

The effects of the inoculation of bacterial microorganisms (*Pseudomonas* sp. and *Bacillus* sp.) on soil quality, aerial biomass and nutritional quality of native grasses under field conditions in the Peruvian highlands

Alberto Arias-Arredondo^{1*}, Samuel Edwin Pizarro Carcausto¹, Edilson J. Requena-Rojas¹, Patricia Verástegui-Martínez¹, Juancarlos Alejandro Cruz Luis¹, Richard Andi Solórzano-Acosta^{1,2}

¹Dirección de Servicios Estratégicos Agrarios, Instituto Nacional de Innovación Agraria (INIA), Av. La Molina 1981, 15024, Lima, Perú

²Facultad de Ciencias Ambientales, Universidad Científica del Sur (UCSUR), Lima 15024, Perú

* Corresponding author: Alberto Arias Arredondo, albertogilmer@gmail.com, ORCID ID: <https://orcid.org/0000-0002-6055-8722>

Abstract

Received: 2025-06-14

Accepted: 2026-04-15

Published online: 2026-04-15

Associated editor: Agnieszka Józefowska

Keywords:

Bacterial inoculation

Plant growth-promoting rhizobacteria

Native grasslands

Soil organic matter

Forage nutritional quality

Peruvian highland ecosystems cover approximately 22 million hectares and provide key ecosystem services that support human well-being and food security. Soil functioning in these ecosystems largely depends on the activity of microbial communities. This study evaluated the effects of *Pseudomonas* sp. and *Bacillus* sp. inoculation on soil chemical properties, aerial biomass production, and nutritional quality of *Festuca dolichophylla*, *Jarava ichu* and *Cinnagrostis vicunarium*. A field experiment was conducted at 4379 m a.s.l. in the central Peruvian highlands. Bacterial inoculation increased soil organic matter and nitrogen availability in plots dominated by *J. ichu* and *F. dolichophylla* inoculated with *Bacillus* sp., compared to non-inoculated controls. Higher soil phosphorus content was observed in *C. vicunarium* pastures inoculated with *Pseudomonas* sp. In terms of biomass production, significant increases were recorded in *C. vicunarium* under both bacterial inoculations and in *F. dolichophylla* associated with *Bacillus* sp., while *J. ichu* showed higher yields with *Pseudomonas* sp. In addition, bacterial inoculation improved forage nutritional quality, particularly total protein, calcium, and phosphorus contents in *J. ichu*, highlighting species-specific plant-microorganism interactions. Overall, the inoculation of beneficial bacteria represents a promising and environmentally sustainable strategy to improve soil quality, forage productivity, and nutritional value in native highland grasslands, contributing to more resilient rangeland systems and the conservation of ecosystem services.

1. Introduction

Highland ecosystems in Peru cover approximately 22 million hectares (Estrada Zuñiga et al., 2018) and provide essential ecosystem services that support national food security, particularly through meat and milk production (Flores, 2016). These ecosystems are mainly composed of grasses and wetlands, including associations of Asteraceae, Plantaginaceae, Poaceae, Fabaceae, Rosaceae, Cyperaceae and Juncaceae (Maldonado Fonkén, 2014). They constitute the nutritional base for grazing systems involving alpacas, sheep and cattle (Oliva et al., 2015). However, native grasslands are generally characterized by low forage nutritional quality, typically exhibiting low crude protein content, high fiber concentrations and limited digestibility, which constrain livestock productivity (Flores et al., 2005).

Most grazing lands in the Peruvian highlands are affected by degradation processes driven by climate change and overgrazing (Flores, 2016), resulting in reductions in vegetation cover and forage nutritional quality (Westoby et al., 1989). These processes negatively impact the production of meat, milk and wool, as well as other ecosystem services, including water regulation (Holechek et al., 2006). Overgrazing and related disturbances alter vegetation structure and productivity, reduce soil microbial communities, and modify soil chemical and physical properties (Wang et al., 2020). This leads to lower litter accumulation (Bai et al., 2012) and, consequently, alterations in nitrogen (N) and phosphorus (P) storage in soils and plants (Hou et al., 2019).

Soil nutrient availability, particularly of N and P, limits vegetation growth and determines plant nutritional quality (Alori et al., 2017). Phosphorus is a key macronutrient for plant

growth and development, representing approximately 0.2% of plant dry weight (Zhu et al., 2011). Highland rangelands are typically established on moderately developed soils characterized by high organic matter contents with limited mineralization and low availability of nitrogen and phosphorus, primarily due to low temperatures that inhibit decomposition processes (Wilcox, 1984). Phosphorus deficiency strongly constrains biomass production and forage nutritional quality in these ecosystems (Carreira et al., 2006).

Phosphorus limitation is commonly addressed through fertilizer application; however, a large proportion of applied phosphorus does not become readily available for plant uptake, and excessive use can lead to environmental impacts such as the eutrophication of water bodies through phosphorus transport (Kang et al., 2011). In developing countries such as Peru, fertilizer availability is limited and costs are often prohibitive for application in native rangelands. Consequently, alternative rangeland management strategies have been proposed, including the use of microorganisms to enhance phosphorus solubilization and plant nutrient uptake (Magadlela et al., 2023). The solubilization of unavailable nutrients is environmentally favorable and economically viable, contributing to biomass production and the regeneration of degraded rangelands (Flatian et al., 2021).

Microbial inoculants, also known as biofertilizers, have been widely studied in agriculture due to their ability to stimulate plant growth and development (Pratap Singh et al., 2016). Based on their mechanisms of action, beneficial soil microorganisms can be classified as stimulants, soil improvers, bioremediators, biocontrollers and biofertilizers (Joshi et al., 2019). Among them, *Bacillus* sp. and *Pseudomonas* sp. are well-known plant growth-promoting rhizobacteria (PGPR) that stimulate host plant development as part of the rhizosphere biota (Bhattacharyya and Jha, 2012). These microorganisms are of particular interest due to their capacity to enhance plant tolerance to abiotic and biotic stress through multiple mechanisms (Tseng et al., 2020).

In grass species, inoculation with PGPR has been widely reported to produce positive outcomes. For example, *Bacillus subtilis* has increased shoot biomass in *Urochloa brizantha* (Rodrigues Manrique et al., 2019) and improved growth in *Phleum pratense* under water stress through osmolyte accumulation (Gagné-Bourque et al., 2016). Similarly, inoculation with *Pseudomonas* sp. and *Bacillus* sp. has resulted in significant increases in biomass in *Festuca dolichophylla* (Santillana Villanueva et al., 2022) and enhanced fresh and dry biomass in *Lolium perenne* (Stamenov et al., 2012). Improvements in dry matter yield and mineral concentrations (P, Mg and Zn) have also been reported for *Lolium multiflorum* (Yolcu et al., 2011). In addition, synergistic effects have been described, such as biomass enhancement in *Lolium perenne* under drought conditions through the co-inoculation of *Bacillus amyloliquefaciens* and water-retaining agents (Su et al., 2017).

Field applications of beneficial microorganisms under high-altitude conditions have demonstrated species-dependent increases in nutrient concentrations in aerial biomass (Santillana Villanueva et al., 2022). Likewise, increases in

macronutrients such as nitrogen and potassium associated with microbial inoculation have been reported across different grassland systems (Hungria et al., 2021). The effectiveness of microbial inoculation is strongly influenced by the microbial species involved, host plant genotype and prevailing environmental conditions (Bastías et al., 2021).

In the Peruvian highlands, native grasslands are dominated by perennial species such as *Festuca dolichophylla*, *Jarava ichu* and *Cinnagrostis vicunarum*, which play a central role in extensive livestock production systems (Arias-Arredondo et al., 2025). These ecosystems are generally established on cold-climate soils characterized by high organic matter accumulation, limited nutrient mineralization and low availability of nitrogen and phosphorus. Despite their ecological and productive importance, studies evaluating the use of beneficial microorganisms to improve soil fertility, forage biomass and nutritional quality in these native grasslands remain scarce.

This study evaluated the effects of *Pseudomonas* sp. and *Bacillus* sp. inoculation on soil properties, aerial biomass production and the nutritional quality of *Festuca dolichophylla*, *Jarava ichu* and *Cinnagrostis vicunarum* under field conditions in the Peruvian highlands.

