



Combined Use of Mycorrhizae and Green Compost for Reducing the Deleterious Effects of Salt Stress in Two Genotypes of Quinoa (*Chenopodium quinoa*)

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Abstract

The present work aims at assessing the effects of arbuscular mycorrhizal fungi (AMF) and/or green compost (Comp) as an effective strategy to boost the productivity of two varieties (Titicaca and Puno) of quinoa (*Chenopodium quinoa* Willd) under salt stress. The quinoa plants were grown for 4 months under controlled conditions in the greenhouse. The experiment was set up in a randomized complete block design with three factors: biofertilizer application (AMF, Compo, and AMF + Comp), quinoa varieties (Titicaca and Puno), and salt stress levels (0, 150, and 300 mM of NaCl). Salt stress impaired the growth, physiological, and biochemical parameters. However, the bipartite combination AMF + Comp efficiently increased growth, stomatal conductance, photosystem II efficiency, photosynthetic pigments protein, and sugar of both quinoa varieties compared to the other treatments and control. AMF + Comp increased the plant's dry weight, compared to the other treatments, by an increment of 133% and 275% under non-stressed conditions (0 mM), 337% and 197% under 150 Mm NaCl, and 311% and 197% under 300 mM NaCl for Titicaca and Puno, respectively. In addition, AMF and/or compost mitigated the negative effects of salinity by improving the soil's physicochemical parameters. The use of AMF and compost and especially their combination could be a good strategy to improve the productivity of quinoa under salinity conditions.

Keywords Organic amendment · Arbuscular mycorrhizal fungi · Salinity · Biochemical parameters · *Chenopodium quinoa*

1 Introduction

Climate change represents the most critical issue of the twenty-first century, remodeling the earth's weather patterns on a global scale. Furthermore, the accentuated greenhouse

gas emissions have intensified water cycle events, adding to global warming, mainly caused by anthropogenic activities. Consequently, estimations have been indicating adverse effects on soil traits, water entities, and air pollution (Ramzan et al. 2022). In addition, drought, salinity, flooding, and other consequent results are expected to increase (Francini and Sebastiani 2019). As far as agriculture is concerned, the sector represents one of the most affected domains. Agriculture commends crop productivity and plays a central role in the global economy. However, the world's population is predicted to attain 9.7 billion by 2050, which is positioning food security as a major agricultural hurdle (Arora 2019; Myers and Ii 2017).

Therefore, crop productivity is strongly influenced by abiotic factors, such as salinity and drought. Thus, sustainable agriculture, which is adapted to changing climate patterns and a growing global population, should rely on the use of adapted crop species that are resilient to abiotic stress (Ferguson 2019). In this sense, agricultural adaptation to stressed soils has been a major issue of paramount

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scientific importance, because of how abiotic stress negatively affects crop plants (Flowers and Colmer 2015). Fortunately, halophytes represent one of the most promising plant groups in sustainable agricultural production (Nikalje et al. 2018), which can be used as tolerant plant crops, holding the potential to minimize the negative effects of salinity on yield and food requirements (Rozentsvet et al. 2017). Quinoa (*Chenopodium quinoa*) was initially domesticated in Andean nations about 7000 years ago. In the second part of the twentieth century, quinoa's potential made it emerge as a plant species that can help attain this goal. In this sense, *C. quinoa* is a facultative halophytic species that represents an interesting model species for studies on abiotic stress, in particular salinity stress responses, which has been the focus of several research practitioners in recent years (Bárzana et al. 2015; Bazile et al. 2016; Razzaghi et al. 2012). Quinoa can tolerate low temperatures ($-8\text{ }^{\circ}\text{C}$) and drought (Benaffari et al. 2022; Hussain et al. 2018). Furthermore, quinoa constitutes a highly nutritious food crop, thanks to the seeds' contenance of essential amino acids (lysine, methionine, threonine), nutritious minerals (Ca, Fe, K, Mg, Mn, P, Zn), and healthy fatty acids (Pereira et al. 2019).

However, quinoa is largely affected by salinity, which is one of the major factors limiting plant growth and yield. Plants grown in saline soils manifest limitations in morphological, physiological, and biochemical processes (Miranda-Apodaca et al. 2020). Furthermore, high levels of salinity increase the production of reactive oxygen species (ROS), inducing the oxidation of membrane lipids, proteins, and nucleic acids (Ahanger and Agarwal 2017). As a consequence, growth inhibition, photosynthetic activity perturbation, and productivity decline occur. However, plants are equipped with various defense mechanisms, such as the antioxidant system, which helps in mitigating generated ROS excess. The antioxidant system consists of many enzymes, such as superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), and polyphenol oxidase (PPO) (Sachdev et al. 2021).

In this regard, several studies have already sought alternatives that can improve defense mechanisms in plants under salinity conditions. One of these alternatives is the use of biostimulants, including arbuscular mycorrhizal fungi (AMF) and compost, as an ecological solution to reduce the deleterious effects of salt stress on plants, without many occurrences of chemical fertilizers (Ait-El-Mokhtar et al. 2020). Biostimulants represent promising eco-friendly tools in sustainable agriculture. Biostimulants like AMF have been pointed out as beneficial means of attenuating the adverse effects of abiotic stress (Ait-El-Mokhtar et al. 2019; Toubali et al. 2020). AMF can improve the water and mineral status of the plant, thanks to the facilitated transfer of water and mineral elements, in particular phosphorus and other micronutrients, through the plant root system (Baslam

et al. 2014). Indeed, the elongation of AMF's extra-radical mycelium increases the contact surface between soil minerals and plant roots. Therefore, the improved water uptake and nutrient assimilation result in ameliorated plant growth as well as better yielding (Bhantana et al. 2021).

Additionally, the use of organic amendments, such as compost, has the advantage of establishing soil remediation and nutrient recycling (Sayara et al. 2020). Thus, several studies have confirmed the positive effects of compost on the biological and chemical properties of dry and degraded soils (Anli et al. 2020; Ren et al. 2018; Sayara et al. 2020). The application of compost to soil has been shown to enhance plant growth by improving water retention, soil organic carbon, and nutrient availability, leading to increased photosynthetic activity, yields, and stress tolerance within plants (Anli et al. 2022; Ullah et al. 2021). Furthermore, different studies have confirmed that the application of compost can significantly improve crop productivity (Agegnehu et al. 2017; Manirakiza and Şeker 2020).

Thus, this study aims to investigate the effects of applying AMF and compost on the growth, yield, photosynthesis, water status, and antioxidant system of two varieties (Titicaca and Puno) of quinoa, subjected to salt stress under greenhouse conditions.

We hypothesize that the application of the double combination AMF + Comp to the soil would attenuate the adverse effects of salt stress by controlling and stimulating different aspects of plant functioning, such as growth, water uptake, photosynthesis, and the ROS sequestration system. To verify our hypothesis, we used a green waste-based compost and an AMF consortium isolated from salt-affected Tafilalet soil and used them alone and/or in combination to improve quinoa productivity and salt tolerance.

2 Material and Methods

2.1 Biological Material

Two varieties of quinoa were used, Titicaca (dense and drooping panicle, orange color of panicles, precocious variety) and Puno (full and branched panicles, purple color of the panicles, precocious variety) (Dao et al. 2020). Seeds of two varieties were obtained from the National Institute for Agricultural Research (Marrakesh, Morocco).

The AMF consortium was isolated from the Tafilalet palm grove located 500 km Southeast of Marrakesh (Morocco). The AMF consortium was composed of 15 species: *Acaulospora delicata*, *Acaulospora leavis*, *Acaulospora* sp., *Claroideoglossum claroideum*, *Glomus aggregatum*, *G. clarum*, *G. claroides*, *G. deserticola*, *G. heterosporum*, *G. macrocarpum*, *G. microcarpum*, *G. versiforme*, *Glomus* sp., *Rhizophagus intraradices*, and *Pacispora boliviana* (Benaffari et al.

Table 1 Different treatments with three levels of salinity (0, 150, and 300 mM) in the experiment under greenhouse conditions

Code	Treatments
Control	Without AMF inoculation or compost amendment
AMF	AMF consortium inoculation
Comp	Compost based on green waste
AMF + Comp	Combination of AMF consortium and compost

AMF, AMF consortium and Comp, compost

Table 2 Physicochemical parameters of used compost

	Compost
pH	7.74 (0.01)
EC (mS cm ⁻¹)	5.46 (0.20)
NTK (%)	1.32 (0.01)
NH ₄ ⁺ (%)	0.09 (0.01)
NO ₃ ⁻ (%)	0.31 (0.01)
TOC (%)	5.72 (0.45)
OM (%)	9.86 (0.78)
C/N	7.49
NH ₄ ⁺ /NO ₃ ⁻	0.29
P _{olsen} (mg kg ⁻¹)	489.95 (20.29)
Na ⁺ (mg kg ⁻¹)	2110.00 (50.00)
K ⁺ (mg kg ⁻¹)	5590.00 (150.00)
Ca ²⁺ (mg kg ⁻¹)	37,380.00 (1840.00)

EC, electrical conductivity; NTK, total Kjeldahl nitrogen; TOC, total organic carbon; OM, organic matter; C/N, ratio of carbon to nitrogen. Presented data are means (SD). SD, standard deviation

2022). Inoculation of quinoa was performed by adding 20 g of the inoculum (roots and substrate containing spores) to the quinoa root system and the different treatments used are listed in Table 1.

The compost used in this study was made from green waste according to Meddich et al. (2016). The characteristics of the compost are shown in Table 2.

