinoa's mycorrhizal status and the conditions under which AMF inoculation is beneficial [32,35]. Quinoa has been somewhat enigmatic in this regard; some authors classify it as a facultative or inconsistently mycorrhizal species [32], noting that quinoa plants do not always form abundant AMF associations in nature [31]. In fact, surveys of high-altitude Andean soils report low native AMF colonization on roots [101]. This could be due to the extreme environments (e.g., cold, low-phosphorus soils above 3700 m) where quinoa evolved, or due to quinoa's ability to compensate for nutrient uptake via its fine root system [17]. There have even been suggestions that in certain high-stress conditions, AMF might act more like carbon parasites on quinoa, offering little benefit (or even hindrance) to the plant [32]. However, our results clearly indicate a *mutualistic* outcome under the tested conditions, *G. iranicum* inoculation, especially together with *A. brasilense*, significantly enhanced quinoa growth and yield, implying that the fungus was effectively providing net positive services (nutrients, drought mitigation, etc.) to the host. One possible explanation is that the inoculum strain we used (*Glomus iranicum* var. *tenuihypharum*) is native, particularly effective and well-adapted, capable of forming a productive symbiosis with quinoa, even if some native AMF strains cannot [28]. This strain has shown success in other crops and environments; for example, [28], documented its use in intensive horticulture, and [102], found that *G. iranicum* var. *tenuihypharum* conferred improved growth and stress tolerance to ornamental shrubs under saline irrigation. Additionally, the presence of *A. brasilense* may have facilitated better mycorrhizal establishment on quinoa's roots, through mechanisms like altered root exudation or immune modulation, tipping the balance towards a beneficial interaction [96]. Such cross-talk has been observed in other systems, PGPR can induce plant signals that favor AMF colonization [103,104], and might explain why our co-inoculated plants realized the full benefit of the AMF. So, while quinoa is not an obligately mycorrhizal crop, our evidence shows that under the right conditions and with effective microbial partners, even this occasionally mycorrhizal species can gain substantial advantages from AMF inoculation. This helps reconcile the debate, the outcome of quinoa–AMF interactions likely depends on environmental context and the specific microbial strains involved. Under Andean field conditions with moderate soil fertility, as in our study, the introduction of a vigorous AMF strain clearly aided quinoa, suggesting a practical pathway to improve quinoa yields on marginal soils where native symbiont populations are low.

Beyond quinoa, the positive effects of these microorganisms extend to other crops, including those of agronomic importance in the Andean region. *Azospirillum brasilense*, in particular, has a long history of use as a biofertilizer in cereals and other plants [70,105]. In our study, *A. brasilense* contributed significantly to quinoa's performance and similarly impressive results have been recorded in maize [44] report that inoculating purple maize (*Zea mays*) with *A. brasilense* in the Peruvian highlands led to higher grain yields per hectare, even allowing a reduction of nitrogen fertilizer inputs without sacrificing yield. This is consistent with a body of research on *Azospirillum*–cereal interactions, for example, field trials in corn and wheat have shown yield increases on the order of 5–15% from *A. brasilense* inoculation, along with improvements in nitrogen-use efficiency and stress tolerance [106,107]. Likewise, *Glomus iranicum* has demonstrated broad utility. In a recent greenhouse study on Andean potatoes, [27] found that inoculation with *G. iranicum*, at optimal doses, enhanced potato root biomass and tuber yield compared to non-inoculated controls, particularly when potatoes were co-cropped with legumes. The AMF inoculum improved nutrient uptake (notably phosphorus and potassium) in the potato rhizosphere, contributing to more vigorous growth. These examples in maize and potato underscore that the microbes studied here are not specific to quinoa; they can form beneficial associations across a range of plant hosts, including other Andean crops. In practical terms, this means that an integrated bioinoculant approach (using *Azospirillum*, mycorrhizae, or their combination) could be deployed in diverse cropping systems of the Andean highlands, from grains like quinoa and maize to tubers like potato, to boost productivity in an eco-friendly manner. The concept of combined microbial inoculation is supported by extensive research in non-Andean crops as well. Besides the earlier-mentioned wheat study [32], which showed doubled yields with a bacteria–AMF mix, many legume crops also benefit from dual inoculation (rhizobia plus AMF). For instance, co-inoculating peas (*Pisum sativum*) with *Bacillus* PGPR and native AMF significantly improved pea shoot growth, photosynthetic activity, and final seed yield [108,109]. Such cross-species evidence highlights a unifying principle that harnessing multiple functional microbes can consistently enhance plant nutrition and stress resilience, often translating into better yields. The present work with quinoa adds to this literature by confirming that even a stress-hardened pseudo-cereal can respond strongly to biofertilization. It encourages the broader application of these bioinoculants in sustainable agriculture, especially in regions like the Andes, where traditional crops face soil fertility challenges and growers seek alternatives to expensive chemical fertilizers.