2. Materials and methods

2.1. Study site and soil characterization

The study was conducted in the central Peruvian highlands, in the Junín region (11.16° S, 75.93° W), at an elevation of 4,379 m a.s.l. (Fig. 1). The site represents high-Andean grassland ecosystems (puna), which are extensively used for livestock grazing. The climate is classified as cold high-altitude, with mean annual temperatures ranging from 3 to 7°C and pronounced diurnal thermal variation. Night-time temperatures frequently drop below 0°C, particularly during the dry season. The coldest month is July, while the highest temperatures are recorded in February (Mantas and Caro, 2023). Precipitation follows a marked seasonal pattern, with the rainy season occurring from October to April and a distinct dry period from May to September. Mean annual precipitation is below 1,600 mm, with most rainfall concentrated between December and March, coinciding with the main growing period of native grasses (Giráldez et al., 2020).

Vegetation in the study area is dominated by native perennial grasses, primarily *Festuca dolichophylla*, *Jarava ichu* and *Cinnagrostis vicunarum*, which constitute the main forage resource for camelids and ruminants under extensive grazing systems. These species typically form monospecific or predominantly mixed stands under natural conditions.

Soils at the study site are shallow to moderately deep and were developed under cold climatic conditions that limit organic matter mineralization. According to the USDA Soil Taxonomy (Soil Survey Staff, 2022), the soils are classified mainly as Andisols, with local inclusions of Entisols, which are characteristic of high-altitude Andean landscapes (Wilcox et al.,

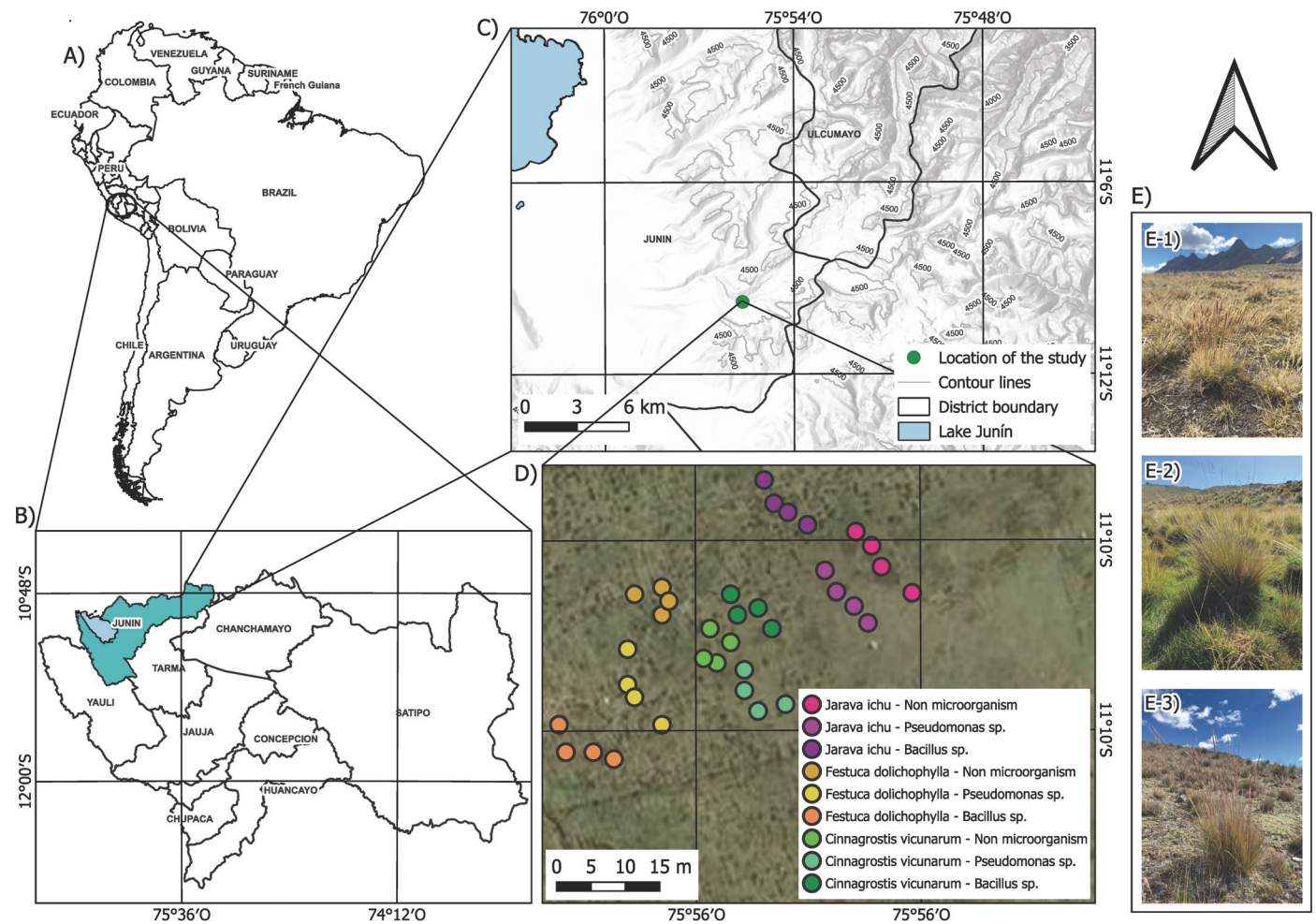


Fig. 1. Location of the study area and experimental layout in the central highlands of Peru. (A) Geographic location of Peru within South America. (B) Location of the Junín region within Peru. (C) Topographic map of the study area showing elevation contours, district boundaries, Lake Junín, and the location of the experimental site. (D) Spatial distribution of experimental plots for *Festuca dolichophylla*, *Jarava ichu* and *Cinnagrostis vicinarum* under different bacterial inoculation treatments (*Bacillus* sp., *Pseudomonas* sp., and non-inoculated control). (E) Representative field photographs of native grassland vegetation: (E-1) *Cinnagrostis vicinarum*, (E-2) *Festuca dolichophylla*, and (E-3) *Jarava ichu*

1988). The soils exhibit loam to sandy-loam textures, high organic matter content, low nitrogen and phosphorus availability, and moderate to high stoniness. Soil pH ranges from slightly acidic to neutral (Arias Arredondo et al., 2021), consistent with volcanic parent material and low-temperature pedogenic processes. Experimental plots were established on gently sloping terrain (<10%), to minimize the influence of surface runoff and erosion on nutrient redistribution.

2.2. Bacterial strains and inoculum preparation

Bacterial strains identified as *Pseudomonas putida* and *Bacillus subtilis*, previously characterized by 16S rRNA gene amplification, were used in this study. These strains were originally isolated from avocado (*Persea americana*) plantations located in the district of Virú, La Libertad, Peru, a region recognized for its high agricultural productivity (Solórzano-Acosta and Quispe, 2024). For the field experiment, the strains were cryopreserved at -80°C and stored in triplicate. Prior to each

inoculation event, bacterial cultures were reactivated at the Plant Protection and Biocontrol Laboratory of the Santa Ana Experimental Station, National Institute for Agrarian Innovation (INIA).

The inoculants, consisting of *Pseudomonas* sp. and *Bacillus* sp., were cultured in 500 mL of mineral medium at 28°C under continuous agitation at 150 rpm. Incubation periods were 96 h for *Pseudomonas* sp. and 72 h for *Bacillus* sp. Bacterial growth was monitored to ensure a final concentration of 1×10^8 CFU mL^{-1} prior to field application. Prepared inoculants were transported to the experimental site in a 10-L cooler with gel packs to maintain refrigerated conditions. For field application, the inoculum was diluted with untreated irrigation canal water in a 20-L backpack sprayer (Huasasquiche et al., 2024a; 2024b). A dose of 1.5 mL of inoculum was mixed with 1 L of water and applied at a rate equivalent to 5 L ha^{-1} . The solution was sprayed directly onto the base of the plant stems according to the experimental design, with five applications performed at 15-day intervals after the onset of the experiment.

2.3. Experimental design and treatments

A field experiment was established in a native high Andean grassland dominated by *Festuca dolichophylla*, *Jarava ichu* and *Cinnagrostis vicunarum*. For each grass species, a completely randomized design was employed with three treatments and four replicates per treatment, resulting in 12 experimental plots per species and a total of 36 plots. The treatments consisted of: (i) a non-inoculated control, (ii) inoculation with *Bacillus subtilis*, and (iii) inoculation with *Pseudomonas putida*. Each experimental plot covered an area of 3 m² and was separated from adjacent plots by a buffer zone minimum distance of 2 m to prevent cross-contamination between treatments. Treatments were randomly assigned within each species to minimize spatial variability. Before the experiment began, all aboveground biomass within each plot was manually cut to a uniform height. To ensure monospecific conditions, non-target plant species were manually removed at the beginning of the experiment and periodically controlled throughout the study period, following standard native grassland management procedures. Maintenance of monospecific plots was conducted every 30 days by manual weeding to prevent species replacement or invasion.

