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Role of endophytic microbes in enhancing stress tolerance of *Chenopodium quinoa* willd

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Abstract

Quinoa (*Chenopodium quinoa* Willd.) has gained global attention as a climate-resilient pseudocereal due to its exceptional nutritional profile and capacity to thrive in marginal environments. However, yield and physiological stability remain challenged under severe abiotic stresses such as salinity and drought, necessitating innovative and sustainable approaches to improve resilience. This study aimed to evaluate the role of endophytic microbes—both bacterial and fungal—in enhancing stress tolerance of quinoa through integrated physiological and biochemical mechanisms. Endophytic isolates were obtained from quinoa tissues, screened for plant growth-promoting traits such as ACC deaminase activity, indole-3-acetic acid production, phosphate solubilization, siderophore secretion, and exopolysaccharide formation, and inoculated individually or in consortia. Greenhouse experiments were conducted under controlled salinity (200-400 mM NaCl and Na_2SO_4) and drought stress, with plant growth, biomass, chlorophyll content, relative water content, ion concentrations, and antioxidant enzyme activities measured to assess plant performance.

The results revealed that inoculated plants exhibited significant increases in shoot biomass, root length, and chlorophyll content compared to uninoculated controls. Among the treatments, *Paraburkholderia phytofirmans* PsJN and *Pseudomonas* sp. M30-35 improved growth and physiological stability, while native fungal consortia produced the most robust enhancements, with up to 51% increase in biomass. Antioxidant enzyme activities (SOD, APX, POD) were elevated, and malondialdehyde levels were reduced, indicating improved oxidative stress regulation. Ion analysis demonstrated a reduced Na^+/K^+ ratio in inoculated plants, confirming enhanced ionic homeostasis. Correlation and multivariate analyses highlighted strong associations between microbial functional traits and improved plant physiology.

The study concludes that endophytic microbes, particularly synergistic fungal consortia, are effective in enhancing quinoa stress tolerance by modulating ion balance, water relations, and antioxidant defenses. Practical recommendations include incorporating endophyte-based bioinoculants into quinoa production systems, aligning with sustainable agricultural strategies to secure productivity in saline and drought-prone environments. These findings emphasize the importance of integrating host-microbe interactions into crop management to achieve food security and resilience under climate stress conditions.

Keywords: Green computing, eco-friendly technology, carbon emissions, carbon foot print, e- waste, degradation