2.2 Experimental Conditions and Treatments

To prepare the quinoa plants, seeds were first disinfected with 10% sodium hypochlorite for 10 min, then rinsed several times with sterile distilled water and put to germinate in Petri dishes containing sterilized filter paper and moistened with sterile distilled water. Then, they were placed in the dark at 20 °C for 48 h (Bois et al. 2006). After germination of the seeds, the seedlings were transferred to pots with a capacity of 3 kg of agricultural soil. The substrate was sterilized in an oven at 180 °C for 3 h, then mixed or not with 5% (w/w) compost according to the treatments. Inoculation

of quinoa with AMF was performed by adding 20 g of the inoculum (roots and substrate containing spores) to the quinoa root system at the time of transplanting.

The quinoa plants were grown for 4 months under controlled conditions in the glasshouse (average temperature of 24 °C, average relative humidity of 69%, and light 330 μmol m⁻² s⁻¹) at the Faculty of Science Semlalia, Cadi Ayyad University, Marrakesh, Morocco. The experiment was set up in a randomized complete block design with three factors: biofertilizer application, quinoa varieties, and salt stress levels (0, 150, and 300 mM of NaCl). For each salinity level, four treatments were considered, in total 12 treatments with 10 replicates per treatment were performed. Each pot (one plant) was considered a replicate. The four treatments for the three groups are mentioned in Table 1.

The agricultural soil used has a sandy texture, consisting of 50% sand. The other physicochemical analyses of the agricultural soil used have the following characteristics: pH = 8.1, electrical conductivity (EC) (mS/cm) = 0.735, available phosphorus (mg/kg) = 7.96, and organic matter (OM) (%) = 0.86.

2.3 Seeds Germination

To evaluate the tolerance of the two studied quinoa genotypes to salinity, we tested the impact of NaCl on seed germination. Seeds of both genotypes were separated and disinfected by soaking in 10% sodium hypochlorite for 10 min. They were then rinsed thoroughly with sterile distilled water. Forty seeds of each genotype were germinated in Petri dishes on two layers of filter paper soaked with 5 mL of sterile distilled water with different concentrations of NaCl (0, 50, 100, 150, 200, 250, and 300 mM). The plates were incubated in an oven in the dark at 18 °C because the ideal average temperature for quinoa germination is around 15 to 20 °C (Maamri et al. 2022). Germination was monitored every 24 h for 6 days. A seed was considered germinated when the radicle emerged. During this experiment, we studied the germination rate, which is expressed as the ratio of the number of germinated seeds to the total number of germinated seeds.

2.4 Mycorrhizal Analysis

Detection of root colonization by AMF was determined using the method described by Phillips and Hayman (1970), which consists of treating roots with 10% of potassium hydroxide (KOH) for 45 min at 90 °C, then placing the roots in lactic acid for 10 min at room temperature to neutralize the remaining KOH, thereby staining them with Trypan blue (0.05%) at 90 °C for 20 min.

The mycorrhizal frequency and intensity were calculated according to the following formulas:

$$\text{Mycorrhizal frequency (F) (\%)} = \left(\frac{\text{Infected root segments}}{\text{Total root segments}} \right) \times 100$$

$$\text{Mycorrhizal intensity (M) (\%)} = \frac{(95n_5 + 70n_4 + 30n_3 + 5n_2 + n_1)}{\text{Total root segments}}$$

where “n5” stands for the number of roots with an infection level of 5 (infection rate 90–100%), “n4” with an infection level of 4 (infection rate 50–90%), “n3” with 3 (infection rate 10–50%), “n2” with 2 (infection rate 1–10%), and “n1” with 1 (infection rate 0–1%).

2.5 Harvesting, Plant Growth, and Yield Parameters

After 4 months (at the fructification period) of treatments' application, plants were harvested. The growth of the quinoa plants was assessed by measuring the shoot height (SH), root length (RL), and biomass production. The dry weight of shoots and roots and the dry weight of seeds were determined by drying at 80 °C for 48 h (Benaffari et al. 2022).

2.6 Physiological Parameters

2.6.1 Chlorophyll Fluorescence, Stomatal Conductance, and Leaf Water Potential

Upon the day of harvest, several physiological parameters were measured at the maturity stage of quinoa plants, such as:

Chlorophyll fluorescence (F_v/F_m) was measured by a fluorometer (OPTI-SCIENCE, OS30p) between 10:00 and 12:00 a.m. Clips were placed on the upper surface of young leaves of the same row. The minimum (F_0) and maximum (F_m) fluorescence emission were measured on the leaves after 20 min of dark adaptation (Hosseinzadeh et al. 2015).

Stomatal conductance (gs) was measured using a portable steady-state diffusion porometer (Leaf Porometer LP1989, Decagon Device, Inc., Washington, DC, USA). Ten measurements per treatment were made on the abaxial side per plant between 9:30 and 11:00 a.m. on sunny days. This parameter is expressed in $\text{mmol H}_2\text{O}/\text{m}^2/\text{s}$ (Harley et al. 1992).

The leaf water potential (Ψ_w) was evaluated using a pressure chamber (Model 600-EXP Super Pressure Chamber, PMS instrument, Albany, OR, USA) before dawn (06:00–08:00 a.m.). Measurements were taken on fully extended mature leaves, from the upper part of the stem of each of the ten plants per treatment (Scholander et al. 1965).

2.6.2 Leaf Photosynthetic Pigments Analysis

The determination of the content of the photosynthetic pigment was performed after grinding 100 mg of fresh fully

developed leaves, located in the central third of the plant, in the presence of 8 mL of 80% acetone. The photosynthetic pigments concentration was measured according to Lichtenthaler (1987). After centrifugation at $10,000 \times g$ for 10 min, the optical density (OD) of the supernatants was recorded using a UV/visible spectrophotometer (UV-3100PC spectrophotometer) at 480, 645, and 663 nm. The concentrations of the photosynthetic pigments were measured as follows:

$$\text{Chlorophyll } \alpha (\text{mg g}^{-1}\text{DW}) = 12.25.(\text{OD}663) - 2.79.(\text{OD}645)$$

$$\text{Chlorophyll } b (\text{mg g}^{-1}\text{DW}) = 21.5.(\text{OD}645) - 5.1.(\text{OD}663)$$

$$\text{Total chlorophyll} (\text{mg g}^{-1}\text{DW}) = \text{Chlorophyll } \alpha + \text{Chlorophyll } b$$

$$\text{Carotenoids} (\text{mg g}^{-1}\text{DW}) = \frac{\text{Acar}}{\text{Em} * 100}$$

2.7 Biochemical Analysis

2.7.1 Total Soluble Sugars and Proteins Quantification in Leaves and Seeds

The concentration of total soluble sugars (TSS) was determined according to the method described by (Dubois et al. 1956). Leaf and seed materials (100 mg) were cold ground in 2 mL ethanol (80%). The homogenates were centrifuged and the extracts were recovered. In test tubes, 1 mL of the supernatant was added to 1 mL of phenol solution (5%) and 5 mL of concentrated sulfuric acid. After shaking, the tubes were allowed to cool for 5 min, after which the optical density was measured at 485 nm.

Total soluble proteins were determined using the technique described by Bradford (1976). Leaf and seed samples (100 mg) were homogenized with 4 mL of 1 M phosphate buffer (pH 7) and then centrifuged at $18,000 \times g$ for 15 min at 4 °C. The absorbance was read at 595 nm.

2.7.2 Leaf Hydrogen Peroxide and Malondialdehyde Contents

Hydrogen peroxide (H_2O_2) content in leaves was evaluated using the method described by Velikova et al. (2000). Briefly, leaves were homogenized with 5 mL 10% (w/v) trichloroacetic acid (TCA) in an ice bath and then centrifuged at $12,000 \times g$ for 10 min at 4 °C. The supernatant (0.5 mL) was recovered to determine the concentration of H_2O_2 and 0.5 mL of sodium phosphate buffer (10 mM, pH 7) and 1 mL of iodic potassium (1 M) were added. After 1 h

of incubation, the absorbance at 390 nm was read and plotted against a standard H_2O_2 curve. The blank was made by replacing the sample extract with 10% TCA.

Lipid peroxidation as malondialdehyde (MDA) equivalent was evaluated in leaf tissues. MDA content was estimated by leaf samples (0.1 g) in 3 mL of 0.1% (w/v) TCA and centrifuged at $18,000 \times g$ for 10 min as described by Madhava Rao and Sresty (2000). The supernatant was mixed with 3 mL of 0.1% TCA containing 0.5% (w/v) thiobarbituric acid (TBA). The mixture was then heated in a water bath at 100 °C for 30 min and immediately cooled in an ice bath. The absorbance was read at 440, 532, and 600 nm. The concentration of MDA ($nmol\ g^{-1}\ DW$) was calculated by using the extinction coefficient of $155\ mM^{-1}\ cm^{-1}$, and the results were expressed as $nmol$ MDA equivalents per gram.

2.7.3 Antioxidant Enzyme Activities

The enzymatic extraction was carried out according to Aroca et al. (2003). 0.1 g of fresh leaf tissues was ground in 4 mL of 0.1 M sodium phosphate buffer (pH 7) with 5% insoluble polyvinylpyrrolidone (PVPP) and 0.1 mM ethylene diamine tetra acetic acid (EDTA). The homogenate was centrifuged at $18,000 \times g$ for 10 min and then the supernatant was collected and used for the measurement of antioxidant enzymes activity.