Bacterial inoculations were applied in liquid form following the inoculum preparation protocol described in Section 2.2, at a rate equivalent to 5 L ha⁻¹. Applications were performed manually using a backpack sprayer, directing the solution to the base of the plant crowns to enhance rhizosphere contact. Inoculations were carried out five times at 15-day intervals, starting in May 2023, immediately after the end of the rainy season, and concluding in July 2023. This period was selected to coincide with early vegetative regrowth and to optimize microorganism establishment before the peak growing season. The experiment remained under natural environmental conditions until January 2024, when final measurements of soil properties, aerial biomass and nutritional quality were conducted.

2.4. Soil sampling and physicochemical analysis

Soil sampling was conducted at the end of the experimental period in January 2024. Within each experimental plot, soil samples were collected from the rhizosphere zone of the grass species. For this purpose, two individual soil cores were extracted per plot at a depth of 0–20 cm using a stainless-steel auger (Shao et al., 2025). The two subsamples were homogenized to obtain one composite sample per plot, resulting in a total of twelve composite soil samples for laboratory analyses. Visible plant residues, stones and coarse fragments were manually removed prior to sample processing. Soil samples were air-dried at room temperature, gently crushed, and passed through a 2-mm sieve (Oishi et al., 2020) for physicochemical analyses.

The physicochemical analyses were conducted at the Soil, Water and Foliar Laboratory (LABSAF) of the Santa Ana Experimental Station. Soil organic matter content (OM, %) was determined using the Walkley–Black wet oxidation method (AS-07). Total nitrogen (N, %) was quantified following the micro-Kjeldahl procedure (AS-08). Available phosphorus (P-Olsen,

mg kg⁻¹) was measured using the Olsen extraction method, suitable for neutral to slightly acidic soils (AS-10) (Olsen and Sommers, 1982). Available potassium (K, mg kg⁻¹) was determined by ammonium acetate extraction (AS-12), following standardized procedures (Semarnat, 2002).

2.5. Plant sampling, biomass determination and nutritional analysis

Plant sampling was carried out at the end of the experimental period in January 2024. Within each experimental plot, aboveground biomass of the grass species was harvested manually at ground level from a central area of 1 m² to avoid edge effects (Arias A et al., 2021). All harvested plant material was placed in labelled paper bags and transported to the laboratory for further processing. Fresh biomass was recorded immediately after harvest using a digital balance. Subsamples were then oven-dried at 80°C until reaching a constant weight to determine dry matter content (Cunniff et al., 2015). Dry biomass yield was calculated on a per hectare basis for each treatment and species.

Dried biomass samples were ground using a Wiley mill and passed through a 1-mm sieve prior to nutritional analyses. Total protein content (TP%) was determined by quantifying total nitrogen following the Kjeldahl method and applying a conversion factor of 6.25, according to AOAC method 984.13. Calcium (Ca%) and phosphorus (P%) contents were analyzed following AOAC methods 927.02 and 965.17 (Horwitz and Latimer, 2005). *In vitro* digestibility of organic matter (IVOMD%) was determined using an Ankom Daisy II incubator (ADII; Ankom Technology Corporation, Fairport, NY, USA), following standardized procedures described by Tassone et al. (2020). All nutritional parameters were expressed on a dry matter basis.

2.6. Statistical analysis

Statistical analyses were performed using R software version 3.8 (R Core Team, 2021). The effects of microbial inoculation on *Festuca dolichophylla*, *Jarava ichu* and *Cinnagrostis vicunarum* plant communities were evaluated using analysis of variance (ANOVA), considering microbial treatment as the main factor. The analyzed soil variables included organic matter (OM), nitrogen (N), phosphorus (P) and potassium (K), while plant variables included total protein (TP), calcium (Ca), phosphorus (P) and *in vitro* organic matter digestibility (IVOMD). When significant differences were detected ($p < 0.05$), mean comparisons among treatments were performed using the Fisher's least significant difference (LSD) test at a 5% significance level (Agbangba et al., 2024). Multivariate relationships among soil properties, biomass production and plant nutritional parameters were explored using principal component analysis (PCA). Prior to PCA, the suitability of the dataset for multivariate analysis was assessed using the Kaiser–Meyer–Olkin (KMO) measure of sampling adequacy and Bartlett's test of sphericity (Groth et al., 2013). These analyses were conducted to identify associations between microbial inoculation treatments and soil and plant response variables.

3. Results and discussion

3.1. Physicochemical soil characterization

The effects of bacterial inoculation on soil physicochemical properties have been reported to be independent of grass species in previous studies (Santillana Villanueva et al., 2022). However, contrasting responses were observed in the present study. Soil organic matter and nitrogen contents were significantly higher in plots dominated by *Jarava ichu* and *Festuca dolichophylla* inoculated with *Bacillus* sp., whereas no significant differences were detected in soils associated with *Cinnagrostis vicunarum* (Fig. 2a and Fig. 2b). The increase in soil nitrogen concentration observed under *F. dolichophylla* inoculated with *Bacillus* sp. contrasts with earlier findings, where higher nitrogen levels were reported for *C. vicunarum* associated with *Bacillus* sp. (Cipriano et al., 2021; Santillana Villanueva et al., 2022). These differences suggest that plant-microorganism interactions are likely species-specific and influenced by root traits and rhizosphere conditions. The positive associa-

tion between *Bacillus* sp. inoculation and soil nitrogen availability may be explained by several mechanisms, including the stimulation of root growth through indole production, which enhances the effective root surface area for nutrient uptake. In addition, *Bacillus* sp. has been shown to stimulate nitrate reductase activity, facilitating the conversion of nitrate into nitrogen forms that are more readily assimilated by plants (Masood et al., 2020).

In contrast, soils associated with *Cinnagrostis vicunarum* and inoculated with *Pseudomonas* sp. showed significantly higher phosphorus concentrations ($p \leq 0.05$) (Fig. 2c). While previous studies have reported phosphorus solubilization mainly associated with *Bacillus* sp. inoculation (de Sousa et al., 2021), the present results indicate a stronger effect of *Pseudomonas* sp. under the studied conditions. The higher soil phosphorus levels observed following *Pseudomonas* sp. inoculation are likely related to its well-documented capacity to solubilize inorganic phosphate through the production of organic acids and other chelating compounds, thereby increasing phosphorus availability to plants (Liu et al., 2018; Ng et al., 2022).