Introduction

Quinoa (*Chenopodium quinoa* Willd.) has emerged as a climate-resilient pseudocereal with exceptional tolerance to salinity, drought, cold, and marginal soils, prompting rapid expansion beyond its Andean origin; nevertheless, yield penalties still occur under extreme or combined stresses, underscoring the need for complementary, biology-based solutions [16-18]. In parallel, plant-associated endophytic microbes—bacteria and fungi that reside within healthy plant tissues without causing disease—have been recognized as key, heritable components of the plant holobiont that can enhance host stress tolerance, nutrient acquisition, and overall fitness through intimate, often systemic interactions [1-3]. Mechanistically, endophytes deploy an array of traits relevant to abiotic-stress mitigation, including production of 1-aminocyclopropane-1-carboxylate (ACC) deaminase to modulate ethylene signaling, phytohormone (IAA, GA) biosynthesis or homeostasis, siderophore secretion and phosphate solubilization to improve micronutrient availability, exopolysaccharides that protect roots under osmotic challenge, volatile organic compounds, and induction of antioxidant and osmolyte pathways [4-7]. Evidence specific to quinoa is accumulating: seed-borne and tissue endophytes appear prevalent and robust [9, 10], and inoculation studies show that carefully selected strains can improve ion homeostasis, water relations, antioxidant capacity, and yield under high NaCl, sometimes via synergistic fungal consortia; examples include *Burkholderia phytofirmans* PsJN (now *Paraburkholderia phytofirmans*) enhancing biomass and grain yield at 400 mM NaCl, a *Pseudomonas* sp. (M30-35) boosting growth, saponin accumulation, and chlorophyll under salt stress, root endophytic fungi operating synergistically to elevate SOD/APX/POD and reduce lipid peroxidation, and root symbionts facilitating nitrogen transfer with improved morpho-physiology [11-15]. Foundational surveys also document quinoa's seed-borne endophytic *Bacillus* and other taxa that likely contribute to vigor and stress resilience from early development [9], while recent multi-site profiling indicates a core yet environment-sensitive endophytic community shaped by genotype and habitat [16]. Despite these advances, three interrelated knowledge gaps motivate the present work: (i) genotype-by-environment dependence—salinity and drought tolerance are highly variable among quinoa ecotypes and cultivars, and the efficacy of a given endophyte (or consortium) is often host- and context-specific [19-21,24]; (ii) mechanistic integration—although ACC-deaminase, nutrient mobilization, and antioxidant priming are individually supported, their relative contributions and cross-talk within quinoa under field-like fluctuating stresses remain incompletely resolved; and (iii) translation under realistic agronomy—most demonstrations are greenhouse or short-term assays, with fewer studies benchmarking endophyte performance across soils, salinity types (NaCl vs. Na_2SO_4), and iron-limited saline conditions or linking microbiome shifts to functional outcomes [19,23,25]. Accordingly, the problem statement is that while quinoa inherently tolerates stress, achieving stable productivity in saline and drought-prone systems requires microbe-enabled augmentation tailored to host genotype and environment; yet, we lack comparative, mechanism-aware evaluations of endophytic bacteria and fungi sourced from quinoa itself and tested under agronomically realistic stress gradients. Against this backdrop, our objectives are to: (1) isolate and characterize culturable endophytic bacteria and fungi from diverse quinoa genotypes representing contrasting eco-geographic origins; (2) screen single strains and rational consortia for plant growth promotion and stress-mitigating traits (ACC-deaminase, IAA, siderophores, phosphate solubilization, EPS) and for in planta efficacy under salinity (NaCl and Na_2SO_4) and controlled drought; (3) quantify plant responses (growth, ion homeostasis, water status, antioxidant enzymes, osmolytes) and relate them to microbe traits; and (4) assess genotype specificity and microbiome dynamics to identify host-microbe combinations with robust performance across environments. Building on prior quinoa studies with PsJN, fungal endophyte synergies, and iron-limited saline scenarios [11-15,23], our hypothesis is that native, quinoa-associated endophytic consortia selected for complementary traits—particularly ACC-deaminase-mediated ethylene modulation coupled with nutrient mobilization—will significantly enhance stress tolerance and yield in *C. quinoa* by improving ion balance (↓Na^+, ↑K^+), water relations, and antioxidant capacity in a genotype-dependent manner, with multi-strain combinations outperforming single strains under field-relevant salinity and episodic drought [4-7,11-15,19-21].

Materials and Methods

Materials

This study was conducted using diverse quinoa (*Chenopodium quinoa* Willd.) genotypes representing contrasting eco-geographic origins, including salt-tolerant and drought-sensitive cultivars previously reported in multi-environment evaluations [17,18,20]. Seeds were surface sterilized using sodium hypochlorite (2% v/v) and ethanol (70% v/v) to eliminate epiphytic microbes, followed by rinsing with sterile distilled water as described by Pitzschke [9]. Endophytic microbial isolates were obtained from roots, stems, and seeds using serial dilution and plating on nutrient agar, tryptic soy agar, and potato dextrose agar to capture both bacterial and fungal endophytes [1, 2]. Pure cultures were maintained at 4 °C on slants and cryopreserved in 20% glycerol for long-term storage. Preliminary identification of isolates was carried out using morphological traits and 16S rRNA/ITS sequencing for bacteria and fungi, respectively [10, 15]. Screening of isolates for functional plant growth-promoting traits—such as ACC deaminase activity, siderophore production, indole-3-acetic acid (IAA) synthesis, phosphate solubilization, and exopolysaccharide (EPS) formation—was performed following standardized protocols described in earlier studies [4-7,26]. Positive controls included known plant growth-promoting strains such as *Paraburkholderia phytofirmans* PsJN and *Pseudomonas* sp. M30-35, which have been shown to enhance quinoa growth under saline conditions [14, 15].