CAT activity was determined as described by Aebi (1984). The reaction mixture contained 0.1 M sodium phosphate buffer (pH 7), 2 mL H_2O_2 (10 mM), and 200 μL of the enzyme extract. The absorbance of the solution was recorded at 240 nm. The CAT activity was expressed in μmol of protein $min^{-1}\ mg^{-1}$ degraded by H_2O_2 .

Peroxidase (POX) activity was determined by the method of Polle et al. (1994). The reaction mixture consisted of 100 μL of enzymatic extract, 0.1 M phosphate buffer (pH 7), 1 mL of 20 mM guaiacol, and 0.5 mL of 10 mM H_2O_2 . The absorbance of the mixture was recorded at 470 nm for 30 s. POX activity was expressed in $EU \cdot min^{-1}\ mg^{-1}$ protein.

PPO activity was estimated by the method of Hori et al. (1997). The test solution contained 2 mL of catechol (10 mM in 0.1 M phosphate buffer (pH 7)); the reaction was started by adding 100 μL of the enzyme extract. The PPO activity was expressed in enzyme unit mg^{-1} protein.

2.8 Soil Analyses

Sol physicochemical characteristics were assessed after plant harvesting on samples taken near the roots to evaluate the effects of AMF and/or compost applied on soil quality. The samples were dried and sieved to measure pH, EC, total organic carbon (TOC), OM, and available phosphorus (P). pH and EC were measured in a diluted soil suspension of 1/5 (v/v), using a pH meter HI 9025 and a conductivity meter HI-9033 (Hanna Instruments, Padua, Italy), respectively.

TOC and OM were measured according to the method described by Aubert (1978), which consists of the oxidation of organic matter by potassium dichromate in the presence of sulfuric acid. The available P content was evaluated according to Olsen and Sommers (1982).

2.9 Statistical Analysis

The results were subjected to multivariate statistical analysis (MANOVA) with CoStat software, version 6.400 (Copyright © 1998–2008 CoHort Software). The statistical treatment includes a variance analysis (ANOVA), followed by a comparison of the means with the Student–Newman–Keuls test at the 5% threshold. The data were subjected to principal components analysis (PCA). The PCA was performed using XLSTAT v. 2016 (Addinsoft, NY, USA).

3 Results

3.1 Seeds Germination

We evaluated the degree of tolerance of the two quinoa genotypes (Titicaca and Puno) to salt stress, by determining the germination rates under different concentrations of NaCl (0, 50, 100, 150, 200, 250, 300 mM) during 6 days (Fig. 1). The results indicated that the germination rate significantly decreased with increasing NaCl concentration, compared to the control.

It appears that both genotypes had almost the same behavior towards salinity. At 150 mM, Titicaca recorded a germination rate of 81%, against 65.83% for Puno. On the other hand, at 300 mM, the germination rates were 72.5 and 50.83% for both Titicaca and Puno genotypes, respectively, on the 6th day of germination.

3.2 Effect of Salt Stress and Biofertilizers on AMF Root Colonization

The results presented in Fig. 2 confirm that the degree of quinoa root colonization by AMF was decreased, following exposure to salt stress. The percentage values for AMF treatment were 31 and 29% under severe concentration (300 mM NaCl), and 41 and 39% in non-stressed conditions (0 mM NaCl) for Titicaca and Puno, respectively. In addition, the findings of this study showed that the application of compost decreased the level of colonization of quinoa roots by AMF under stressful and non-stressful conditions. However, the estimation of the mycorrhizal intensity revealed that the application of AMF alone gave the highest mycorrhizal intensity by 34 and 28% for Titicaca, and 28 and 21% for Puno under 0 mM NaCl and 300 mM NaCl conditions, respectively.

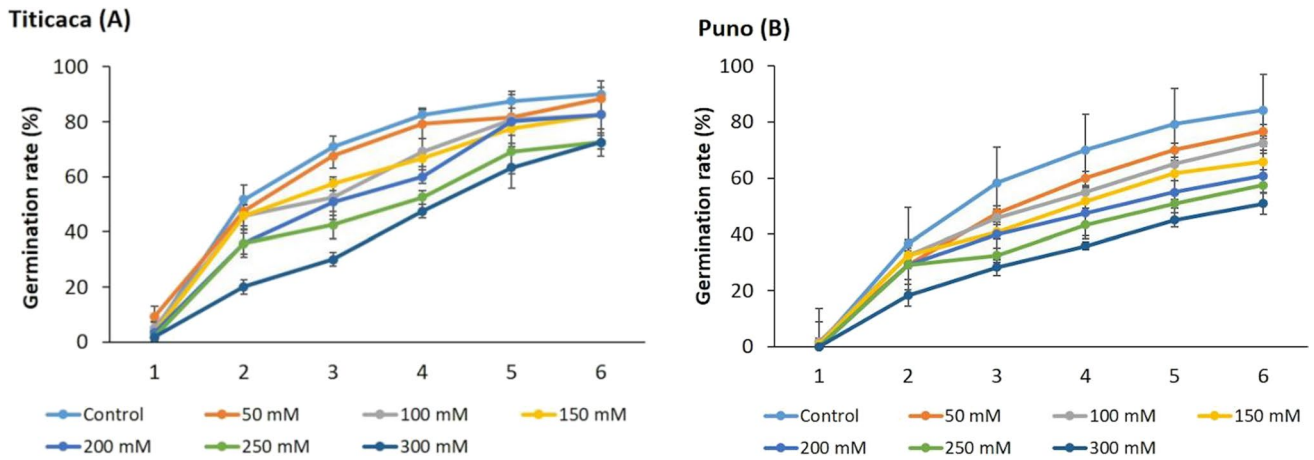


Fig. 1 Germination rate of both quinoa varieties, Titicaca (A) and Puno (B), in the presence of different concentrations of NaCl for 6 days

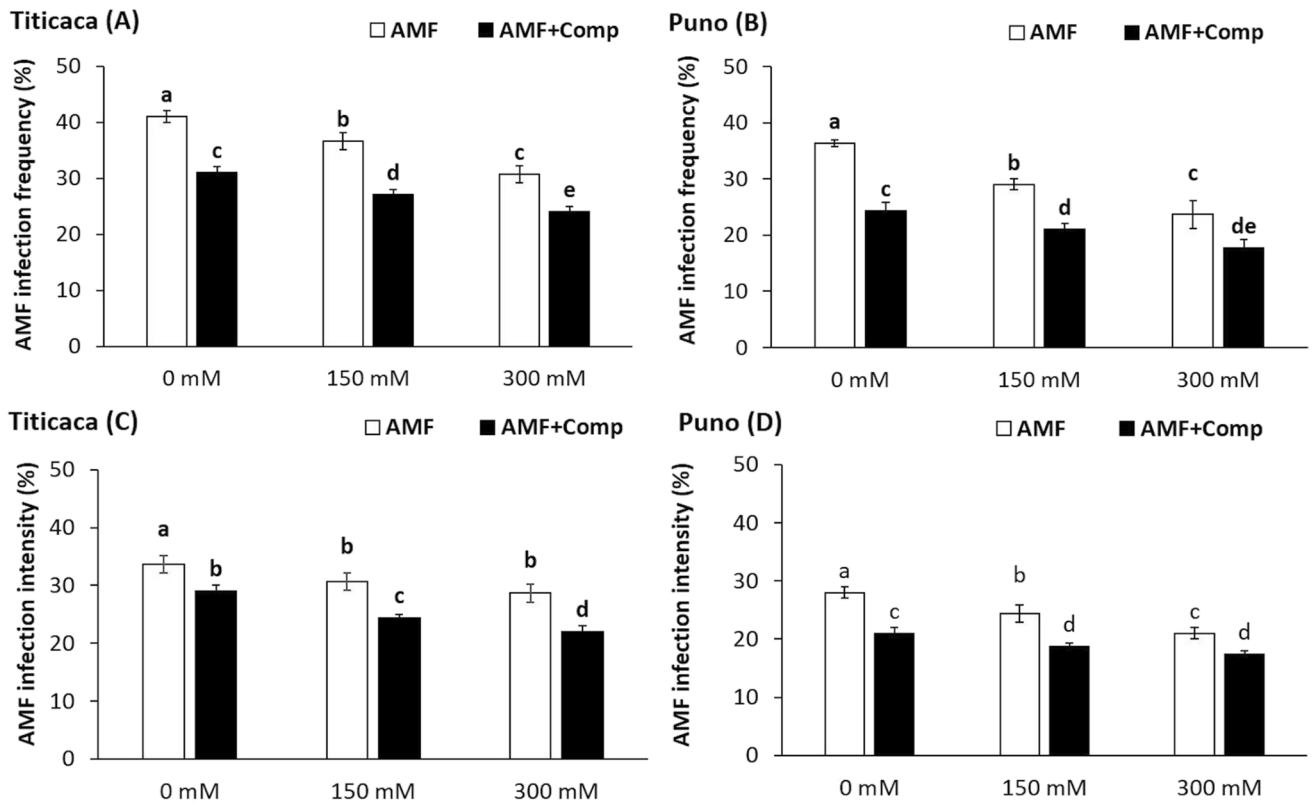


Fig. 2 Effects of salt stress and biofertilizers on the AMF infection frequency (A and B) and intensity (C and D) of both quinoa genotypes. AMF, AMF consortium; Comp, compost. Data presented are

means \pm SD. Bars sharing the same letters in each graphic are not significantly different at $p < 0.05$

3.3 Effect of Salt Stress and Biofertilizers on Plants Growth

According to the results shown in Table 3, the application of salt stress resulted in a negative effect on growth (total dry biomass, aerial and root elongation, and seeds dry weight)

in both quinoa genotypes. Nevertheless, the applied biofertilizers enhanced these parameters compared to the control plants, both in the absence and presence of salinity.