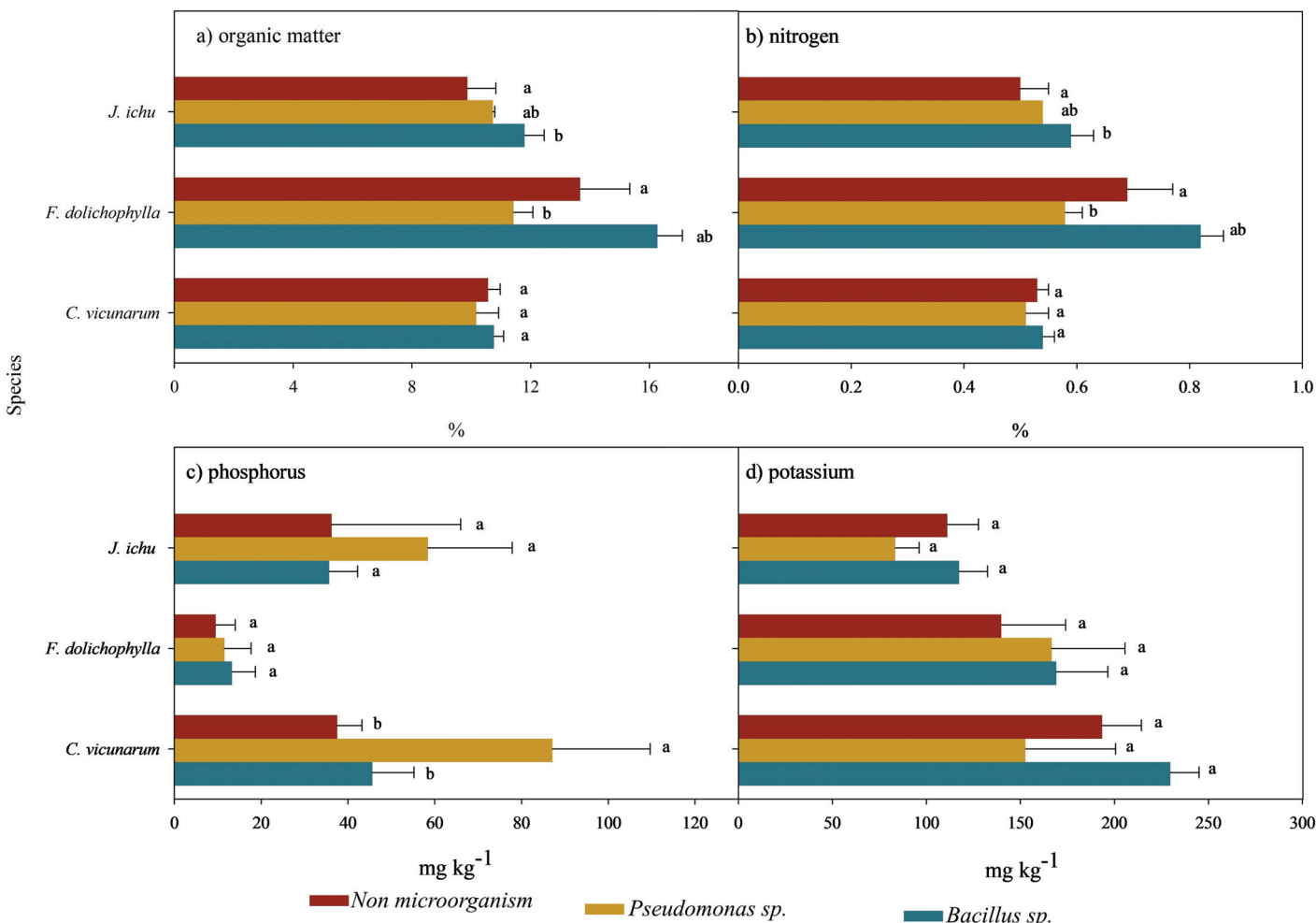


Fig. 2. Effect of microorganisms on the physicochemical characteristics of the soil. (a) organic matter (OM), (b) nitrogen (N), (c) phosphorus (P) and (d) potassium (K) in three types of native grasses. Mean ± standard error. Different letters indicate significant differences. ANOVA results are shown with $p \leq 0.05$

No significant differences in soil potassium content were detected among the three grass species or bacterial inoculation treatments (Fig. 2d). Consistent with previous findings, studies suggest that *Bacillus* sp. and *Pseudomonas* sp. do not exhibit a strong or direct role in potassium solubilization in natural grassland soils (Ng et al., 2022; Stamenov et al., 2012; Yolcu et al., 2011). In contrast, in agricultural systems, specific strains such as *Bacillus cereus* have been shown to significantly increase soil potassium availability, as observed in potato cropping systems (Ali et al., 2021). In such cases, enhanced potassium availability has been associated with the production of organic acids and other metabolites capable of mobilizing mineral-bound potassium (Meena et al., 2014), a mechanism that may be less effective or limited in native grassland soils.

The significant increases in soil organic matter, nitrogen and phosphorus contents may be attributed to microbially induced changes in soil physical and biochemical properties. In particular, the production of extracellular polymeric substances (EPS), characterized by high water-holding capacity, can improve soil aggregation and nutrient retention (Chung et al., 2021). Additionally, phosphorus solubilization mechanisms, including organic acid production, proton release and phosphatase activity, increase phosphorus availability and may indirectly promote nitrogen accumulation and organic matter stabilization within the soil (Rawat et al., 2021). These combined processes likely explain the observed increases in soil organic matter, nitrogen, and phosphorus.

3.2. Yield and nutritional quality of grasses

Grasslands dominated by *Cinnagrostis vicunarum* and inoculated with *Pseudomonas* sp. exhibited significantly higher total protein content compared with plots inoculated with *Bacillus* sp. and non-inoculated controls ($p \leq 0.05$; Fig. 3a). This response suggests a species-specific interaction between *C. vicunarum* and *Pseudomonas* sp., highlighting the importance of host plant–microorganism compatibility. Species-dependent responses to microbial inoculation have also been reported in other plant systems. For instance, inoculation with *Bacillus* sp. and *Pseudomonas* sp. in *Vigna unguiculata* resulted in differential effects on physiological traits, including chlorophyll content and fresh biomass, which are closely associated with protein accumulation (Sivasankari and Anandharaj, 2014). These findings support the notion that the effectiveness of plant–microorganism associations is largely determined by plant species and their specific interactions with inoculated microorganisms.

Unlike previous research indicating that *Bacillus* sp. enhance the nutrient content of *F. dolichophylla*, the present study found that inoculation type did not result in significant changes in nutrient levels for this species (Fig. 3a) (Stamenov et al., 2012). Nevertheless, inoculations with *Bacillus* sp. and *Pseudomonas* sp. showed significant effects compared to the control on the percentage of total protein in *J. ichu* ($p \leq 0.05$, Fig. 3a). This increase in total protein yield in *J. ichu* could be associated with the ability of *Bacillus* sp. to promote the production of phytohormones such as auxins and gibberellins,

which stimulate the growth of *J. ichu* plants as reported in previous studies (Gutiérrez-Mañero et al., 2001; Yousuf et al., 2017). *Bacillus* sp. and *Pseudomonas* sp. are confirmed plant growth-promoting rhizobacteria (PGPR) that enhance host plant growth (Bhattacharyya and Jha, 2012), especially in *J. ichu*. This reaffirms the importance of both microorganisms in sustainable agriculture (Tseng et al., 2020).

In contrast, inoculations significantly affected the calcium and phosphorus percentages in *J. ichu* ($p \leq 0.05$), but had no effect on *C. vicunarum* or *F. dolichophylla* (Fig. 3b, c). These findings are consistent with previous studies on forage crops (*Lolium perenne*) inoculated with *Pseudomonas* sp. and *Bacillus* sp. that increased organic production (Stamenov et al., 2017), crude protein concentration and P, S, Mg, Cu, Zn and Fe in *Lolium multiflorum* (Yolcu et al., 2011). However, other investigations have described positive effects of *Bacillus* sp. on the macro- and micronutrient content of *F. dolichophylla* (Santillana Villanueva et al., 2022), which contrasts with the findings of this study.

Regarding IVOMD in plants, no significant differences were observed in the three inoculated grass species (Fig. 3d), which is in agreement with previous studies (Mehrvarz and Chaichi, 2008). However, improvements in this characteristic have been reported in silage forages (Lara et al., 2015).

The effect of inoculations on biomass yield differed among plant species. *C. vicunarum* showed significant increases with all inoculation treatments, whereas *F. dolichophylla* produced higher biomass when inoculated with *Bacillus* sp., and *J. ichu* exhibited greater yields in soils treated with *Pseudomonas* sp. These species-specific responses suggest that growth promotion by bacterial inoculation is strongly dependent on plant–microorganism compatibility, potentially mediated by the differential stimulation of plant growth processes under field conditions (Gutiérrez-Mañero et al., 2001; Yousuf et al., 2017). In addition, biological nitrogen inputs and the facilitation of nutrient uptake through microbial-derived compounds, such as exopolysaccharides, may contribute to the observed increases in biomass (Guimarães et al., 2022). The positive response observed in *J. ichu* is consistent with previous reports under highland conditions (Cipriano et al., 2021), as illustrated in Fig. 3e.

In this study, a higher positive response capacity was observed in *J. ichu* following inoculation with the rhizobacterium *Pseudomonas* sp. compared to *F. dolichophylla*, which differs from the results reported by Eduardo-Palomino et al., (2024). Other studies, such as those by Ventura Espinoza et al., (2024), showed an increase in aerial biomass in *Medicago sativa* pastures inoculated with similar microorganisms.

In fact, the effect of solubilizing bacteria helps plants to access insoluble forms of phosphate through the excretion of protons and organic acids, which makes phosphate available for plant uptake (Akhtar et al., 2021; Su et al., 2017). Additionally, inoculation of plants with PGPR triggers molecular-level effects, inducing plant physiological responses and regulating genes involved in ion uptake and translocation. This results in improved efficiency in the recovery of soil nutrients (Pii et al., 2015), such as N, Fe, Mn, K and Zn (Ali et al., 2021; Çakmakçı et al., 2007).

