



Soil Selenium Addition for Producing Se-Rich Quinoa and Alleviating Water Deficit on the Peruvian Coast

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Abstract

In Peru, quinoa is cultivated in agricultural systems exposed to abiotic stresses. Selenium biofortification enriches crops and enhances their defense system against water deficit. This study aimed to determine the effect of soil Se application for enhancing Se content in quinoa grains and plant tolerance under water deficit. Selenium rates were applied at 0, 0.25, 0.5, 1.0, and 2.0 mg kg⁻¹, under irrigated and water-deficit conditions. Gas exchange, SPAD index, Se content, and proline were quantified in leaves. Dry mass was recorded in grains and shoots, whereas Se content, free amino acids, total proteins, Se and macronutrient accumulation, and Se-recovery were quantified only in grains. The water deficit diminished the transpiration rate and grain dry mass, but it increased SPAD index. The grain dry mass was increased at 0.25 and 0.5 mg kg⁻¹ Se whereas it was reduced at 1.0 and 2.0 mg kg⁻¹ Se. Selenium content in grains and leaves and Se accumulation by grains increased concerning Se rates in soil water conditions. Under water deficit, the best photosynthetic rate, instantaneous carboxylation efficiency, water use efficiency, shoot dry mass, and total proteins were at 0.5 mg kg⁻¹ Se. In grains, free amino acids and N, P, and K accumulations were maximum at 2 and 0.25 mg kg⁻¹ Se, respectively. Selenium biofortification enriched quinoa grains with selenium. The antioxidant non-enzymatic activity might be one of water deficit tolerance mechanisms promoted by Se on quinoa var INIA Salcedo and would be enhanced mainly at 0.5 mg kg⁻¹ Se.

Keywords Biofortification · *Chenopodium quinoa* · Drought mitigation · Plants' defense system · Antioxidant non-enzymatic activity

1 Introduction

Selenium (Se) is one of the essential micronutrients for humans and animals and has a key role in the functioning of biological processes. Selenium is present in the active centers of antioxidant enzymes, which in turn maintain the integrity of components and membranes cell. Likewise, Se reduces the risk of cardiovascular diseases and cancer, promotes proper thyroid hormone metabolism, improves mental disorders, and strengthens the immune system (Hossain et al. 2021; Kieliszek 2019; Sarwar et al. 2020). Although Se is associated with relevant biological processes in animals,

many staple foods worldwide contain insufficient Se levels for the human diet. Low Se intake causes human health disorders such as chronic degenerative diseases (Das et al. 2017; Hossain et al. 2021; Kieliszek 2019; Lopes et al. 2017). Thus, the development of strategies to increase the level of Se in the diet is crucial to avoid serious human illnesses. For instance, biofortification represents a sustainable strategy to enhance the nutritional quality of plant-based foods (Hossain et al. 2021).

In the field, the agronomic biofortification is achieved increasing the Se bioavailability for crops growing on Se-deficient soils. Biofortification has been successfully used to ensure adequate Se intake to reduce Se deficiency in humans. This is particularly important since plants are one of the main sources of available Se, i.e., Se in plants tends to be present in organic forms, which have greater bioaccessibility (Hossain et al. 2021; Raina et al. 2021; Sarwar et al. 2020; Zhou et al. 2021). Research shows that this strategy enriches a wide range of crops grown in Se-deficient soils,

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such as rice (Andrade et al. 2018; Lessa et al. 2019), wheat (Lara et al. 2019), potato (de Oliveira et al. 2019), common bean (Vega-Ravello et al. 2022), coffee (Mateus et al. 2021), radish (Cipriano et al. 2022b), and sorghum (Cipriano et al. 2022a). Moreover, selenate represents the best source for biofortification, mainly when Se is applied in oxidic soils due to its higher availability compared with selenite (Ahmad et al. 2021; Araujo et al. 2020; Cipriano et al. 2022b; dos Santos et al. 2022; Ekanayake et al. 2015).

Overall, the lack of water affects crop productivity by reducing photosynthesis and plant growth. It has become a latent threat to food security since it alters the food chain. Research in crop management has produced new technologies to deal with the low water availability; such technologies have been developed based on the study of the plant water tolerance mechanisms. One of the most widely used ways to cope with this adverse condition is enhancing the plant defense system through the activation of the enzymatic and non-enzymatic antioxidant systems (Farooq et al. 2012; Hussain et al. 2019; Nahar et al. 2016; Sharma et al. 2019).