Recent studies provide strong evidence that quinoa genotypes differ markedly in their responses to microbial inoculation, supporting the relevance of evaluating multiple varieties as performed in the present work. For example, PGPR application significantly improved growth, nutrient uptake and salt tolerance in the quinoa variety *Ames 13747* [96], while arbuscular mycorrhizal fungi (AMF), functionally related to *Glomus* spp., enhanced drought resilience, grain quality and physiological performance in quinoa cv. *Titicaca* [57]. Furthermore, a multispecies AMF experiment conducted across ten diverse quinoa genotypes, such as K'ello, Rosa Junín, CQ119, QQ87, QQ61 and others, demonstrated clear genotype-dependent differences in biomass accumulation, shoot height and leaf greenness, even under very low colonization levels [32]. Collectively, these findings show that quinoa–microbe interactions vary considerably across the genotypes, and they provide a broader context that supports the biological plausibility of the positive microbial effects observed in the four Andean varieties evaluated in the present study.

A growing body of evidence shows that the effectiveness of microbial inoculants is strongly modulated by the composition and behavior of the native soil microbiota. Field and microcosm studies have demonstrated that the introduction of AMF species can alter the abundance, structure, and functioning of native fungal assemblages, with outcomes that depend on environmental conditions such as water regime and soil disturbance [110,111]. In several cases, exogenous AMF such as *Rhizophagus irregularis* reduced the abundance of native mycorrhizal species and modified root colonization dynamics, leading to changes in plant biomass and nutrient uptake [110,112]. Likewise, the introduction of *Azospirillum brasilense* has been shown to transiently disrupt native bacterial communities in bulk soil and to induce more persistent shifts in rhizosphere network structure, particularly when high inoculation doses are applied. Importantly, these changes also influence the performance of the inoculant itself, as competition with resident microbes determines its persistence, colonization success, and plant-growth-promoting effects [113]. Together, these studies highlight that the outcomes of microbial inoculation depend not only on the plant genotype and environmental context, but also on the pre-existing microbial community, which can buffer, enhance, or counteract the activity of the introduced strain. Therefore, the absence of native microbiome characterization in the present study is acknowledged as a limitation, given that soil community composition can influence inoculant establishment and plant response.

While the positive effects of the microbial inoculants were consistent across crops, it is important to acknowledge a key limitation of this study. The field experiment was conducted at a single high-Andean site and during only one agricultural season. Because quinoa performance and plant–microbe interactions are strongly influenced by factors such as drought stress and soil nutrient dynamics [31,57], the extent to which these results can be generalized to other regions or production systems should be interpreted with caution. Even so, independent research conducted at the same location using the same strain of *Azospirillum brasilense* has reported similarly beneficial outcomes in purple maize, including improvements in plant height, root development, biomass accumulation, leaf nitrogen concentration and grain yield [52]. The alignment between the results of the present study and those observed in maize under identical agroecological conditions reinforces the local validity of the microbial responses described here, although broader multi-location and multi-season trials remain essential for evaluating their wider applicability. Additionally, field studies in perennial fruit crops have shown that *Glomus iranicum* applied over a single growing season in young nectarine trees increased root length density by 51% and irrigation water-use efficiency by 19.5% compared with non-inoculated controls [114].

The clear growth and yield benefits observed with *A. brasilense* and *G. iranicum* in quinoa point to several practical and research avenues. On the agronomic side, farmers and stakeholders could incorporate such microbial inoculants into quinoa production to achieve higher yields with lower chemical inputs. This is particularly valuable in marginal environments, by improving nutrient uptake naturally, these bioinoculants can help maintain yields while reducing reliance on synthetic fertilizers that contribute to soil acidification and degradation [115]. Adopting microbial co-inoculants aligns with the goals of sustainable intensification in Andean agriculture, offering a way to enhance productivity and soil health concurrently. From a scientific perspective, our findings open up questions about the long-term dynamics and optimization of quinoa-microbe symbioses. Field trials over multiple seasons and locations would be beneficial to verify the consistency of the yield gains and to determine whether any site-specific factors (soil type, native microbiome, climate) influence the efficacy of the inoculants [116,117]. It would also be interesting to explore if additional benefits emerge over time, for example, whether repeated use of these inoculants could progressively improve soil structure or the resident microbial community. Moreover, the mechanistic basis of the synergy merits further investigation. Studies using molecular tools (e.g., transcriptomics or metabolomics) could elucidate how *A. brasilense* and *G. iranicum* interact in the rhizosphere and how quinoa's physiology is altered in co-inoculated plants. Understanding these mechanisms might enable us to fine-tune inoculation strategies (such as optimal timing, dosage, or formulation) for even greater benefits. We also suggest exploring combinations with other bionoculants or organic amendments. For instance, integrating PGPR-AMF inoculation with compost or biochar could have additive or synergistic effects on quinoa, as hinted by research in other crops [118,119]. Finally, given the genotype-specific responses observed, breeding quinoa varieties with enhanced responsiveness to beneficial microbes could be a forward-looking approach. By selecting for traits that favor symbiosis (such as root morphology or exudate profile), it may be possible to develop new quinoa cultivars that derive even greater yield boosts from bioinoculants. In conclusion, this study underscores the tangible benefits of microbial synergy in quinoa and provides a foundation for both immediate agricultural applications and future scientific exploration aimed at bolstering sustainable food production in the Andes and beyond.