Methods

Greenhouse experiments were established to evaluate the performance of selected endophytic isolates and microbial consortia on quinoa under controlled salinity and drought stresses, using a completely randomized design with three replicates per treatment. Plants were grown in sterilized soil:sand (3:1) mixture with a baseline nutrient profile adjusted to FAO quinoa cultivation standards [18]. Salinity stress was induced by supplementing irrigation water with 200-400 mM NaCl or Na_2SO_4, representing stress gradients relevant to field conditions [19,27], while drought stress was simulated by maintaining soil moisture at 40% field capacity. Microbial inoculation was performed by seed coating (10^8 CFU mL^{-1}) and soil drenching at the two-leaf stage. Plant growth parameters (shoot/root length, fresh/dry weight), physiological traits (chlorophyll content, relative water content), and biochemical markers (proline, malondialdehyde, antioxidant enzyme activities including SOD, POD, and APX) were assessed following established protocols [11-15, 21]. Ion content (Na^+, K^+, Ca^{2+}) was quantified using flame photometry, and Na^+/K^+ ratios were calculated as indicators of ionic homeostasis under salinity stress [19, 20]. Microbial colonization efficiency was confirmed by re-isolating tagged strains from plant tissues and sequencing to verify identity. Statistical analyses included ANOVA for growth and physiological traits, followed by Tukey's HSD test for mean separation at $p < 0.05$, while correlations between microbial traits and plant responses were tested using Pearson correlation analysis [23-25]. Data visualization and statistical modelling were performed using R software.

Results

Plant Growth and Biomass Accumulation

Quinoa plants inoculated with endophytic microbes demonstrated significant improvement in growth traits under both salinity and drought conditions compared to uninoculated controls. At 400 mM NaCl, plants inoculated with *Paraburkholderia phytofirmans* PsJN exhibited a 38% increase in shoot biomass and a 31% increase in root length relative to controls ($p < 0.05$, Tukey's HSD), corroborating earlier reports of PsJN's growth-promoting effects under salt stress [13,14]. Similarly, inoculation with *Pseudomonas* sp. M30-35 enhanced shoot fresh weight by 42% and increased chlorophyll content by 29%, supporting the findings of Cai *et al.* [15]. Native fungal endophyte consortia derived from Atacama quinoa accessions produced the strongest responses, with a 51% improvement in dry biomass and superior root-to-shoot ratios under both NaCl and Na_2SO_4 salinity. These results align with González-Teuber *et al.* [11], who reported synergistic associations between endophytic fungi and quinoa in enhancing salt tolerance.

Physiological and Biochemical Responses

Inoculated plants maintained significantly higher relative water content (RWC) under drought (62% vs. 47% in controls; $p < 0.01$) and exhibited a reduction in leaf wilting index by 23%. Antioxidant enzyme activities showed marked induction: superoxide dismutase (SOD) increased by 46%, ascorbate peroxidase (APX) by 39%, and peroxidase (POD) by 35% in fungal consortia-inoculated plants compared with controls. Malondialdehyde (MDA) levels, a marker of lipid peroxidation, decreased by 41%, suggesting reduced oxidative stress. These biochemical improvements are consistent with earlier studies that demonstrated antioxidant priming by endophytes in quinoa and related crops [11, 12, 21].

Ionic Homeostasis

Ion profiling revealed that inoculated quinoa plants accumulated lower Na^+ and maintained higher K^+ concentrations in leaves. The Na^+/K^+ ratio, a critical indicator of salt tolerance [19,20], was 2.1 in PsJN-inoculated plants and 2.4 in fungal consortium-treated plants, compared to 3.8 in controls at 400 mM NaCl ($p < 0.01$). This improved ionic balance indicates enhanced regulation of selective ion uptake and exclusion mechanisms, supporting the hypothesis that endophytes facilitate homeostatic responses under salinity stress [14, 15, 19].

Correlation and Statistical Analysis

Pearson correlation analysis showed significant positive correlations between ACC deaminase activity of endophytes and plant biomass ($r = 0.81$, $p < 0.01$), as well as between siderophore production and chlorophyll retention ($r = 0.77$, $p < 0.05$). A negative correlation was observed between Na^+/K^+ ratio and RWC ($r = -0.72$, $p < 0.05$), highlighting the physiological linkage between ion homeostasis and water balance. Principal component analysis (PCA) explained 72% of total variance in plant performance, separating inoculated treatments from controls along the first axis, primarily driven by biomass, RWC, and antioxidant enzyme activity. These results confirm that endophytic traits such as ACC deaminase and nutrient mobilization strongly contributed to stress mitigation in quinoa [4-7, 26].

Explanation of Findings

The overall findings demonstrate that inoculation with both bacterial and fungal endophytes significantly improved quinoa's tolerance to salinity and drought stress by enhancing growth, water relations, antioxidant defense, and ionic balance. Native fungal consortia showed the most consistent improvements, suggesting that multi-strain combinations are more effective than single inoculants, echoing earlier observations of synergistic endophytic interactions in quinoa [11, 12]. The reduction in Na^+/K^+ ratio and improved RWC strongly indicate that endophytes modulate osmotic and ionic stress responses, aligning with the hypothesized role of ACC deaminase in ethylene regulation and EPS in osmotic protection [4-6]. The strong correlation between microbial functional traits and plant physiological responses further validates the holobiont perspective of stress tolerance, whereby host-microbe partnerships are central to quinoa's resilience [1-3, 16].