Although Se is not an essential element for higher plants, Se is beneficial to plant's physiological and metabolic functions. For instance, Se can trigger the plant's defense system and stimulate the tolerance level of plants to abiotic stress such as drought. Likewise, Se decreases water loss, regulates photosynthesis, and improves biomass production through activities of antioxidant enzymes and non-enzymatic antioxidants. These reduce the production and accumulation of reactive oxygen species (ROS) (Adnan 2020; Chauhan et al. 2019; Hawrylak-Nowak et al. 2018; Hossain et al. 2021; Lanza and Reis 2021; Sarwar et al. 2020). Several studies on water deficit have demonstrated that there is a positive effect of Se on crops such as olive (Proietti et al. 2013), wheat (Nawaz et al. 2017), maize (Bocchini et al. 2018), rice (Andrade et al. 2018), sweet potato (Huang et al. 2020), and common bean (Vega-Ravello et al. 2022).

Quinoa is a grain with high nutritional value due to its quality and protein content, even higher than that of many cereals. It was the main food of ancient cultures of the Andes. This Andean superfood with many health benefits has conquered the world market, and greater production areas and higher yields are expected to take place to supply the growing demand (FAO/RLC 2011; Filho et al. 2017; Jacobsen et al. 2003b; Patel 2015). In addition, the genetic diversity of the crop and its great adaptability to adverse conditions have allowed its production in several ecosystems (FAO/RLC 2011; Hinojosa et al. 2018; Jacobsen et al. 2003a; Saddiq et al. 2021). This quinoa's growth plasticity and the nutritional quality of its grains are potential characteristics to sustain food security worldwide. Thus, Food and Agricultural Organization (FAO) declared 2013 as the

“International year of quinoa” (Patel 2015). On the other hand, in 2005, the Peruvian government declared several Andean crops, including quinoa, as National Natural Heritage, promoting their genetic material conservation and production chain activities (El Peruano 2005). Additionally, international interest in this natural food of high nutritional value encouraged Peru to establish on June 30th of every year as the “National Day of Andean grains,” which also includes amaranth, cañihua, and tarwi (El Peruano 2013), as previously reported by Jacobsen et al. (2003b). Peru is the world leader in quinoa production and exports (FAOSTAT 2022). Quinoa cultivation is mechanized and has surface irrigation (Gómez and Aguilar 2016); however, it should still improve because the lack of water on the Peruvian coast is the main constraint for agricultural production (INEI 2013). Therefore, some lots are shifting to drip irrigation. Thus, government policies should be addressed toward implementing technical irrigation and other technologies to increase water use efficiency or plant tolerance to water deficit. In this context, the addition of Se could be one possibility for mitigating the water deficit in the region.

Research on Se content in quinoa grains is not widely performed. One study reported values of Se below the detection limit (Nascimento et al. 2014), 0.039 (Ruales and Nair 1993), and 33 mg Se per kg dry mass (Al-anbari and Al-taweel 2019) in quinoa grains; the first two are considered low. To the best of our knowledge, there are no previous studies on Se application for biofortifying quinoa grains nor assessing how Se in the plant may contribute to its development in low soil water availability conditions.

Given the nutritional importance of the balanced supply of all essential amino acids by quinoa grains for humans and the water resource limitation for its production in Peru, we developed the present study to Se-enrich quinoa grains, food with high nutritional properties, and improve the quinoa tolerance to water deficit, mainly.

We stated that soil Se application enhances the quality nutrition of quinoa grains and the quinoa crop's capacity to tolerate water deficit. In addition, our results will contribute to improving population health in Peru, at some extent. The agronomic biofortification strategy has been successful reducing the high anemia rate in children under 3 years old through the iron genetic biofortification of the potato, one of the most widely consumed staple crops (PMA 2010). However, to the best of our knowledge, there are no studies evaluating the agronomic biofortification in quinoa. In this context, our study aims to increase Se content in Andean grains widely consumed in Peru to contribute to the struggle against hidden hunger and determine Se's physiological and metabolic benefits on quinoa crop under water deficit, even more when water shortage is a latent threat to food security.

2 Material and Methods

2.1 Soil Description and Experimental Design

The pot study was carried out in a greenhouse located at Soil Science Department, Universidad Nacional Agraria La Molina—UNALM, La Molina, Lima, Peru. The soil was collected from the 0–20-cm depth in an Entisol profile from alluvial plain located on the campus of UNALM (12° 04' 54.5" S latitude, 76° 57' 08.3" W longitude, 239 m above sea level), air-dried, and sieved through a 2-mm mesh. Next, a composite soil sample was analyzed following methodologies suggested by Ministry of Agriculture and Irrigation (MINAGRI) of Peru (Bazán 2017) and soil properties are shown in Table 1. Total soil Se content was 0.26 mg kg⁻¹ and was determined following to the 3051A method of the United State Environmental Protection Agency (USEPA 2007).