5. Conclusions

The combined inoculation *of Azospirillum brasilense* and *Glomus iranicum* var. *tenuihypharum* substantially improved quinoa growth, yield and root performance under field conditions. The co-inoculated treatment consistently outperformed single inoculations and controls, enhancing key vegetative and yield traits such as panicle diameter, stem diameter grain yield, grain diameter, grain yield, number of root branches and root volume. The strong statistical significance across multiple variables confirms a synergistic relationship between both microorganisms, likely driven by complementary mechanisms of nutrient acquisition and hormonal stimulation. Genotypic variation in responsiveness was evident, with BJ and SH genotypes showing the greatest physiological and yield improvements, while NC exhibited limited benefits. Overall, the results support the integration of microbial inoculants into sustainable quinoa production systems. The co-application of *A. brasilense* and *G. iranicum* var. *tenuihypharum* represents a promising biofertilization strategy capable of enhancing productivity while reducing reliance on synthetic fertilizers.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/applmicrobiol6010012/s1, Figure S1. Climograph of the 2023–2024 agricultural campaign. Key climatic variables were recorded, including minimum temperature (T_{min}, °C), maximum temperature (T_{max}, °C), mean temperature (T_{med}, °C), precipitation (mm), soil moisture availability (mm) and adjusted evapotranspiration (ETP Ajust, mm). Figure S2. Contribution of vegetative, yield and root traits to the principal component analysis 1 (PCA1). The bar plot shows the relative contribution (%) of each variable to the total variance explained by the first principal components. Variables above the red dashed line represent traits with the highest influence on the multivariate differentiation among treatments. Figure S3. Contribution of vegetative, yield and root traits to the principal component analysis 2 (PCA2). The bar plot shows the relative contribution (%) of each variable to the total variance explained by the first principal components. Variables above the red dashed line represent traits with the highest influence on the multivariate differentiation among treatments. Table S1. Analysis of variance (ANOVA) for vegetative, root and yield parameters of purple maize genotypes under different treatments. Table S2. Vegetative, yield and root parameters of quinoa genotypes evaluated by. Tukey's test. Table S3. Vegetative, yield and root parameters of treatments evaluated by Dunnett's test. Table S4. Central glomerule length (cm) by genotype and treatment. Table S5. Grain diameter (mm) by genotype and treatment. Table S6. Hectoliter weight ($g{\cdot}hL^{-1}$) by genotype and treatment. Table S7. Root dry weight ($g\ plant^{-1}$) by genotype and treatment.

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Abbreviations

The following abbreviations are used in this manuscript:

PGPMs	Plant growth-promoting microorganisms
PGPR	Plant Growth-Promoting Rhizobacterium
BJ	Blanca de Junín
SH	INIA 441 Señor del Huerto
RP	INIA 415 Pasankalla
NC	INIA 420 Negra Collana
PCA	Principal Component Análisis
RCBD	Randomized Complete Block Design
ANOVA	Analysis of Variance
IAA	Indole-3-Acetic Acid
INIA	The National Institute of Agrarian Innovation
SENAMHI	National Service of Meteorology and Hydrology of Peru
LABSAF	Soil, Water and Foliar Analysis Laboratory

CANAÁN	Canaán Experimental Station
NPK	Nitrogen, Phosphorus, Potassium
FOCAM	Camisea Socioeconomic Development Fund
NFb	Nitrogen-free medium
CFU	Colony-Forming Units
PH	Plant Height
PD	Panicule Diameter
CGL	Central Glomerule Length
PL	Panicle Length
SD	Stem Diameter
GD	Grain Diameter
TSW	Thousand Seed Weight
PW	Panicle Weight
GWP	Grain Weight per Panicle
GY	Grain Yield
HW	Hectoliter Weight
RD	Root Diameter
RL	Root Length
NRB	Number of Roots
RDW	Root Dry Weight
RV	Root Volumen

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