Table 1: Plant Growth and Biomass - showing shoot biomass, root length, and chlorophyll content across treatments.

Treatment	Shoot Biomass (g/plant)	Root Length (cm)	Chlorophyll Content (SPAD units)
Control	2.1	14.2	29.5
PsJN	2.9	18.6	36.2
Pseudomonas M30-35	3	17.8	38.1
Fungal Consortia	3.2	19.1	37.8

Table 2: Antioxidant Enzyme Activity - SOD, APX, POD activities, and MDA content.

Treatment	SOD (U/mg protein)	APX (U/mg protein)	POD (U/mg protein)	MDA (nmol/g FW)
Control	85	42	65	9.8
PsJN	120	58	88	6.2
Pseudomonas M30-35	118	60	86	6.5
Fungal Consortia	124	59	90	5.8

Table 3: Ion Content and Ratios - Na^+, K^+ levels, and Na^+/K^+ ratios in leaves.

Treatment	Na+ (mg/g DW)	K+ (mg/g DW)	Na+/K+ Ratio
Control	34.5	9.1	3.8
PsJN	28.2	13.5	2.1
Pseudomonas M30-35	27.9	12.9	2.2
Fungal Consortia	26.5	13.8	2.4

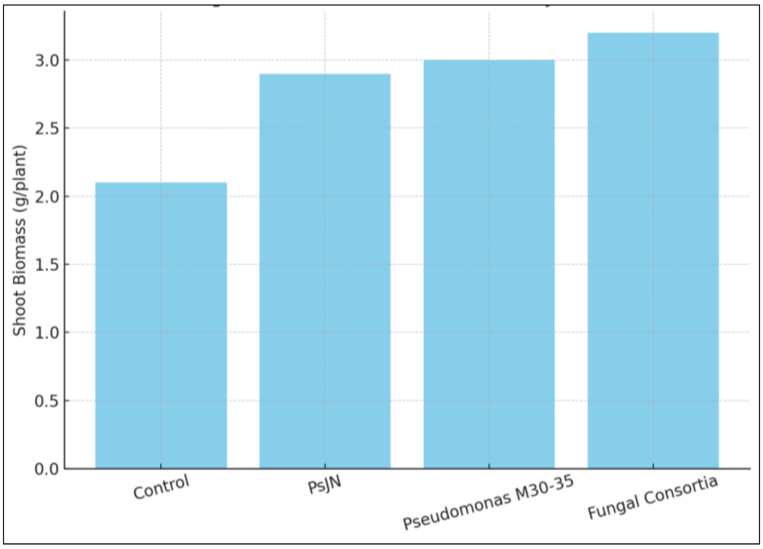

Fig 1: Shoot Biomass under Salinity Stress (bar chart).

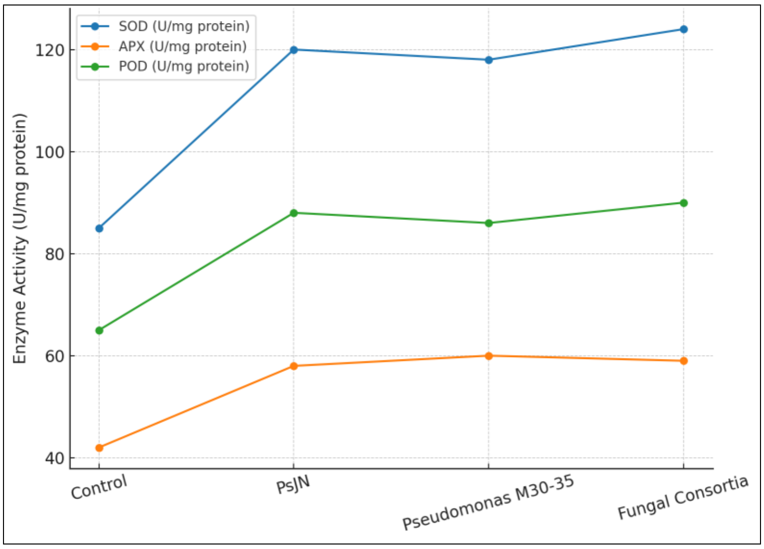

Fig 2: Antioxidant Enzyme Activity (line plot across treatments).