Pots were filled with 7 kg of soil. Fertilization for N, P, and K followed the recommendation of Malavolta (Malavolta 1981), being applied 210, 200, and 150 mg kg⁻¹ of N, P, and K, respectively. Nitrogen and K rates were split to three and two applications, respectively, and P rate was added at once before transplanting. Selenium rates—0.00, 0.25, 0.50, 1.00, and 2.00 mg kg⁻¹—at two soil water conditions (irrigated and water deficit) were applied in the soil as sodium selenate (Na₂SeO₄, Sigma-Aldrich, Saint Louis, MO, USA) after transplanting. Therefore, the experiment was set up as a completely randomized design in a 5 × 2 factorial scheme (5 Se rates and 2 soil water conditions) with four replicates, totaling 40 experimental plots.

Chenopodium quinoa W. var INIA Salcedo seeds, an early Peruvian variety adapted to the Altiplano, inter-Andean valleys, and coast, were sown seedling tray and then transplanted to each pot. Six seeds were sown per cell and thinned 10 days later at one seedling in each cell.

2.2 Establishment of Water Deficit

Germination-emergence and grain-filling stages are critical periods for water deficit because of determining productivity (Gómez and Aguilar 2016). All pots were irrigated to reach soil moisture close to water holding capacity (WHC) from the beginning of the experiment until the grain-filling stage began. Therefore, water deficit treatments were differentiated

at 59 days after transplanting (DAT), when the quinoa plants started the grain-filling stage. These treatments were subjected to water deficit for 5 days, where water deficit was assessed by the fraction of transpirable soil water (FTSW) following procedure carried and described by Vega-Ravello et al. (2022). Then, water deficit treatments were re-irrigated to WHC.

2.3 Gas Exchange and SPAD Chlorophyll Index Measurements

Gas exchange and SPAD chlorophyll index were assessed on the last day of the water deficit (64 DAT) between 8:00 and 11:00 a.m. on the youngest fully expanded leaf. A portable photosynthesis system (CIRAS-3, PPSsystem, Hitchin, UK) was used to measure stomatal conductance (g_s —mol H₂O m⁻² s⁻¹), transpiration rate (E —mmol H₂O m⁻² s⁻¹), and photosynthetic rate (A —μmol CO₂ m⁻² s⁻¹). Instantaneous carboxylation efficiency ($E_i C_i$ —mol air⁻¹) and water use efficiency (WUE —μmol CO₂ mmol⁻¹ H₂O) were estimated through to ratio A/C_i (internal CO₂ concentration in the substomatal chamber) and A/E , respectively. CIRAS-3 was configured to density of the photosynthetically active photon flux of 1000 μmol m⁻² s⁻¹, vapor pressure deficit of 2.66 kPa, pump flow of 500 μmol s⁻¹, and the block temperature of 25 °C.

The SPAD chlorophyll index was assessed using a portable chlorophyll meter (SPAD-502, Konica-Minolta, Japan). The value recorded was the average of three regions of each leaf (basal, medium, and apical region). Also, in each leaf region, three measures were obtained to calculate the average value per region.

2.4 Biometric Measurements and Chemical Analysis

Quinoa (*C. quinoa*) plants were grown during 150 days, and at the end of harvest maturity with a grain moisture content of ~12–14% (Gómez and Aguilar 2016), plant shoots were harvested and separated into leaves, stems, and grains, which were dried in a forced-air oven at 70 °C for 48 h. Then, dry mass of leaves and grains were milled to be digested in nitric acid according to the USEPA 3051A method (USEPA 2007), with focus to determine P, K, and Se contents. Phosphorus and K contents were measured by ICP-OES, whereas Se content was determined by atomic absorption spectrometry with graphite furnace atomization (GFAAS)

Table 1 Soil physical and chemical properties

pH _(1:1 in water)	EC _(1:1) (dS m ⁻¹)	SOM ^a (%)	P ^b (mg kg ⁻¹)	K ^b (mg kg ⁻¹)	CEC ^c (cmol _c kg ⁻¹)	Ca ^d	Mg ^d	K ^d	Na ^d	Clay (%)	Silt	Sand
8.09	0.83	1.15	21.4	379	14.88	12.06	1.57	0.74	0.51	32	30	38