The deleterious effect of salt stress was observed on all growth parameters (shoot height, root elongation, and plant dry weights) and yield (seeds dry weights), within

Table 3 Growth performance of non-amended and non-inoculated quinoa (control), and quinoa inoculated with arbuscular mycorrhizal fungi (AMF) and/or amended with compost (comp) subjected to different concentrations of NaCl

	Treatments	Shoot height (cm)		Root elongation (cm)		Plant dry weight (g/plant)		Seeds dry weight (g/plant)	
		Titicaca	Puno	Titicaca	Puno	Titicaca	Puno	Titicaca	Puno
0 mM	Control	51.66 (2.08) e	32.00 (2.00) f	9.33 (2.08) c	7.33 (1.52) b	4.83 (0.40) ef	2.73 (0.06) e	1.5 (0.10) fg	1.36 (0.66) d
	AMF	61.66 (2.08) d	51.33 (4.16) d	16.66 (1.52) a	14.00 (2.00) a	8.83 (1.06) c	4.00 (0.22) c	2.21 (0.20) ef	1.68 (1.00) c
	Comp	82.33 (1.52) b	73.66 (1.52) b	15.66 (0.57) a	14.66 (0.57) a	10.06 (1.20) b	5.43 (0.08) b	4.78 (0.20) d	2.53 (0.50) b
	AMF + Comp	89.66 (2.51) a	80.33 (1.52) a	18.00 (1.00) a	16.00 (1.00) a	11.30 (0.95) a	7.53 (0.11) a	14.00 (0.50) a	6.00 (2.64) a
150 mM	Control	43.33 (3.05) f	29.33 (2.51) fg	9.00 (1.00) c	6.33 (1.50) b	1.80 (0.52) h	2.23 (0.14) f	1.24 (0.15) gh	1.16 (0.23) f
	AMF	60.00 (3.00) d	49.00 (2.64) de	13.00 (1.00) b	14.00 (1.00) a	3.83 (0.5) fg	3.36 (0.02) d	1.46 (0.15) fg	1.23 (1.00) e
	Comp	78.33 (1.52) c	70.66 (1.52) bc	13.00 (1.00) b	14.33 (2.08) a	5.40 (0.96) e	4.03 (0.08) c	2.60 (0.45) e	1.45 (1.00) c
	AMF + Comp	88.00 (2.00) a	78.33 (2.51) a	17.00 (1.00) a	14.66 (1.52) a	7.86 (0.35) cd	5.13 (0.02) b	10.13 (1.09) b	5.16 (0.51) a
300 mM	Control	41.33 (1.52) f	26.33 (1.52) g	8.00 (1.00) c	6.16 (1.44) b	1.71 (0.60) h	1.65 (0.02) f	1.04 (0.13) h	0.76 (0.06) f
	AMF	58.66 (1.52) d	46.66 (1.52) e	12.00 (1.00) b	9.66 (2.51) b	3.03 (0.15) gh	2.14 (0.02) e	1.09 (0.36) gh	1.00 (1.00) ef
	Comp	75.66 (2.51) c	68.33 (1.52) c	13.33 (1.52) b	13.66 (1.52) a	4.43 (0.40) efg	3.13 (0.02) d	3.03 (0.55) e	1.20 (1.00) ef
	AMF + Comp	85.33 (1.52) ab	77.66 (1.52) a	16.00 (2.00) a	14.50 (1.80) a	7.06 (0.40) d	4.16 (0.01) c	7.529 (0.61) c	3.76 (0.51) ab

AMF, AMF consortium and *Comp*, compost. Presented data are means (SD). Columns sharing the same letters are not significantly different ($p < 0.05$)

the two genotypes of quinoa, cultivated under greenhouse conditions. The results revealed that plant growth traits of both genotypes were significantly influenced by salinity (300 mM) (Table 3). However, all applied biofertilizer treatments mitigated the negative effect of salt stress and improved the growth of quinoa, compared to the controls. The application of compost and AMF, separately or in combination, significantly increased shoot and root biomass under stressed (150 mM and 300 mM NaCl) and non-stressed (0 mM) conditions, compared to non-inoculated and non-amended plants for both genotypes. For instance, the highest plant growth effect was obtained when the compost was applied in combination with AMF (AMF + Comp). Under 300 mM NaCl, the combination increased the growth parameters, plant dry weight (PDW, 311% for Titicaca and 197% for Puno), seeds dry weight (SDW, 204% for Titicaca and 486% for Puno), SH (106% for Titicaca and 195% for Puno), and root elongation (RE, 100% for Titicaca and 135% for Puno), compared to the control plants.

3.4 Effect of Salt Stress and Biofertilizers on Photosynthetic Efficiency, Stomatal Conductance, and Leaf Water Potential

Data presented in Fig. 3 showed that salt stress caused significant reductions in stomatal conductance in plants. Under the same conditions, the biofertilizer treatments significantly increased this parameter in both Titicaca and Puno genotypes, compared to untreated plants, especially in plants treated by AMF + Comp.

The effect of biofertilizers and salt stress on photosystem II efficiency is presented in Fig. 3. The results indicated that salinity negatively affected photosynthetic efficiency as assessed by the Fv/Fm ratio in all treatments. Treatments of plants with AMF + Comp significantly improved this parameter both in the absence and presence of salinity for the two genotypes.

The application of 300 mM NaCl significantly reduced water potential (Fig. 3). Nevertheless, the treatment of plants with biofertilizers significantly improved this

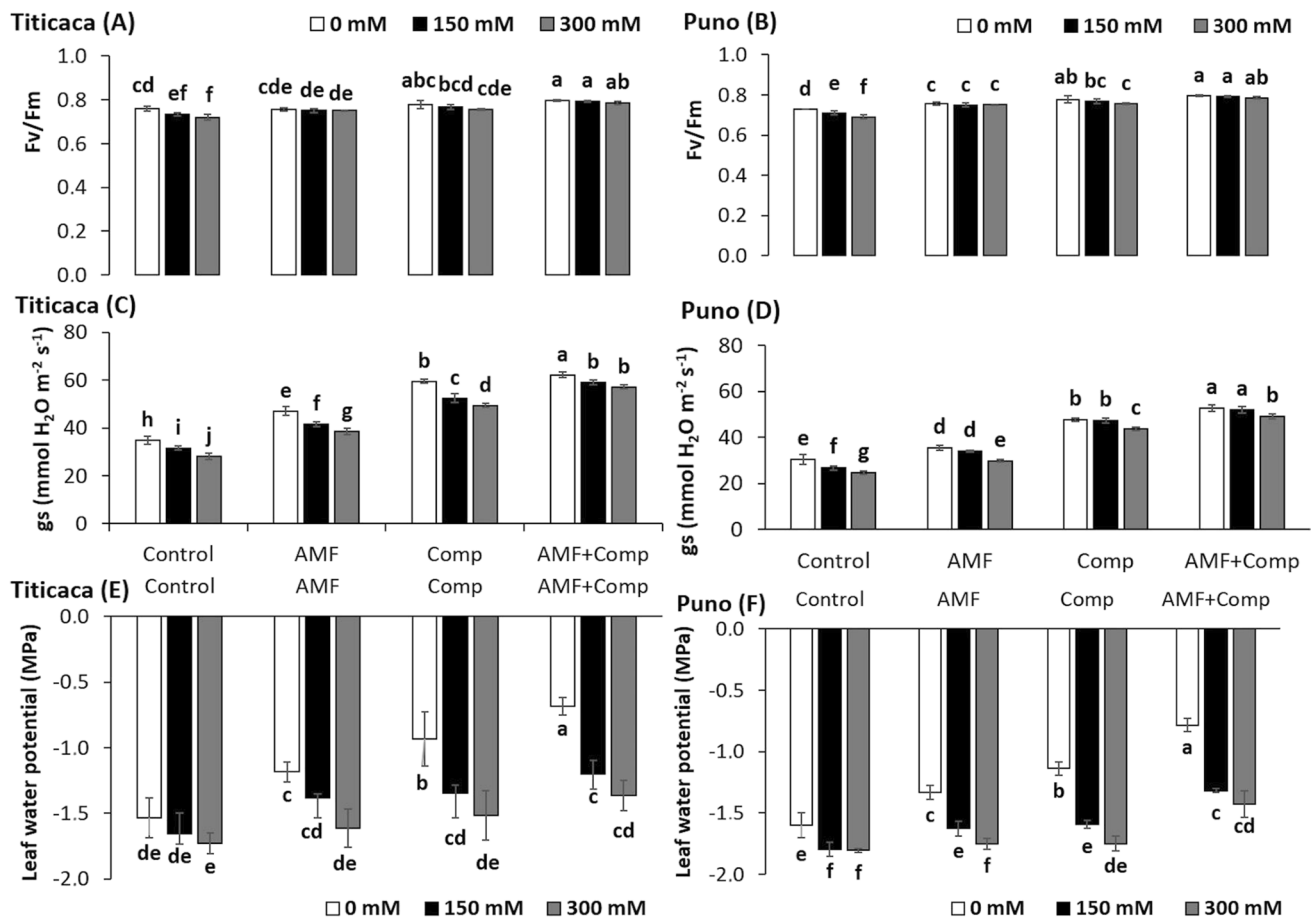


Fig. 3 Effects of salt stress and biofertilizers on chlorophyll fluorescence (Fv/Fm) (A and B), stomatal conductance (gs) (C and D), and leaf water potential (E and F) of both quinoa genotypes. AMF, AMF

consortium; Comp, compost. Data presented are means \pm SD. Bars sharing the same letters in each figure are not significantly different at $p < 0.05$

parameter. Plants treated with AMF + Comp showed the greatest improvements by 37 and 35% for Puno and Titicaca, respectively.