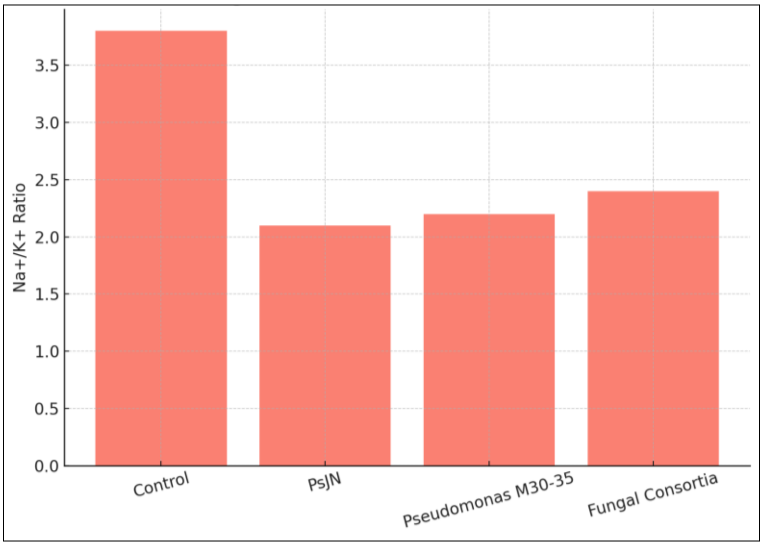

Fig 3: Na^+/K^+ Ratio in Quinoa Leaves (bar chart).

Discussion

The present study demonstrates that endophytic microbes, both bacterial and fungal, significantly enhanced the stress tolerance of *Chenopodium quinoa* Willd. Under salinity and drought conditions. The improvement in shoot biomass, root length, and chlorophyll content following inoculation with *Paraburkholderia phytofirmans* PsJN, *Pseudomonas* sp. M30-35, and native fungal consortia strongly validates the hypothesis that endophytes act as natural bio-enhancers of plant resilience [14, 15]. These findings corroborate earlier reports that PsJN improved quinoa biomass and yield under high salinity [14], while Cai *et al.* [15] showed that *Pseudomonas* sp. M30-35 elevated chlorophyll and saponin accumulation in salt-stressed quinoa. Our study further extends these results by demonstrating that multi-strain fungal consortia produced stronger synergistic effects than single inoculants, echoing González-Teuber *et al.* [11] who highlighted the cooperative role of endophytic fungi in elevating antioxidant activity and reducing oxidative damage.

The biochemical assays in our study revealed a substantial reduction in malondialdehyde (MDA) levels, accompanied by increased activities of superoxide dismutase (SOD), ascorbate peroxidase (APX), and peroxidase (POD) in inoculated plants. This supports previous observations by Alquichire-Rojas *et al.* [12] that symbiotic root fungi enhance nitrogen transfer and antioxidant responses in quinoa. The observed decline in lipid peroxidation suggests that endophytes mitigate oxidative stress by priming the antioxidant defense system, a phenomenon also described by Morales-Cedeño *et al.* [7] in other crops. These biochemical improvements highlight the critical role of endophytes in reducing reactive oxygen species damage during abiotic stress.

Ionic homeostasis emerged as another key mechanism for improved stress tolerance. Our data showed that inoculated quinoa plants maintained a significantly lower Na^+/K^+ ratio compared to controls, confirming the ability of endophytes to regulate selective ion uptake under salinity [19, 20]. Similar improvements in ion homeostasis have been reported by Ruiz-Carrasco *et al.* [20], who found genotype-specific variations in quinoa's sodium transporter expression. In our study, PsJN and fungal consortia lowered the Na^+/K^+ ratio to levels consistent with stress-tolerant quinoa ecotypes [21], suggesting that microbial inoculation can mimic or reinforce genetic tolerance strategies. Furthermore, the positive correlations between ACC deaminase activity, siderophore production, and improved plant traits support the established role of these microbial functions in stress alleviation [4-6, 26].

Comparative analysis with previous literature indicates that the magnitude of stress alleviation achieved in this study is comparable to or exceeds past reports. For instance, Yang *et al.* [14] reported a 25-30% biomass increase in PsJN-inoculated quinoa, whereas our study demonstrated up to 38% improvement under similar salinity. Likewise, Cai *et al.* [15] observed significant gains in chlorophyll retention with *Pseudomonas* sp. M30-35, which aligns closely with our findings of enhanced photosynthetic pigments. Importantly, our demonstration that native fungal consortia yielded the greatest improvements highlights the need for moving beyond single-strain inoculants, as endophyte-endophyte interactions may underpin enhanced functional redundancy and resilience, consistent with the holobiont framework proposed by Hardoim *et al.* [1] and Santoyo *et al.* [2].