^aSOM soil organic matter, ^bAvailable values, ^cCEC cation exchange capacity, ^dExchangeable values

(AAAnalyst™ 800 AAS, Perkin Elmer). On the other hand, nitrogen content was determined by digestion with sulfuric acid and titration by the Kjeldahl method (Malavolta et al. 1997). The QA/QC protocol for Se analyses was assured with the addition of two standard/certified reference materials—White Clover-BCR402 (Institute for Reference Materials and Measurements—IRMM, Geel, Belgium) and Peach Leaves-SRM 1547 (National Institute of Standards & Technology—NIST, Gaithersburg, MD, USA)—in each batch of digestion, with Se recovery values being close to 87%.

Nutrient accumulation in grains is expressed as the total amount of nutrient found in grains and was obtained by multiplying the nutrient content and the dry mass of grains. Se-recovery is Se use efficiency by quinoa grain. It was calculated as the percentual relationship between the amount of Se accumulated by grains and the amount of Se applied to the soil of the same treatment (Vega-Ravello et al. 2022).

2.5 Biochemical Analysis

Dry mass of quinoa grains and leaves was used for biochemical analysis. Proline content was analyzed in leaves, and free amino acid and total protein contents were quantified in grains.

Proline was extracted from leaves, 0.20 g of ground dry mass was weighed, and 10 mL of 3% sulphosalicylic acid was added. First, the mixture was shaken with a VORTEX and then with a rotary shaker at 160 RPM for 1 h, centrifuged at 5000 RPM for 10 min, and the supernatant was collected to quantify proline content (Bates et al. 1973).

For extraction of amino acids and proteins, 0.20 g of ground dry mass of grains was homogenized in 10 mL of potassium phosphate at pH 7.8 (extraction buffer solution), shaken with a VORTEX, placed at 40 °C water bath for 30 min, and centrifuged at 5000 RPM for 10 min, and the supernatant was collected for further assessments. Aliquots from extracted solution were used to determine free amino acids (Yemm and Cocking 1955) and total proteins (Bradford 1976).

2.6 Statistical Analysis and Data Processing

Results were analyzed using programming language R (R Core Team 2022). Statistical differences were determined by analysis of variance (ANOVA), and treatment means were compared by Tukey's test at 5% probability. Also, the combined effect of treatments on variables studied was evaluated through principal component analysis (PCA) of individuals. The graphics were created, and regression models were fitted using the SigmaPlot for Windows software, version 11.0 (Systat Software Chicago, IL, USA).

3 Results

3.1 Gas Exchange and SPAD Chlorophyll Index

Water deficit significantly modified ($p \leq 0.05$) gas exchange behavior, irrespectively of soil Se addition. More specifically, water deficit reduced stomatal conductance (g_s), transpiration rate (E), photosynthetic rate (A), instantaneous carboxylation efficiency (E_iC), and water use efficiency (WUE) (Fig. 1a, b, c, d, e) and increased SPAD chlorophyll index (Fig. 1f).

Under water deficit, Se application did not improve g_s ; however, a slight tendency to increase was observed at a rate of 0.5 mg kg⁻¹ Se (Fig. 1a). Photosynthetic rate and E_iC were enhanced by Se supply and were maximum at this same rate (Fig. 1c, d). Likewise, rates of 0.5 and 1 mg kg⁻¹ Se showed the highest WUE ; nevertheless, only when Se was added at 1 mg kg⁻¹ the WUE under water deficit was higher by 57% compared to its irrigated treatment (Fig. 1e). On the other hand, E drastically reduced by 69% (Fig. 1b), and the SPAD chlorophyll index increased by 7% (Fig. 1f) due to the lack of water, both in relation to the irrigated condition.

3.2 Production of Dry Mass

Grain dry mass production changed due to the studied factors (Se rates and soil water conditions); however, there was no significance for the interaction between those two factors ($p \leq 0.05$) (Fig. 2a, b). Conversely, shoot dry mass was affected ($p \leq 0.05$) by the interaction of these factors (Fig. 2c).

The water deficit reduced grain dry mass by 8% with respect to the irrigated condition (Fig. 2a). At Se rates, grain dry mass production tended to increase at 0.25 mg kg⁻¹ and was maximum at 0.5 mg kg⁻¹. Conversely, at Se rates of 1 and 2 mg kg⁻¹, grain dry mass reduced by 10 and 6%, respectively, when compared with control (Fig. 2b).