3.5 Effect of Salt Stress and Biofertilizers on Photosynthetic Pigments Quantification in Quinoa Leaves

Photosynthetic pigments content (chlorophyll *a*, chlorophyll *b*, total chlorophyll, and carotenoids) of both genotypes decreased with increasing levels of salinity (Table 4). The application of severe salinity level (300 mM NaCl) significantly reduced the levels of chlorophyll *a*, chlorophyll *b*, total chlorophyll, and carotenoids to 10, 57, 39, and 28%, respectively, in Titicaca leaves, while the respective reductions of these pigments in Puno leaves were reported to be 86, 66, 78, and 85%, respectively, compared to their respective control plants (0 mM NaCl). However, the application of biofertilizers induced a significant increase in

these photosynthetic pigments, compared to the control plants. For Puno, the highest amounts of the photosynthetic pigments were recorded in AMF + Comp treatment by 47, 27, 123, and 46% for chl *a*, chl *b*, total chl, and carotenoids, while for Titicaca, it was noticed that the same treatment improved the levels of chlorophyll *a*, chlorophyll *b*, total chlorophyll, and carotenoids by 18, 9, 13, and 27%, respectively, under 300 mM NaCl conditions.

3.6 Effect of Salt Stress and Biofertilizers on Sugar and Protein Content in Quinoa Plants

The results on the effect of salt stress and biofertilizer application on the sugar and protein contents of quinoa seeds and leaves are presented in Table 5. Exposure to salinity caused a significant decrease in sugar and protein contents, while AMF and/or compost significantly increased these contents in both genotypes under 300 mM NaCl conditions, compared to control plants. The highest

Table 4 Photosynthetic pigments and carotenoids of non-amended and non-inoculated quinoa (control), and quinoa inoculated with arbuscular mycorrhizal fungi (AMF) and/or amended with compost (comp) subjected to different concentrations of NaCl

	Treatments	Chl a content (mg/g FW)		Chl b content (mg/g FW)		Total chlorophyll content (mg/g FW)		Carotenoids content (mg/g FW)	
		Titicaca	Puno	Titicaca	Puno	Titicaca	Puno	Titicaca	Puno
0 Mm	Control	1.19 (0.35) e	1.15 (0.18) e	3.04 (0.16) e	1.39 (0.1) e	4.24 (0.43) g	2.55 (0.037) f	9.42 (0.14) i	6.96 (0.28) e
	AMF	3.23 (0.14) c	2.22 (0.03) c	3.85 (0.14) c	2.74 (0.12) c	7.09 (0.25) c	4.96 (0.14) b	13.71 (0.31) g	9.89 (0.20) b
	Comp	4.73 (0.19) b	3.12 (0.07) b	5.08 (0.29) b	3.32 (0.05) b	9.82 (0.43) b	6.44 (0.12) c	18.18 (1.06) d	12.45 (0.08) c
	AMF+Comp	5.57 (0.31) a	4.17 (0.05) a	6.55 (0.13) a	5.29 (0.03) a	12.12 (0.44) a	9.46 (0.06) a	25.64 (1.02) a	20.17 (0.17) a
150 Mm	Control	1.19 (0.01) e	1.04 (0.06) e	2.18 (0.70) e	0.80 (0.00) ef	3.37 (0.29) h	1.84 (0.06) g	8.67 (0.43) ei	5.77 (0.40) g
	AMF	3.03 (0.03) c	2.16 (0.05) c	3.27 (0.02) d	1.73 (0.10) d	6.30 (0.12) e	3.89 (0.15) e	12.58 (0.90) h	7.07 (0.20) d
	Comp	3.15 (0.08) c	2.56 (0.04) c	4.36 (0.38) b	2.70 (0.15) d	6.30 (0.04) d	5.26 (0.1) f	16.46 (0.73) e	9.69 (1.63) f
	AMF+Comp	4.54 (0.24) b	3.76 (0.03) ab	6.00 (0.32) a	4.07 (0.14) ab	10.52 (0.39) b	7.84 (0.17) d	23.38 (0.21) b	15.94 (0.11) d
300 mM	Control	1.10 (0.17) e	1.00 (0.06) f	1.94 (0.15) g	0.40 (0.00) f	3.05 (0.29) h	1.40 (0.06) g	7.38 (0.44) j	4.77 (0.14) g
	AMF	2.07 (0.01) d	1.78 (0.05) cd	3.19 (0.19) d	0.84 (0.10) e	5.27 (0.12) e	2.62 (0.15) e	11.84 (0.49) h	5.07 (0.32) d
	Comp	3.01 (0.03) c	2.26 (0.04) c	3.43 (0.07) d	1.50 (0.15) e	6.45 (0.05) e	3.76 (0.1) f	15.42 (0.41) f	8.69 (0.56) f
	AMF+Comp	4.96 (0.34) b	3.14 (0.03) b	5.99 (0.06) b	3.17 (0.14) b	10.55 (0.02) b	6.28 (0.17) d	20.24 (0.29) c	14.94 (0.18) d

AMF, AMF consortium; Comp, compost; Chl a, chlorophyll a and Chl b, chlorophyll b. Presented data are means (SD). Columns sharing the same letters are not significantly different ($p < 0.05$)

sugar content was recorded in the plants treated with the AMF + Comp by 124 and 111%, respectively, in seeds and leaves for Titicaca, and 126 and 122% for Puno under the severe concentration of NaCl 300 mM. Similarly, the protein content was significantly improved by the AMF + Comp treatment with 96 and 95%, respectively, in seeds and leaves for Titicaca, and 119 and 56% for Puno under 300 mM of NaCl. In addition, the protein and sugar content was higher in the seeds than in the leaves for both varieties whatever the level of salinity applied.

3.7 Effect of Salt Stress and Biofertilizers on Malondialdehyde and Hydrogen Peroxide Content in Quinoa Leaves

The application of 300 mM NaCl resulted in a high MDA and H₂O₂ content in leaves (Fig. 4). However, plants treated with biofertilizers showed a significant reduction in these two parameters, compared to the non-treated plants. Low levels of MDA and H₂O₂ were noticed in plants treated with the dual application of AMF and compost under non-saline and saline conditions, respectively. The percentages of

reduction recorded in MDA and H₂O₂ content were 71 and 117% respectively for Titicaca, and 89 and 41% for Puno under 300 mM of NaCl.

3.8 Effect of Salt Stress and Biofertilizers on Antioxidant Enzyme Activities in Quinoa Leaves

To assess the antioxidant enzymes involved in attenuating the generated oxidative stress, the activities of CAT, POX, and PPO were evaluated (Fig. 5). The activities of the antioxidant enzymes increased in both genotypes with increasing levels of salinity. The activities of these antioxidant enzymes were significantly higher in plants grown under salinity and without biofertilizers, with a significant difference compared to plants grown with AMF and compost, especially the combined treatment. The activities of CAT, POX, and PPO were increased by 79, 58, and 38% in Titicaca plants when treated with AMF + Comp under the highest level of salinity (300 mM NaCl), while the respective increases in the enzymatic activities in Puno plants were 122, 59, and 40%, compared to control plants under 300 mM NaCl.

Table 5 Total soluble sugar and protein content of non-amended and non-inoculated quinoa (control), and quinoa inoculated with arbuscular mycorrhizal fungi (AMF) and/or amended with compost (comp) subjected to different concentration of NaCl

	Treatments	Leaves sugar content (mg/g FW)		Seeds sugar content (mg/g FW)		Leaves protein content (mg/g FW)		Seeds protein content (mg/g FW)	
		Titicaca	Puno	Titicaca	Puno	Titicaca	Puno	Titicaca	Puno
0 mM	Control	140.64 (3.62) f	132.81 (1.06) g	177.46 (6.60) h	149.68 (0.94) j	83.68 (2.48) f	69.74 (0.44) e	95.46 (1.70) g	91.56 (0.83) h
	AMF	155.65 (3.80) e	151.50 (0.59) e	288.55 (4.59) d	259.87 (0.56) e	89.40 (0.83) e	86.53 (0.59) b	144.29 (0.94) d	135.30 (1.34) e
	Comp	179.99 (7.59) d	157.47 (0.36) d	312.17 (5.32) c	292.78 (0.78) d	109.38 (5.57) c	88.40 (0.35) b	168.95 (1.06) c	156.52 (1.11) b
	AMF+Comp	233.63 (8.35) a	190.45 (1.34) a	342.08 (2.86) a	318.06 (1.93) a	143.24 (5.83) a	93.88 (0.47) a	228.06 (0.91) a	166.93 (0.71) a
150 mM	Control	114.13 (1.13) h	102.91 (1.69) j	160.15 (1.10) i	136.57 (0.71) k	74.88 (1.77) g	60.05 (0.98) f	80.26 (5.67) h	87.61 (0.27) j
	AMF	133.53 (2.04) g	131.16 (0.56) g	233.60 (3.22) f	235.53 (1.36) h	76.28 (1.82) g	73.14 (2.63) d	106.16 (5.63) f	104.26 (0.97) g
	Comp	143.24 (1.56) f	136.21 (0.49) f	293.17 (1.57) d	256.43 (0.72) f	104.32 (2.13) cd	77.99 (2.83) c	141.08 (4.43) d	140.42 (0.69) d
	AMF+Comp	221.98 (1.86) b	179.08 (0.65) b	326.91 (2.07) b	301.98 (0.41) b	134.04 (4.34) b	92.67 (0.24) a	186.45 (1.724) b	156.91 (0.91) b
300 mM	Control	91.06 (2.48) j	78.81 (1.78) k	136.41 (4.59) j	131.31 (0.31) l	67.45 (1.83) h	58.78 (0.69) f	84.55 (5.65) h	69.22 (0.77) k
	AMF	103.30 (2.79) i	105.75 (0.56) i	221.07 (2.58) g	223.44 (0.71) i	70.48 (1.82) gh	68.08 (2.63) e	90.85 (4.30) g	89.14 (0.18) i
	Comp	120.05 (2.33) h	120.53 (0.51) h	245.17 (7.44) e	249.12 (1.23) g	99.65 (2.13) d	75.23 (2.83) d	127.58 (2.76) e	124.66 (0.95) f
	AMF+Comp	192.11 (1.89) c	175.52 (1.03) c	305.50 (1.07) c	297.60 (1.54) c	131.40 (0.88) b	91.93 (0.76) a	166.32 (3.89) c	151.91 (0.92) c