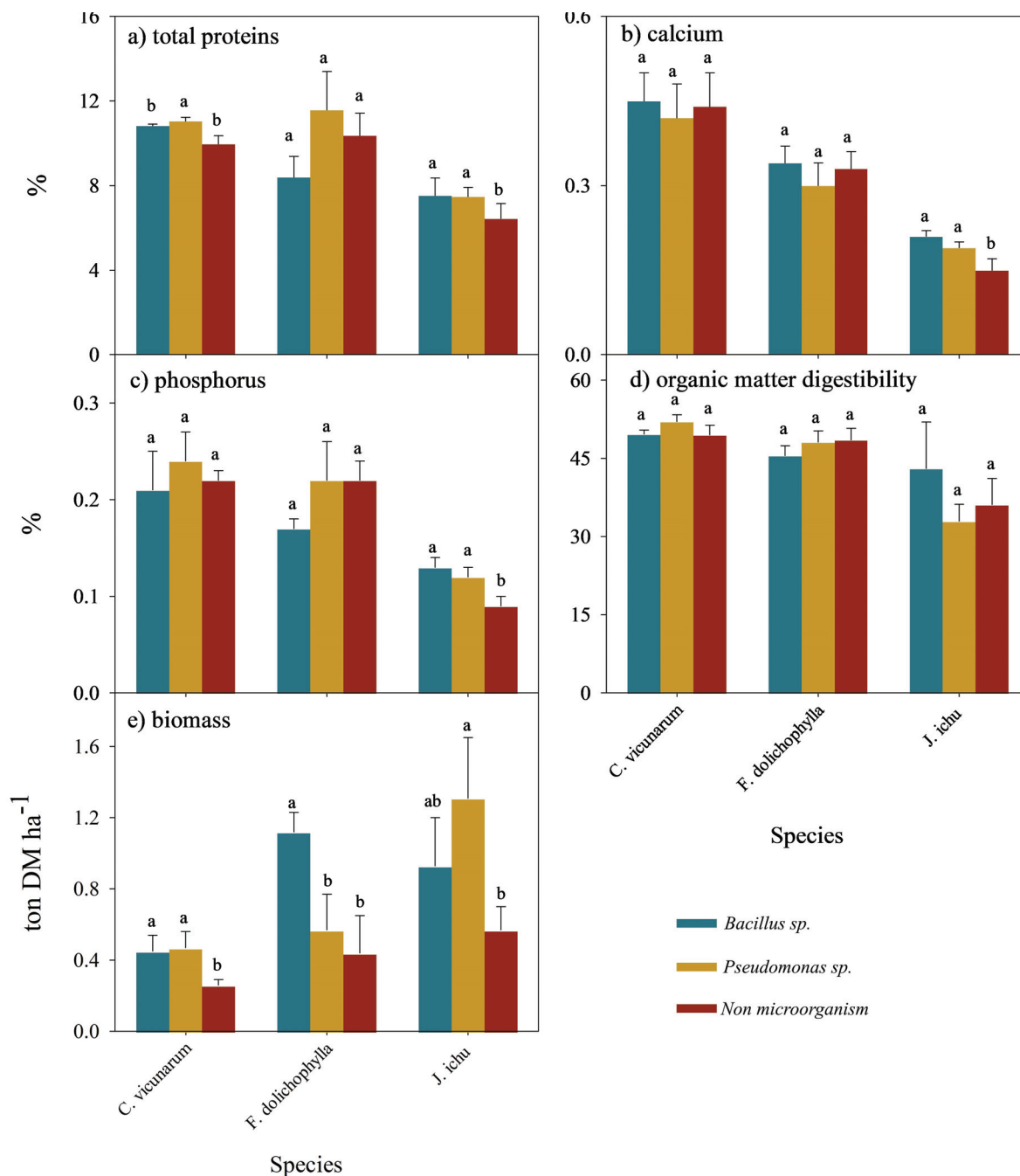


Fig. 3. Effect of microorganisms on foliar characteristics: biomass and nutritional quality

For the analyzed variables, Principal Component Analysis (PCA) indicated that the first principal component (PC1) explained 43.6% of the total variance, while the second principal component (PC2) accounted for 27.8% (Fig. 4). The PCA revealed clear associations between soil properties, bacterial inoculation, and native grass species. Soil nitrogen (N) and organic matter (OM) were closely associated with the combination of *Bacillus sp.* and *F. dolichophylla*, whereas soil phosphorus (P) was mainly associated with *Pseudomonas sp.* and *C. vicinarum*. Potassium (K) was related to the interaction between *Pseudomonas sp.* and *F. dolichophylla*.

Most vegetation-related parameters, including organic matter digestibility (IVOMD), phosphorus, calcium, and total protein, were grouped together and associated primarily with *Pseudomonas sp.* in combination with *F. dolichophylla*, as well as with *Bacillus sp.* and *C. vicinarum*. In contrast, biomass yield was mainly associated with the *Bacillus sp.* and *J. ichu* interaction and contributed predominantly to the variability explained by PC2.

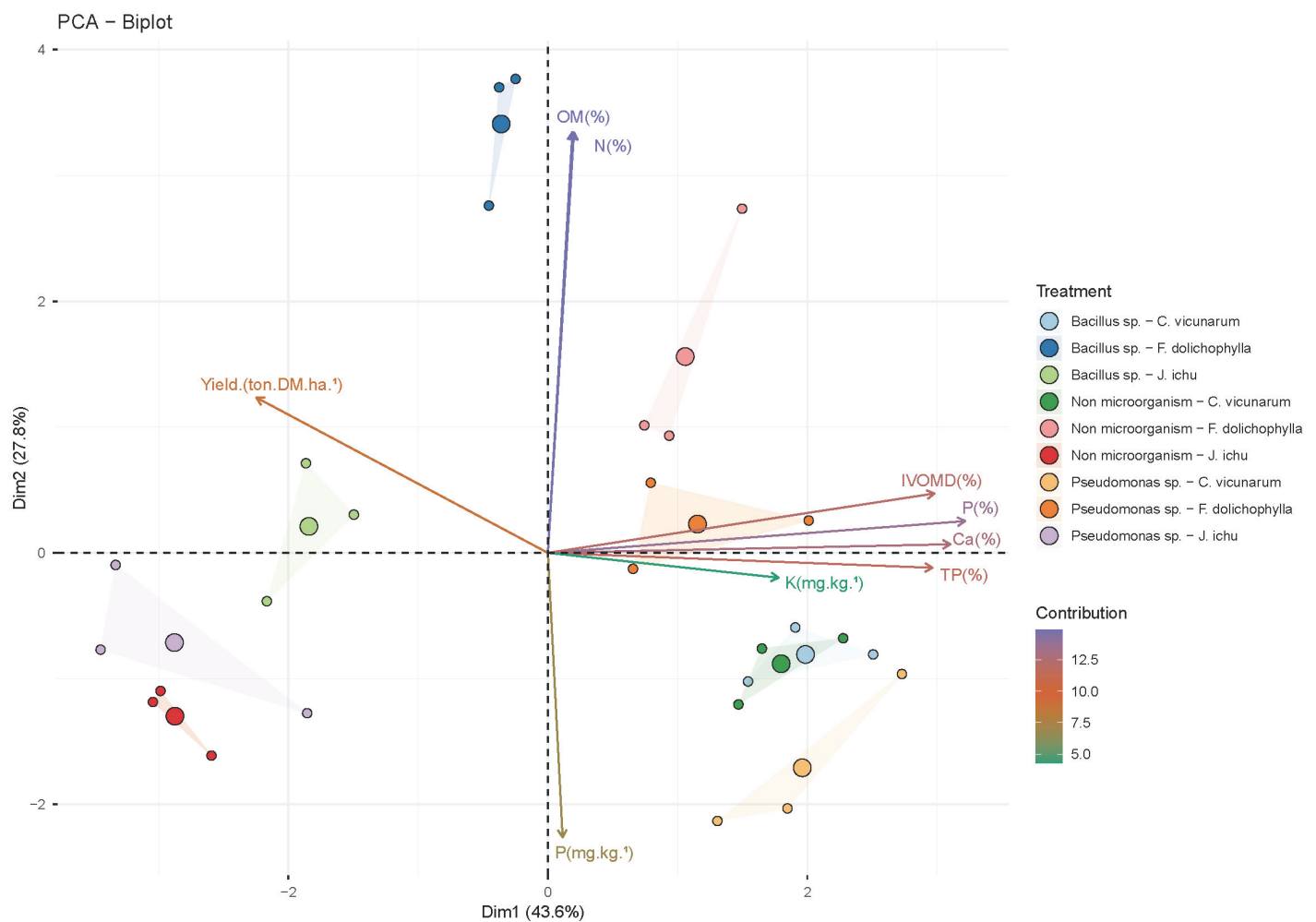


Fig. 4. Principal component analysis (PCA) of soil and nutritional quality

4. Conclusions

The results of this study demonstrate that inoculating plant growth-promoting rhizobacteria (PGPR), specifically *Bacillus* sp. and *Pseudomonas* sp., significantly enhances soil fertility and forage performance in high-altitude Andean grasslands. However, these beneficial effects are highly species-specific, highlighting the critical importance of host plant–microorganism compatibility for rangeland management.