Selenium addition did not influence shoot dry mass production in irrigated treatments. However, under water deficit, shoot dry mass increased when Se was applied at assessed rates, being the maximum value of shoot dry mass found at 0.5 mg kg⁻¹ (Fig. 2c).

3.3 Proline Content in Leaves, Free Amino Acid, and Total Protein Contents in Grains

Proline content in leaves, free amino acid, and total protein contents in grains were significantly affected ($p \leq 0.05$) by the interaction of soil water condition and Se rates (Fig. 3). Leaves from both systems, irrigated and water deficit, exhibited similar proline contents with increasing Se supply. At

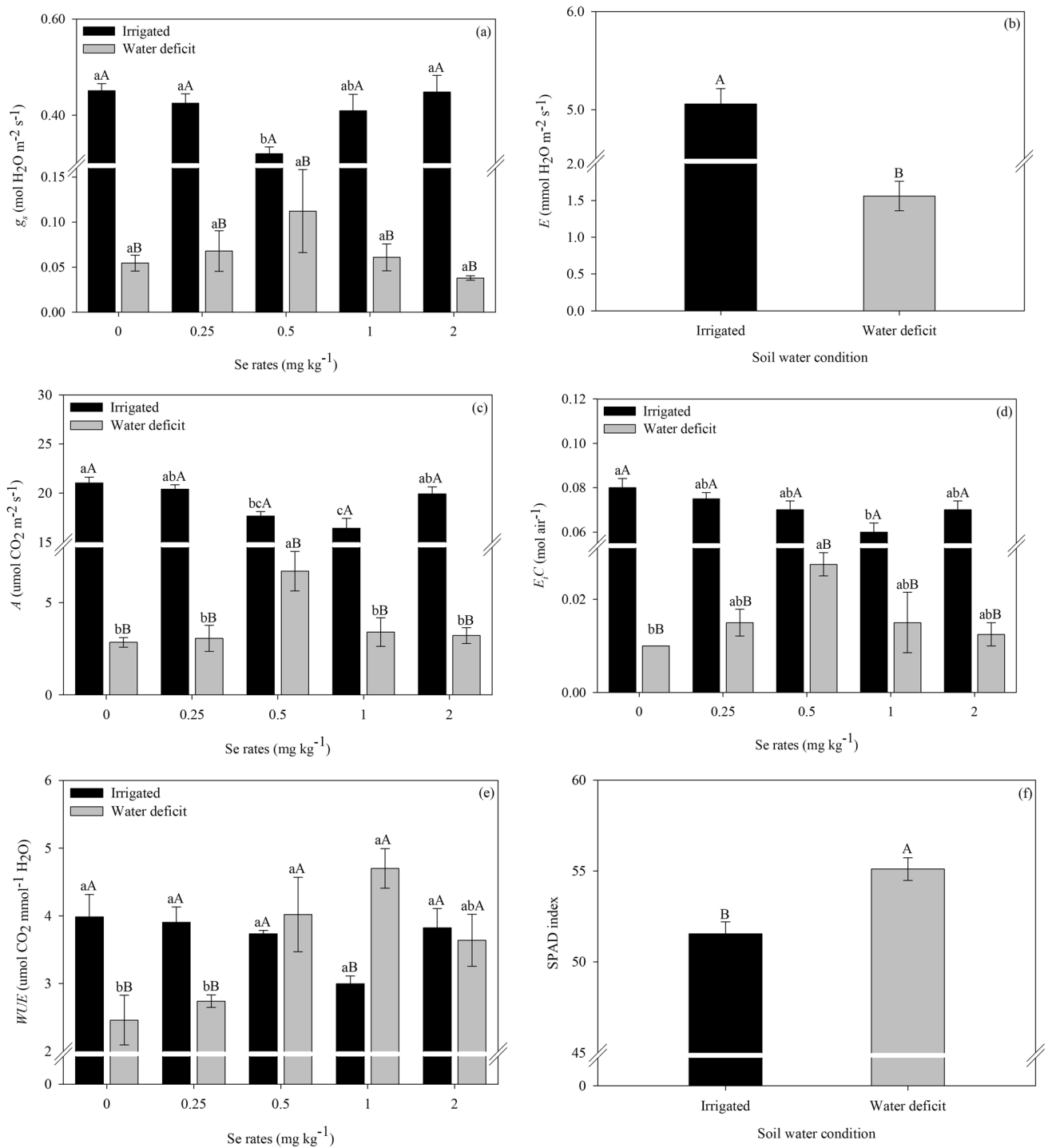


Fig. 1 Stomatal conductance— g_s (a), transpiration rate— E (b), photosynthetic rate— A (c), instantaneous carboxylation efficiency— E_iC (d), water use efficiency— WUE (e), and the SPAD index (f) in leaves of quinoa after water deficit. Uppercase letters compare the means of