AMF, AMF consortium and Comp, compost. Presented data are means (SD). Columns sharing the same letters are not significantly different ($p < 0.05$)

3.9 Soil Analysis

Results of soil analyses after the cultivation of quinoa and application of the different treatments are shown in Table 6. Compared to the initial properties, the soil organic matter and available P were significantly improved after 4 months of quinoa cultivation and biofertilizers application. The pH values decreased in the soil of Puno plants treated with AMF+Comp under stressed conditions (300 mM NaCl). The application of compost alone or combined with AMF significantly improved OM by 172 and 227%, TOC by 56 and 88%, and available P content by 17 and 24% respectively for Titicaca under 300 mM NaCl conditions compared to the control. While the respective improvements of OM, TOC, and available P for Puno were 194 and 215%, 43 and 81%, and 31 and 29% under 300 Mm NaCl conditions compared to the control.

3.10 Principal Component Analysis

PCA was performed to gain an overview of the data obtained and to analyze the relationships between variables (Fig. 6).

PC2 divided the salinity treatments by stress intensity. The 0 mM NaCl treatment samples were placed on top, the 150 mM NaCl treatment samples in the center, and the 300 mM NaCl treatment samples below the ordination. PC1 represents a strong contrast between growth, physiological, and water parameters, all positively associated with comp treatments alone and/or in combination with AMF under 0 mM and 150 mM salinity and parameters related to the antioxidant activity (POX, PPO, and CAT) and stress markers (H_2O_2 and MDA) negatively associated with AMF treatment at 300 mM salinity. PCA revealed that the results obtained showed that the two varieties responded in the same way to the different salinity concentrations and treatments applied.

4 Discussion

Abiotic stress, such as salinity, represents a severe constraint on crop productivity. It causes huge economic losses every year in the world (Ghorbanpour and Varma 2017). Hence, organic and biological amendments based on green waste

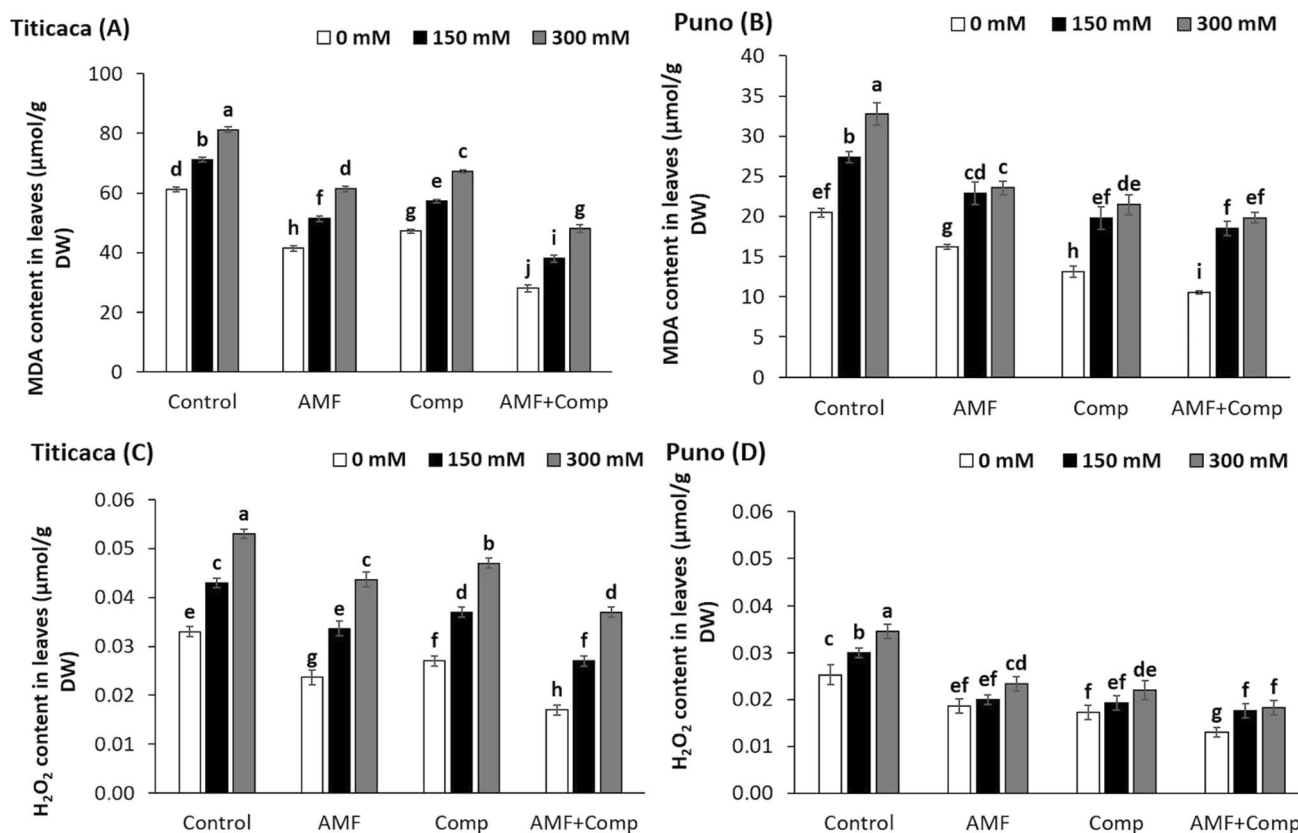


Fig. 4 Effects of salt stress and biofertilizers on malondialdehyde (MDA) and H₂O₂ of both quinoa varieties. AMF, AMF consortium; Comp, compost. Data presented are means \pm SD. Bars sharing the same letters in each graphic are not significantly different ($p < 0.05$)

and AMF were selected to improve the biomass and tolerance of quinoa, due to their great nutritional content. Quinoa plants are acknowledged as allies for global food security (Alandia et al. 2020). These plants are widely grown in Morocco, where salinity is one of the main factors limiting the growth of this crop.

Salinity has deleterious effects on plants at different stages of their growth and development. Several works have reported the negative effects of soil salinity on crops (Machado and Serralheiro 2017; Negrão et al. 2017). The findings demonstrated that irrigation of quinoa with saline water significantly decreased crop water productivity, harvest index, and ultimate dry biomass (Bouras et al. 2022). In this study, the depressive effects of salt on seed germination were demonstrated by the significant decrease in their germination rate with increasing NaCl concentration. Our results are in agreement with studies conducted on quinoa (Abdel-Farid et al. 2020), alfalfa (Ben-Laouane et al. 2020), and faba bean (Benidire et al. 2017). The negative effects of salt at the stage of germination can be the result of an osmotic stress response, which could be due to a decrease in the water potential of the external environment, following elevated rates of salinity. Consequently, the absorption of

water becomes difficult, which inhibits plants' germination (Johnson and Puthur 2021; Safdar et al. 2019).

According to our results, we noticed negative effects of salinity on AMF colonization for both varieties of quinoa plants. These results are in agreement with several studies showing that mycorrhizal infection decreased when plants were subjected to salinity (Ait-El-Mokhtar et al. 2020; Ben-Laouane et al. 2020). Salt stress induces inhibition of AMF spore germination and hyphal growth, thereby decreasing mycorrhizal colonization (Rydlová and Püschel 2020). Furthermore, compost application significantly decreased mycorrhizal frequency and intensity in AMF-inoculated plants under unstressed and stressed conditions. The application of organic amendments, including compost and mineral nutrients, can reduce AMF colonization and root activity due to the release of mineralized P into the soil and/or diffusion of decomposition products, thereby reducing the establishment and maintenance of AMF colonization (Jiang et al. 2021; Xiao et al. 2020).