Specifically, *Bacillus* sp. inoculation was found to be most effective in increasing soil organic matter and nitrogen availability, which directly translated into higher biomass yield and improved nutritional quality for *Jarava ichu* and *Festuca dolichophylla*. In contrast, *Pseudomonas* sp. exhibited a stronger synergistic interaction with *Cinnagrostis vicunarum*, significantly increasing soil phosphorus concentrations and foliar protein content.

These findings suggest that restoration and management programs in the Peruvian highlands should prioritize the selection of specific bacterial strains based on the dominant native grass species to optimize ecosystem productivity and for-

age quality. Utilizing tailored microbial inoculants represents a sustainable strategy to mitigate nutrient limitations in high-altitude ecosystems while reducing reliance on chemical fertilizers.

Acknowledgments

Soil laboratory analyses were conducted in collaboration with the LABSAF team, which provided the essential infrastructure and equipment. The authors also express their sincere gratitude to Ofelia Pinillos Monge, Head of the Plant Protection and Biocontrol Laboratory at the Santa Ana Agricultural Center, for granting access to the facilities used in the preparation of microbial inoculants.

Conflict of interest

The authors declare no conflict of interest. The authors declare that they have no known competing financial interests or personal relationships that could have influenced the work reported in this paper.

Author Contributions

Alberto Arias-Arredondo – Conceptualization, Data Collection, Research, Methodology, Validation, Writing – original draft. **Samuel Pizarro** – Research, Analysis, Validation, Writing – revision and editing. **Edilson J. Requena-Rojas** – Research, Validation, Writing – review and editing. **Patricia Verástegui-Martínez** – Conceptualization, Validation, Writing – revision and editing. **Juancarlos Cruz Luis** – Fundraising, Validation, Supervision, Writing – review. **Richard Solórzano-Acosta** – Fundraising, Validation, Supervision, Drafting – review. All authors read and approved the final manuscript.

References

- Agbangba, C.E., Sacla Aide, E., Honfo, H., Glèlè Kakai, R., 2024. On the use of post-hoc tests in environmental and biological sciences: A critical review. *Heliyon* 10(3), e25131. <https://doi.org/10.1016/j.heliyon.2024.e25131>
- Akhtar, N., Syakir Ishak, M.I., Bhawani, S.A., Umar, K., 2021. Various Natural and Anthropogenic Factors Responsible for Water Quality Degradation: A Review. *Water* 13(19), 2660. <https://doi.org/10.3390/w13192660>
- Ali, A.M., Awad, M.Y.M., Hegab, S.A., Gawad, A.M. A.E., Eissa, M.A., 2021. Effect of potassium solubilizing bacteria (*Bacillus cereus*) on growth and yield of potato. *Journal of Plant Nutrition* 44(3), 411–420. <https://doi.org/10.1080/01904167.2020.1822399>
- Alori, E.T., Glick, B.R., Babalola, O.O., 2017. Microbial Phosphorus Solubilization and Its Potential for Use in Sustainable Agriculture. *Frontiers in Microbiology* 8. <https://doi.org/10.3389/fmicb.2017.00971>
- Arias, A.A., Cruz, L.J., Pantoja, A.C., Contreras, P.J., Lopez, R.M., 2021. Rendimiento y calidad de Avena sativa asociada con Vicia sativa en la región puna del Perú. *Revista de Investigaciones Veterinarias del Perú* 32(5), e21339. <https://doi.org/10.15381/rivep.v32i5.21339>
- Arias Arredondo, A.G., Cruz Luis, J.A., Pantoja Aliaga, C.E., Yali Rupay, F., Bermúdez Alvarado, W.S., Morales Sebastian, E.R., 2021. Rendimiento forrajero y valor nutritivo de dos variedades de Avena sativa (Criolla y Mantaro-15), en la sierra central del Perú. *Revista de Investigación e Innovación Agropecuaria y de Recursos Naturales* 8(2), 54–60. <https://doi.org/10.53287/pccm3923xs47i>
- Arias-Arredondo, A., Yalli, T., Cruz, J., Requena, E., Solórzano-Acosta, R., 2025. Assessment of soil characteristics and the productive potential of native Poaceae forage species in the central highlands of Peru. *Journal of Ecological Engineering* 26(8), 1–15. <https://doi.org/10.12911/22998993/202702>
- Bai, Y., Wu, J., Clark, C.M., Pan, Q., Zhang, L., Chen, S., Wang, Q., Han, X., 2012. Grazing alters ecosystem functioning and C:N:P stoichiometry of grasslands along a regional precipitation gradient. *Journal of Applied Ecology* 49(6), 1204–1215. <https://doi.org/10.1111/j.1365-2664.2012.02205.x>
- Bastías, D.A., Gianoli, E., Gundel, P.E., 2021. Fungal endophytes can eliminate the plant growth–defence trade-off. *New Phytologist* 230(6), 2105–2113. <https://doi.org/10.1111/nph.17335>
- Bhattacharyya, P.N., Jha, D.K., 2012. Plant growth-promoting rhizobacteria (PGPR): Emergence in agriculture. *World Journal of Microbiology and Biotechnology* 28(4), 1327–1350. <https://doi.org/10.1007/s11274-011-0979-9>
- Çakmakçı, R., Dönmez, M.F., Erdoğan, Ü., 2007. The Effect of Plant Growth Promoting Rhizobacteria on Barley Seedling Growth, Nutrient Uptake, Some Soil Properties, and Bacterial Counts. *Turkish Journal of Agriculture and Forestry* 31(3), 189–199.
- Carreira, J.A., Viñeola, B., Lajtha, K., 2006. Secondary CaCO₃ and precipitation of P-Ca compounds control the retention of soil P in arid ecosystems. *Journal of Arid Environments* 64(3), 460–473. <https://doi.org/10.1016/j.jaridenv.2005.06.003>
- Chung, K.-S., Shin, J.-S., Lee, J.-H., Park, S.-E., Han, H.-S., Rhee, Y.K., Cho, C.-W., Hong, H.-D., Lee, K.-T., 2021. Protective effect of exopolysaccharide fraction from *Bacillus subtilis* against dextran sulfate sodium-induced colitis through maintenance of intestinal barrier and suppression of inflammatory responses. *International Journal of Biological Macromolecules* 178, 363–372. <https://doi.org/10.1016/j.ijbiomac.2021.02.186>
- Cipriano, M.A.P., Freitas-Iório, R.deP., Dimitrov, M.R., de Andrade, S.A.L., Kuramae, E.E., Silveira, A.P.D.da., 2021. Plant-Growth Endophytic Bacteria Improve Nutrient Use Efficiency and Modulate Foliar N-Metabolites in Sugarcane Seedling. *Microorganisms* 9(3), 479. <https://doi.org/10.3390/microorganisms9030479>
- Cunniff, J., Purdy, S.J., Barraclough, T.J.P., Castle, M., Maddison, A.L., Jones, L.E., Shield, I.F., Gregory, A.S., Karp, A., 2015. High yielding biomass genotypes of willow (*Salix* spp.) show differences in below ground biomass allocation. *Biomass and Bioenergy* 80, 114–127. <https://doi.org/10.1016/j.biombioe.2015.04.020>
- de Sousa, S.M., de Oliveira, C.A., Andrade, D.L., de Carvalho, C.G., Ribeiro, V.P., Pastina, M.M., Marriel, I.E., de Paula Lana, U.G., Gomes, E.A., 2021. Tropical *Bacillus* Strains Inoculation Enhances Maize Root Surface Area, Dry Weight, Nutrient Uptake and Grain Yield. *Journal of Plant Growth Regulation* 40(2), 867–877. <https://doi.org/10.1007/s00344-020-10146-9>
- Eduardo-Palomino, F., Gibson, D.J., Barberá, P., Castro, J., Trillo, F., La Torre, M.I., Walters, S.A., 2024. International Biological Flora: *Festuca dolichophylla*. *Journal of Ecology* 112(7), 1655–1682. <https://doi.org/10.1111/1365-2745.14343>
- Estrada Zuñiga, A.C., Cárdenas Rodríguez, J., Ñaupari Vásquez, J., Zapana Pari, J.G., 2018. Capacidad de carga de pastos de puna húmeda en un contexto de cambio climático. *Revista de Investigaciones Altoandinas* 20(3), 361–368. <https://doi.org/10.18271/ria.2018.399>
- Flatian, A.N., Anas, I., Sutandi, A., Ishak., 2021. The ability of some microbes to solubilize the hardly soluble phosphorous and potassium from various sources in vitro. *IOP Conference Series: Earth and Environmental Science* 648(1), 012143. <https://doi.org/10.1088/1755-1315/648/1/012143>
- Flores, E., Cruz, J., Ñaupari, J., 2005. Utilización de praderas cultivadas en secano y praderas naturales para la producción lechera. *Boletín Técnico CICCA-FDA-INCAGRO*, Lima.
- Flores, E.R., 2016. Climate Change: High Andean Rangelands and Food Security. *Revista de Glaciares y Ecosistemas de Montaña* (1), 73–80. <https://doi.org/10.36580/rgem.i1.73-80>
- Gagné-Bourque, F., Bertrand, A., Claessens, A., Aliferis, K.A., Jabaji, S., 2016. Alleviation of Drought Stress and Metabolic Changes in Timothy (*Phleum pratense* L.) Colonized with *Bacillus subtilis* B26. *Frontiers in Plant Science* 7. <https://doi.org/10.3389/fpls.2016.00584>
- Giráldez, L., Silva, Y., Zubieta, R., Sulca, J., 2020. Change of the Rainfall Seasonality Over Central Peruvian Andes: Onset, End, Duration and Its Relationship With Large-Scale Atmospheric Circulation. *Climate* 8(2), 23. <https://doi.org/10.3390/cli8020023>
- Groth, D., Hartmann, S., Klie, S., Selbig, J., 2013. Principal components analysis. *Methods in Molecular Biology* 930, 527–547. https://doi.org/10.1007/978-1-62703-059-5_22
- Guimarães, G.S., Rondina, A.B.L., Santos, M.S., Nogueira, M.A., Hungria, M., 2022. Pointing Out Opportunities to Increase Grassland Pastures Productivity via Microbial Inoculants: Attending the Society's Demands for Meat Production with Sustainability. *Agronomy* 12(8), 1748. <https://doi.org/10.3390/agronomy12081748>
- Gutiérrez-Mañero, F.J., Ramos-Solano, B., Probanza, A., Mehrouachi, J., R. Tadeo, F., Talon, M., 2001. The plant-growth-promoting rhizobacteria *Bacillus pumilus* and *Bacillus licheniformis* produce high amounts of physiologically active gibberellins. *Physiologia Plantarum* 111(2), 206–211. <https://doi.org/10.1034/j.1399-3054.2001.1110211.x>