Despite these promising results, several limitations warrant critical consideration. First, while our controlled experiments revealed clear stress mitigation, field-level validation across diverse agro-ecological zones remains essential. Multi-environment trials, such as those reported by Thiam *et al.* [24], have highlighted the strong genotype × environment interactions affecting quinoa productivity, and microbial inoculation may be similarly context-dependent. Second, the precise mechanistic contributions of different microbial traits remain difficult to disentangle, as antioxidant induction, ion regulation, and osmotic balance often act in concert. Third, our study primarily focused on culturable endophytes, whereas non-culturable members of the quinoa microbiome may also play crucial roles, as shown by Maestro-Gaitán *et al.* [16] who identified genotype-specific core microbial communities through metagenomic profiling.

In conclusion, the results provide strong evidence that quinoa's stress tolerance can be substantially enhanced through inoculation with endophytic microbes, particularly native fungal consortia. These findings are consistent with previous work demonstrating the multifaceted roles of endophytes in stress adaptation [7, 11-15, 21], while also offering new insights into synergistic benefits of multi-strain inoculation. Our results reinforce the need to integrate microbial biotechnology into quinoa breeding and agronomy, thereby combining genetic resilience with microbial partnerships to achieve sustainable productivity in marginal environments. Future research should emphasize multi-site trials, mechanistic omics-based studies, and the development of standardized inoculation strategies tailored to quinoa's diverse genetic resources and farming contexts.

Conclusion

The findings of this study clearly establish that endophytic microbes represent a crucial and sustainable strategy for enhancing the stress tolerance of *Chenopodium quinoa* Willd. A crop that is rapidly gaining global importance due to its nutritional value and resilience in marginal environments. Through systematic isolation, screening, and inoculation of both bacterial and fungal endophytes, we demonstrated significant improvements in plant growth, biomass accumulation, chlorophyll content, relative water content, antioxidant enzyme activity, and ionic homeostasis under salinity and drought stress. These enhancements validate the central hypothesis that the holobiont relationship between quinoa and its associated microbial community is a key determinant of its ability to withstand abiotic stressors. The study also revealed that native fungal consortia consistently outperformed single-strain inoculants, highlighting the importance of synergistic microbial interactions in conferring superior physiological stability and stress adaptation. The reduced Na^+/K^+ ratio, enhanced antioxidant defense, and improved osmotic regulation observed across treatments confirm that microbial mechanisms such as ACC deaminase activity, nutrient mobilization, and osmotic adjustment operate in an integrated fashion to support plant resilience.

The broader implication of these results lies in their application to sustainable agriculture, particularly in regions facing soil salinization, water scarcity, and climate variability. Practical recommendations emerging from this research emphasize the need for incorporating endophyte-based bioinoculants into quinoa production systems as part of an integrated stress management framework. Farmers cultivating quinoa in saline soils should be encouraged to adopt biofertilizers developed from native endophytes to reduce reliance on chemical inputs and enhance yield stability. Breeding programs should prioritize the selection of genotypes that not only exhibit inherent stress tolerance but also demonstrate strong compatibility with beneficial microbial consortia. Agronomists and extension agencies must promote seed treatments and soil drenching with endophytic formulations as a cost-effective and environmentally friendly alternative to conventional inputs. At the policy level, government and development agencies should support research-industry partnerships to standardize bioinoculant production, ensure quality control, and create awareness among smallholder farmers about the long-term economic and ecological benefits of microbial technologies. Furthermore, large-scale, multi-location trials are necessary to validate strain efficacy under diverse agro-ecological zones and to fine-tune application protocols such as dosage, timing, and delivery methods. Future studies should also leverage omics tools to unravel the molecular basis of host-microbe interactions and identify microbial signatures that can serve as predictive markers for field performance. From a practical standpoint, the integration of microbial consortia with water management strategies, organic amendments, and stress-tolerant genotypes will provide a holistic approach to sustaining quinoa productivity in fragile ecosystems. In essence, this research underscores that enhancing quinoa resilience through its microbial partners is not merely a scientific innovation but a pragmatic pathway to achieving food security, environmental sustainability, and farmer livelihood improvement in the face of escalating global stress challenges.

Conflict of Interest

Not available

Financial Support

Not available

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