The obtained results of the present study revealed that the growth of both genotypes, Titicaca and Puno, was not significantly influenced by the low salinity level (150 mM NaCl), indicating the halophytic behavior of quinoa (Moog

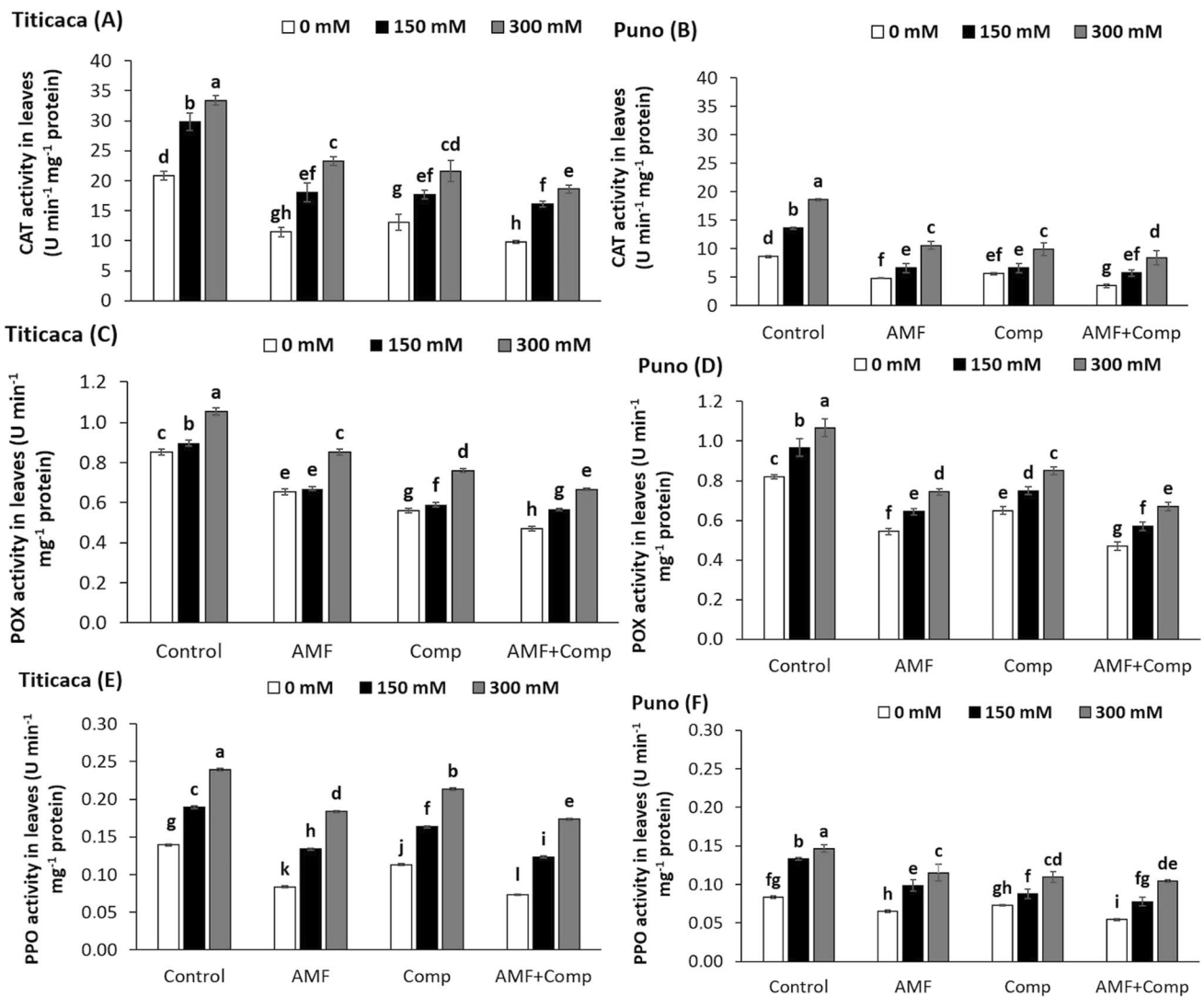


Fig. 5 Effects of salt stress and biofertilizers on catalase (CAT), peroxidase (POX), and polyphenol oxidase (PPO) activities in shoot part of both quinoa varieties. AMF, AMF consortium; Comp, compost.

Data presented are means \pm SD. Bars sharing the same letters in each graphic are not significantly different ($p < 0.05$)

et al. 2022). Our results revealed that the Titicaca genotype was more salinity-tolerant compared to Puno. The inhibition of plant growth and development by salinity could be due to the osmotic and toxic effects of excess salt (Negrão et al. 2017). Decreased water potential causes a reduction in water uptake by plants, resulting in stomatal closure, reduced photosynthesis, and decreased leaf area, leading to a reduction in plant growth rate (Negrão et al. 2017; Safdar et al. 2019).

This behavior has been reported by several authors in other crops, such as alfalfa (Ben-Laouane et al. 2020), faba bean (Benidire et al. 2017), and bean (Abdel Motaleb et al. 2020). Our research confirmed the results found by Kellogg et al. (2021), who showed that AMF increased growth traits in quinoa plants. However, AMF showed remarkable growth of quinoa plants under non-stressed and stressed conditions

compared to the controls (García-Parra et al. 2022). Consequently, they improved the agronomic parameters.

Our results are in agreement with those obtained by Finlay (2008), who observed a positive impact on plant growth when AMF and compost were combined. Thus, plant biomass increment could be due to the growth promotion mechanisms that occurred by the beneficial microorganisms, such as phytohormone production and mineral nutrients solubilization (Finlay 2008). Similarly, Achiba et al. (2010) demonstrated that compost supply in the soil enriches the rhizosphere with micro- and macro-nutrient elements and counteracts nutrient depletion. The significant increase in growth parameters and grain weight after compost application could be attributed to the increase in soil organic matter and water retention (Goswami et al.

Table 6 Main characteristics of different treatments on agricultural soil physicochemical parameters after harvest

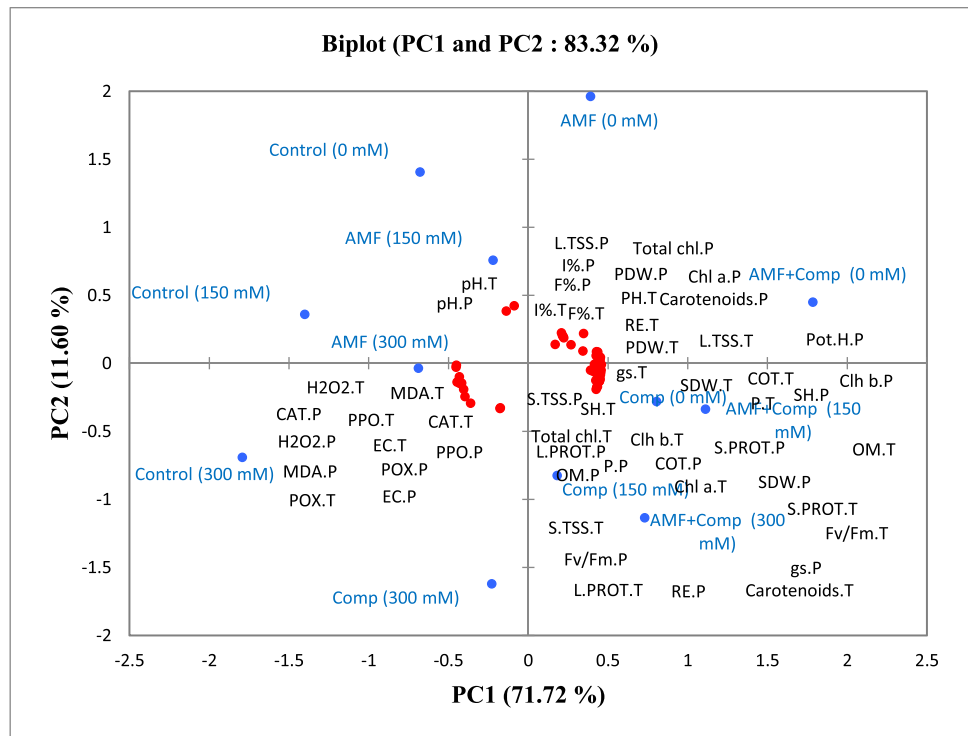
Treatments	pH		EC (mS/cm ²)		TOC (%)		OM (%)		P-Olsen (ppm)		
	Titicaca	Puno	Titicaca	Puno	Titicaca	Puno	Titicaca	Puno	Titicaca	Puno	
0 mM	Control	8.12 (0.01) a	8.24 (0.01) a	0.74 (1.00) c	0.76 (1.00) c	0.56 (0.02) d	0.5 (0.01) e	0.97 (0.04) f	0.87 (0.01) f	9.75 (0.64) d	9.07 (0.06) e
	AMF	8.23 (0.01) a	8.44 (0.04) a	0.73 (1.52) cd	0.75 (1.52) cd	1.22 (0.01) c	1.05 (0.04) d	2.12 (0.01) d	1.83 (0.07) d	27.12 (1.01) c	25.09 (1.00) c
	Comp	7.75 (1.95) b	7.90 (0.17) ab	0.75 (0.57) c	0.78 (1.00) c	1.56 (0.01) b	1.43 (0.03) b	2.72 (0.02) b	2.49 (0.06) b	37.12 (1.95) b	35.91 (0.57) b
	AMF+Comp	7.86 (1.36) ab	7.91 (1.15) ab	0.76 (1.52) c	0.79 (2.08) c	1.88 (0.01) a	1.81 (0.01) a	3.27 (0.01) a	3.15 (0.01) a	50.95 (1.36) a	40.15 (1.15) a
150 mM	Control	7.91 (0.01) ab	7.92 (0.03) ab	0.82 (1.52) b	0.83 (0.57) b	0.48 (0.01) e	0.38 (0.01) f	0.84 (0.01) f	0.66 (1.33) f	9.23 (1.08) e	8.37 (0.54) f
	AMF	7.81 (0.01) ab	7.88 (0.01) b	0.81 (2.00) b	0.82 (1.52) b	0.87 (0.01) c	0.76 (0.01) d	1.51 (0.03) e	1.33 (0.03) e	23.89 (1.59) b	22.60 (2.19) d
	Comp	7.72 (0.03) b	7.72 (0.02) bc	0.83 (4.04) b	0.84 (4.04) b	1.44 (0.01) b	1.36 (0.02) c	2.52 (0.02) c	2.37 (0.02) b	33.07 (1.10) b	31.40 (0.52) bc
	AMF+Comp	7.73 (0.03) ab	7.79 (0.01) bc	0.83 (1.52) b	0.84 (1.00) b	1.71 (0.02) a	1.42 (0.01) b	2.98 (0.03) b	2.48 (0.02) b	44.99 (1.06) a	35.63 (1.33) b
300 mM	Control	7.87 (0.01) a	7.89 (0.00) b	1.22 (1.00) a	1.24 (1.00) a	0.39 (0.02) e	0.28 (0.02) f	0.68 (0.03) f	0.49 (0.03) f	7.50 (0.50) f	8.03 (1.05) f
	AMF	7.78 (0.01) ab	7.83 (0.01) b	1.13 (2.08) ab	1.16 (3.05) ab	0.76 (0.02) c	0.65 (0.01) d	1.32 (0.04) e	1.14 (0.02) e	22.18 (1.00) d	21.06 (1.09) d
	Comp	7.63 (0.03) ab	7.62 (0.03) c	1.20 (3.51) a	1.21 (1.00) a	1.38 (0.01) b	1.28 (0.02) c	2.40 (0.01) c	2.23 (0.03) bc	31.78 (0.67) b	27.33 (1.52) c
	AMF+Comp	7.69 (0.01) ab	7.72 (0.04) d	1.21 (0.57) a	1.23 (1.00) a	1.57 (0.01) a	1.33 (0.02) b	2.74 (0.02) b	2.31 (0.03) bc	43.78 (0.92) a	31.14 (1.03) bc