- Holechek, J.L., Baker, T.T., Boren, J.C., Galt, D., 2006. Grazing Impacts on Rangeland Vegetation: What We Have Learned: Livestock Grazing at Light-to-Moderate Intensities Can Have Positive Impacts on Rangeland Vegetation in Arid-to-Semi-arid Areas. *Rangelands* 28(1), 7–13. [https://doi.org/10.2111/1551-501X\(2006\)28.1%255B7:GIORVW%255D2.0.CO;2](https://doi.org/10.2111/1551-501X(2006)28.1%255B7:GIORVW%255D2.0.CO;2)
- Horwitz, W., Latimer, G.W., 2005. Official methods of analysis of AOAC International 18th edition. Association of Official Analytical Chemistry International, Maryland.
- Hou, D., He, W., Liu, C., Qiao, X., Guo, K., 2019. Litter accumulation alters the abiotic environment and drives community successional changes in two fenced grasslands in Inner Mongolia. *Ecology and Evolution* 9(16), 9214–9224. <https://doi.org/10.1002/ece3.5469>
- Huassasquiche, L., Alejandro, L., Ccori, T., Cántaro-Segura, H., Samaniego, T., Quispe, K., Solórzano, R., 2024a. *Bacillus subtilis* and *Rhizopagus intraradices* Improve Vegetative Growth, Yield, and Fruit Quality of *Fragaria* × *ananassa* var. San Andreas. *Microorganisms* 12(9), 1816. <https://doi.org/10.3390/microorganisms12091816>
- Huassasquiche, L., Ccori, T., Alejandro, L., Cántaro-Segura, H., Samaniego, T., Solórzano, R., 2024b. Interaction between *Trichoderma* sp., *Pseudomonas putida*, and Two Organic Amendments on the Yield and Quality of Strawberries (*Fragaria* × *ananassa* cv. San Andreas) in the Huaral Region, Peru. *Applied Microbiology* 4(3), 1110–1123. <https://doi.org/10.3390/applmicrobiol4030075>
- Hungria, M., Rondina, A.B.L., Nunes, A.L.P., Araujo, R.S., Nogueira, M.A., 2021. Correction to: Seed and leaf-spray inoculation of PGPR in brachiarias (*Urochloa* spp.) as an economic and environmental opportunity to improve plant growth, forage yield and nutrient status. *Plant and Soil* 466(1), 675–675. <https://doi.org/10.1007/s11104-021-05052-2>
- Joshi, H., Somdutt, Choudhary, P., Mundra, S.L., 2019. Role of Effective Microorganisms (EM) in Sustainable Agriculture. *International Journal of Current Microbiology and Applied Sciences* 8(3), 172–181. <https://doi.org/10.20546/ijcmas.2019.803.024>
- Kang, J., Amoozegar, A., Hesterberg, D., Osmond, D.L., 2011. Phosphorus leaching in a sandy soil as affected by organic and inorganic fertilizer sources. *Geoderma* 161(3), 194–201. <https://doi.org/10.1016/j.geoderma.2010.12.019>
- Lara, E.C., Basso, F.C., Assis, F.B. de, Souza, F.A., Berchielli, T.T., Reis, R.A., 2015. Changes in the nutritive value and aerobic stability of corn silages inoculated with *Bacillus subtilis* alone or combined with *Lactobacillus plantarum*. *Animal Production Science* 56(11), 1867–1874. <https://doi.org/10.1071/AN14686>
- Liu, H., Mi, Z., Lin, L., Wang, Y., Zhang, Z., Zhang, F., Wang, H., Liu, L., Zhu, B., Cao, G., Zhao, X., Sanders, N.J., Classen, A.T., Reich, P.B., He, J.-S., 2018. Shifting plant species composition in response to climate change stabilizes grassland primary production. *Proceedings of the National Academy of Sciences* 115(16), 4051–4056. <https://doi.org/10.1073/pnas.1700299114>
- Magadela, A., Lembede, Z., Egbewale, S.O., Olaniran, A.O., 2023. The metabolic potential of soil microorganisms and enzymes in phosphorus-deficient KwaZulu-Natal grassland ecosystem soils. *Applied Soil Ecology* 181, 104647. <https://doi.org/10.1016/j.apsoil.2022.104647>
- Maldonado Fonkén, M., 2014. An introduction to the bofedales of the Peruvian High Andes. *Mires and Peat* 15(5), 1–13. <https://doi.org/10.19189/001c.128519>
- Mantas, V., Caro, C., 2023. User-Relevant Land Cover Products for Informed Decision-Making in the Complex Terrain of the Peruvian Andes. *Remote Sensing* 15(13), 3303. <https://doi.org/10.3390/rs15133303>
- Masood, S., Zhao, X.Q., Shen, R.F., 2020. *Bacillus pumilus* promotes the growth and nitrogen uptake of tomato plants under nitrogen fertilization. *Scientia Horticulturae* 272, 109581. <https://doi.org/10.1016/j.scienta.2020.109581>
- Meena, V.S., Maurya, B.R., Bahadur, I., 2014. Potassium solubilization by bacterial strain in waste mica. *Bangladesh Journal of Botany* 43(2), 235–237.
- Mehrvarz, S., Chaichi, M.R., 2008. Effect of phosphate solubilizing microorganisms and phosphorus chemical fertilizer on forage and grain quality of barely (*Hordeum vulgare* L.). *American-Eurasian Journal of Agricultural Environmental Sciences* 3(6), 855–860.
- Ng, C.W.W., Yan, W.H., Tsim, K.W.K., So, P.S., Xia, Y.T., To, C.T., 2022. Effects of *Bacillus subtilis* and *Pseudomonas fluorescens* as the soil amendment. *Heliyon* 8(11), e11674. <https://doi.org/10.1016/j.heliyon.2022.e11674>
- Oishi, M., Kubota, Y., Mochizuki, O., 2020. Crushing Mechanism for Soil Particles. *World Journal of Mechanics* 10(6), 69–82. <https://doi.org/10.4236/wjm.2020.106006>
- Oliva, M., Rojas, D., Morales, A., Oliva, C., Oliva, M.A., 2015. Contenido nutricional, digestibilidad y rendimiento de biomasa de pastos nativos que predominan en las cuencas ganaderas de Molinopampa, Pomacochas y Leymebamba, Amazonas, Perú. *Scientia Agropecuaria* 6(3), 211–215. <https://doi.org/10.17268/sci.agropecu.2015.03.07>
- Olsen, S.R., Sommers, L.E., 1982. Phosphorus. [In:] A.L. Page (Eds.), *Methods of Soil Analysis: Part 2 Chemical and Microbiological Properties*. John Wiley Sons, Ltd., Nueva Jersey, 403–430.
- Pii, Y., Mimmo, T., Tomasi, N., Terzano, R., Cescio, S., Crecchio, C., 2015. Microbial interactions in the rhizosphere: Beneficial influences of plant growth-promoting rhizobacteria on nutrient acquisition process. A review. *Biology and Fertility of Soils* 51(4), 403–415. <https://doi.org/10.1007/s00374-015-0996-1>
- Pratap Singh, D., Bahadur Singh, H., Prabha, R., 2016. *Microbial Inoculants in Sustainable Agricultural Productivity*. Springer, India.
- R Core Team., 2021. *R: A Language and environment for statistical computing*. Foundation for Statistical Computing, Vienna.
- Rawat, P., Das, S., Shankhdhar, D., Shankhdhar, S.C., 2021. Phosphate-Solubilizing Microorganisms: Mechanism and Their Role in Phosphate Solubilization and Uptake. *Journal of Soil Science and Plant Nutrition* 21(1), 49–68. <https://doi.org/10.1007/s42729-020-00342-7>
- Rodrigues Manrique, A.E., Lima Mazzuchelli, R.deC., Ferreira Araujo, A.S., Fernando de Araujo, F., 2019. Conditioning and coating of *Urochloa brizantha* seeds associated with inoculation of *Bacillus subtilis* 1. *Pesquisa Agropecuaria Tropical* 49, e55536. <https://doi.org/10.1590/1983-40632019v4955536>
- Santillana Villanueva, N., Tineo Bermudez, A., Mamani Mamani, G., Aylas Chavez, M., Gonzales Guzman, W., Espinoza-Montes, F., 2022. Contribution of native endophytic bacteria to nutrient accumulation in high Andean poaceae. *Revista de Investigaciones Veterinarias del Perú* 33(5), e23790–e23790. <https://doi.org/10.15381/rivep.v33i5.23790>
- Semarnat., 2002. Normas Oficiales Mexicanas Normas Oficiales Mexicanas NOM-001-003-SEMARNAT-1997. Conagua, 1–65.
- Shao, T., Yue, Y., Dong, W., Lin, J., Ma, Y., Zhou, Z., Gao, X., Guo, H., Long, X., Zhao, J., Zhang, Y., 2025. Rhizosphere remediation of saline-alkali soils by *Helianthus tuberosus*: Linking microbial-metabolite synergies to carbon sequestration. *Science of The Total Environment* 1002, 180533. <https://doi.org/10.1016/j.scitotenv.2025.180533>
- Sivasankari, B., Anandharaj, M., 2014. Isolation and Molecular Characterization of Potential Plant Growth Promoting *Bacillus cereus* GGBSTD1 and *Pseudomonas* spp. GGBSTD3 from Vermisources. *Advances in Agriculture* 2014(1), 248591. <https://doi.org/10.1155/2014/248591>
- Soil Survey Staff, 2022. *Keys to Soil Taxonomy*. United States Department of Agriculture, Washington.
- Solórzano-Acosta, R.A., Quispe, K.R., 2024. Assessing the role of field isolated *Pseudomonas* and *Bacillus* as growth-promoting rhizobacteria on avocado (*Persea americana*) seedlings. *Journal of Sustainable Agriculture and Environment* 3(3), e12114. <https://doi.org/10.1002/sae2.12114>
- Stamenov, D., Jarak, M., Đurić, S., Milošev, D., Hajnal-Jafari, T., 2012. Plant growth promoting rhizobacteria in the production of English ryegrass. *Plant, Soil and Environment* 58(10), 477–480. <https://doi.org/10.17221/132/2012-PSE>