AMF, AMF consortium; Comp, compost; EC, electric conductivity; TOC, total organic content; OM, organic matter and P, phosphorus. Presented data are means (SD). Columns sharing the same letters are not significantly different ($p < 0.05$)

2017). The ability of the AMF and compost combination to improve plant growth under stressful conditions has been reported by several authors, notably in date palm (Toubali et al. 2020), tomato (Copetta et al. 2011), *Canna indica* (El Faiz et al. 2015), and shrub (Kohler et al. 2015).

Photosynthetic efficiency is a crucial trait that influences plant growth and survival under environmental conditions. Our study showed that salinity impaired stomatal conductance and chlorophyll fluorescence (Fv/Fm) functioning as found in several studies (Ait-El-Mokhtar et al. 2020; Chandrasekaran et al. 2019; Ouhaddou et al. 2022). Salinity significantly reduced the Fv/Fm ratio and stomatal conductance (gs) of both quinoa genotypes, with significant differences between applied treatments. It is well documented that salt stress negatively affects photosynthetic activities (Hafez et al. 2021; Kwon et al. 2019). A similar reduction in the maximum rate of CO₂ assimilation can be expected, which could lead to photo-inhibition of PSII (Najar et al. 2019). In plants, salinity usually causes a rapid decline in PSII activity due to the inhibition of PSII repair caused by excessive ROS production (Pan et al. 2021). In this study, the inoculated and amended plants revealed an improvement in the gs and Fv/Fm ratio compared to the control plants under non-saline and saline conditions, which is in agreement with Benaffari et al. (2022), who found that quinoa plants treated with AMF improved physiological parameters. This increase in the photochemical efficiency of PSII could be due to the accumulation of some osmolytes, such as glycine betaine and proline that can maintain cell turgor and protect the PSII complex and CO₂-fixing enzymes under salt stress (Khanna-Chopra et al. 2019). Mathur et al. (2019) and Mathur and Jajoo (2020) reported that inoculation with AMF helps plants to maintain the integrity and stability of PSI and PSII under abiotic stress. The increase in leaf water potential by salinity in treated compared to untreated plants in this investigation would confirm that applied biofertilizers could help plants adapt to severe saline conditions by maintaining a favorable water status (Franzini et al. 2019; Mokabel et al. 2022). Salinity significantly decreased the levels of total chlorophyll, carotenoids, and chlorophyll *a* and *b*. This decrease could be due to the increase in chlorophyll degrading enzymes, such as chlorophyllases (Siddiqui et al. 2020). However, these parameters were significantly improved when biofertilizers were applied alone and/or in combination. AMF hyphae are likely to increase Mg uptake, which can increase total chlorophyll content in mycorrhizal quinoa plants (Benaffari et al. 2022). Previous works showed that the improvement of chlorophyll synthesis is linked to adequate uptake of mineral elements, particularly Mg and N (Begum et al. 2019; Hashem et al. 2018). In addition, P in synergy with N plays a major physiological role in the process of photosynthesis.

Fig. 6 Principal component analysis (PCA) for both varieties; T, Titicaca; P, Puno; Comp, compost; AMF, AMF consortium; PDW, plant dry weight; SDW, seeds dry weight; Fv/Fm, chlorophyll fluorescence; gs, gas exchange; LWP, leaf water potential; Chla, chlorophyll *a*; Chlb, chlorophyll *b*; Tchl, total chlorophyll; L.TSS, leaf total soluble sugar; S.TSS, seed total soluble sugars; L.Prot, leaf proteins; S.Prot, seed protein; CAT, catalase; PPO, polyphenoloxidase; POX, peroxidase; EC, electrical conductivity; TOC, total organic carbon; OM, organic matter; P, soil available P



The tested biofertilizers increased soluble sugar and protein content in plants of both quinoa genotypes compared to the control, with a better result noted for the AMF + Comp combination. Copetta et al. (2011) also concluded that the use of AMF and compost could improve fruit quality by ameliorating their biochemical composition, including sugar and protein levels. The improvement of photosynthesis increases protein synthesis and sugar content. This would positively influence the growth and yield of quinoa plants. Several studies revealed that plant adaptation to salt stress is associated with osmotic adjustment by accumulating organic solutes (Abdel Latif et al. 2019; Siddiqui et al. 2020).

Sugars are important osmolytes that could contribute to the osmotic adjustment of glycophytes subjected to salinity conditions (Ashraf and Harris 2004). Their main functions are osmoprotection, osmotic adjustment, carbon storage, radical scavenging, and protein structure stabilization (Parida and Das 2005). Indeed, these solutes can protect cell membrane by balancing the osmotic potential of the cytosol with that of the vacuole and the external environment. According to our findings, salt stress reduced total soluble sugar in quinoa leaves while AMF and compost application increased this parameter under stressful conditions as well (Ahanger et al. 2014). The accumulation of sugars would protect membranes from salinity-induced dehydration by regulating the cellular osmotic potential, thus maintaining a good water status of the plants (Achour et al. 2015; Parida and Das 2005).

In this study, applied biofertilizers increased the accumulation of sugar and protein levels in quinoa plants, suggesting their role as osmoregulators. Our findings agree with results found in other studies using AMF and/or compost under saline conditions. Quinoa plants treated with AMF and/or compost accumulated more sugar content during the salt stress exposition, likely to maintain high hydration as well as turgor level, which maintains the main physiological activities under saline conditions. In addition, the carbohydrate accumulation in saline conditions reduced the osmotic potentials in host cells. The sugar content in inoculated and amended quinoa was higher than in non-treated plants. Under saline conditions, the higher content of soluble proteins in AMF-treated plants grown in soil amended with compost may explain the strengthening of the non-enzymatic antioxidant defense system by AMF and compost.

Similarly, Li et al. (2019) and Toubali et al. (2020) recorded that the evaluated antioxidant enzymes (CAT, POX, and PPO) were enhanced during the application of salt stress compared to the control. Indeed, stress-induced ROS accumulation is counteracted by several complexes and processes, such as the enzymatic antioxidant defense system (Devireddy et al. 2021; Hussain et al. 2018). In our study, the significant increase in the activity of these enzymes detected in quinoa plants is presumed to limit cellular damage and improve the antioxidant capacity of the plant to defend itself against stress. In addition, the application of AMF and compost decreased the activity of the antioxidant enzymes PPO and POD, increasing the resistance of quinoa to salt stress.

Our study showed the improvement of soil physicochemical properties at harvest. Under salt stress, AMF and compost application mainly increased soil quality, such as OM and P content, compared to the control treatment. After compost application, the decrease in soil pH can be attributed to the mineralization of organic matter and CO₂ release (Huang and Chen 2009). Significant increases in available OM and P, especially with the application of compost alone or in combination with AMF, were noted and resulted from the high content of OM and P available in the compost. Similar results were recorded by Gaiotti et al. (2017).

5 Conclusion

The application of salinity, particularly the high concentration (300 mM NaCl), caused depressive effects on the growth, physiological, and biochemical mechanisms of quinoa plants. However, the application of native biofertilizers, especially the dual combination of arbuscular mycorrhizal fungi and compost, significantly improved the growth, physiological, biochemical, and tolerance of the host plants to salt stress. The comparison of both varieties revealed that Titicaca showed less reduction in shoot height, root elongation, and seed dry weight. In addition, the biostimulants application exhibited higher activities of antioxidant enzymes, including catalase, peroxidase, and polyphenol oxidase, suggesting that Titicaca was more tolerant to salinity than Puno. Based on these results, the quinoa Titicaca genotype can be successfully cultivated under saline soils.

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Data Availability Not applicable.

Declarations

Conflict of Interest The authors declare no competing interests.

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