- Stamenov, D.R., Djuric, S., Hajnal-Jafari, T., Andjelkovic, S., 2017. Influence of *Pseudomonas* and *Bacillus* Strains Isolated from *Lolium perenne* Rhizospheric Soil in Vojvodina (Serbia) on Plant Growth and Soil Microbial Communities. *Polish Journal of Microbiology* 66(2), 269–272. <https://doi.org/10.5604/01.3001.0010.7879>
- Su, A.-Y., Niu, S.-Q., Liu, Y.-Z., He, A.-L., Zhao, Q., Paré, P.W., Li, M.-F., Han, Q.-Q., Ali Khan, S., Zhang, J.-L., 2017. Synergistic Effects of *Bacillus amyloliquefaciens* (GB03) and Water Retaining Agent on Drought Tolerance of Perennial Ryegrass. *International Journal of Molecular Sciences* 18(12), 2651. <https://doi.org/10.3390/ijms18122651>
- Tassone, S., Fortina, R., Peiretti, P.G., 2020. In Vitro Techniques Using the DaisyII Incubator for the Assessment of Digestibility: A Review. *Animals* 10(5), 1–24. <https://doi.org/10.3390/ani10050775>
- Tseng, Y.-H., Rouina, H., Groten, K., Rajani, P., Furch, A.C.U., Reichelt, M., Baldwin, I.T., Nataraja, K.N., Uma Shaanker, R., Oelmüller, R., 2020. An Endophytic *Trichoderma* Strain Promotes Growth of Its Hosts and Defends Against Pathogen Attack. *Frontiers in Plant Science* 11. <https://doi.org/10.3389/fpls.2020.573670>
- Ventura Espinoza, C.A., Cornejo Maldonado, A.S., Palacin Guerra, P.S., Jara Claudio, F.R., 2024. Efecto de la biofertilización en la biomasa de alfalfa y engorde de cuyes. *Manglar* 21(1), 41–45. <https://doi.org/10.57188/manglar.2024.004>
- Wang, Z., Jimoh, S.O., Li, X., Ji, B., Struik, P.C., Sun, S., Lei, J., Ding, Y., Zhang, Y., 2020. Different responses of plant N and P resorption to overgrazing in three dominant species in a typical steppe of Inner Mongolia, China. *PeerJ* 8, e9915. <https://doi.org/10.7717/peerj.9915>
- Westoby, M., Walker, B., Noy-Meir, I., 1989. Opportunistic Management for Rangelands Not at Equilibrium. *Journal of Range Management* 42(4), 266–274. <https://doi.org/10.2307/3899492>
- Wilcox, B., 1984. The puna–high elevation grassland of the Andes. *Rangelands Archives* 6(3), 99–101.
- Wilcox, B.P., Allen, B.L., Bryant, F.C., 1988. Description and classification of soils of the high-elevation grasslands of central Peru. *Geoderma* 42(1), 79–94. [https://doi.org/10.1016/0016-7061\(88\)90024-9](https://doi.org/10.1016/0016-7061(88)90024-9)
- Yolcu, H., Turan, M., Lithourgidis, A., Cakmakci, R., Koc, A., 2011. Effects of plant growth-promoting rhizobacteria and manure on yield and quality characteristics of Italian ryegrass under semi arid conditions. *Australian Journal of Crop Science* 5(13), 1730–1736. <https://doi.org/10.3316/informit.005337271984855>
- Yousuf, J., Thajudeen, J., Rahiman, M., Krishnankutty, S., P. Alikunj, A., A. Abdulla, M.H., 2017. Nitrogen fixing potential of various heterotrophic *Bacillus* strains from a tropical estuary and adjacent coastal regions. *Journal of Basic Microbiology* 57(11), 922–932. <https://doi.org/10.1002/jobm.201700072>
- Zhu, F., Qu, L., Hong, X., Sun, X., 2011. Isolation and Characterization of a Phosphate-Solubilizing Halophilic Bacterium *Kushneria* sp. YCWA18 from Daqiao Saltern on the Coast of Yellow Sea of China. *Evidence-Based Complementary and Alternative Medicine* 2011(1), 615032. <https://doi.org/10.1155/2011/615032>