soil water conditions at each Se rate, and lowercase letters compare the means of Se rates at each soil water condition, according to Tukey's test (at 5% probability). Vertical bars indicate standard errors of average values: (a), (c), (d), and (e) $n=4$, and (b) and (f) $n=20$

water deficit, the lowest Se rates (0.25 and 0.5 mg kg⁻¹) tended to maximize the proline content in leaves, which progressively returned to the control level at the highest Se rates (1 and 2 mg kg⁻¹), without showing statistical differences.

Comparing soil water conditions within the same Se rate, proline content was different only when Se was not added (control), being 32% lower under water deficit than the value reported to irrigated treatment. Although the statistic

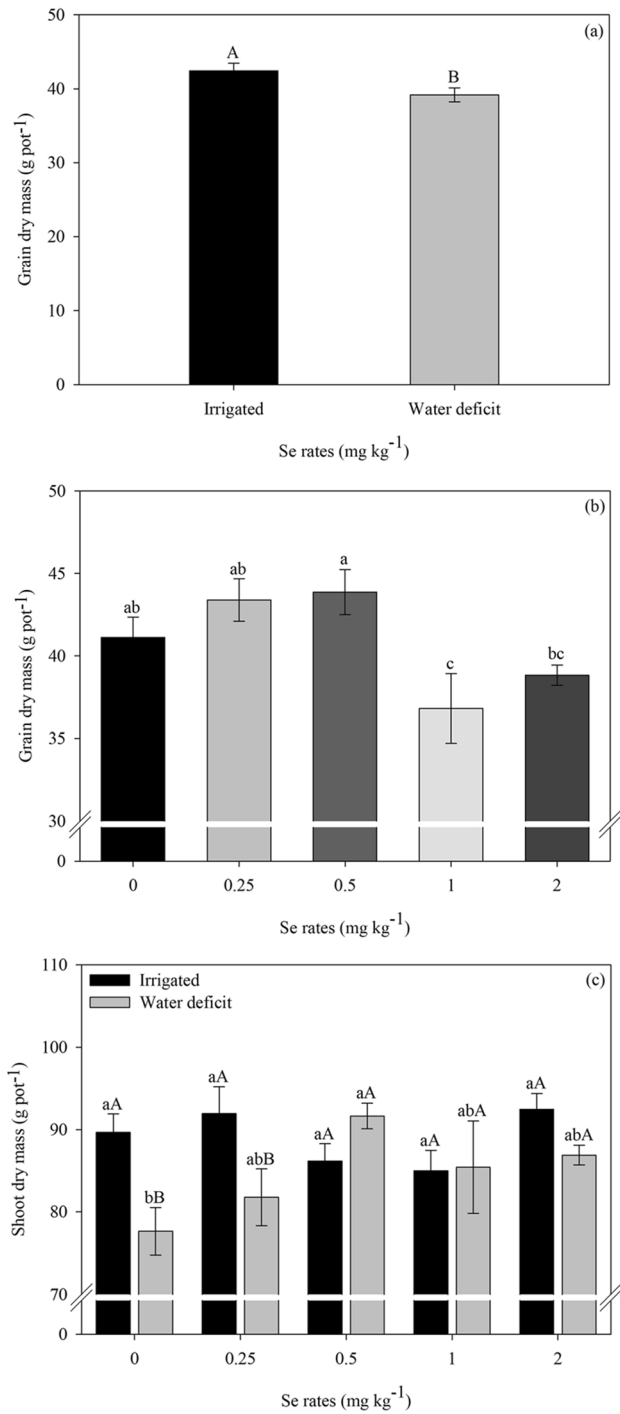


Fig. 2 Production of grain dry mass (a and b) and shoot dry mass (c) of quinoa. Uppercase letters compare the means of soil water conditions at each Se rate, and lowercase letters compare the means of Se rates at each soil water condition, according to Tukey’s test (at 5% probability). Vertical bars indicate standard errors of average values: (a) $n=20$, (b) $n=8$, and (c) $n=4$

indicated that Se did not support proline increases at water deficit treatments, these proline contents were equal to their irrigated treatments (Fig. 3a).

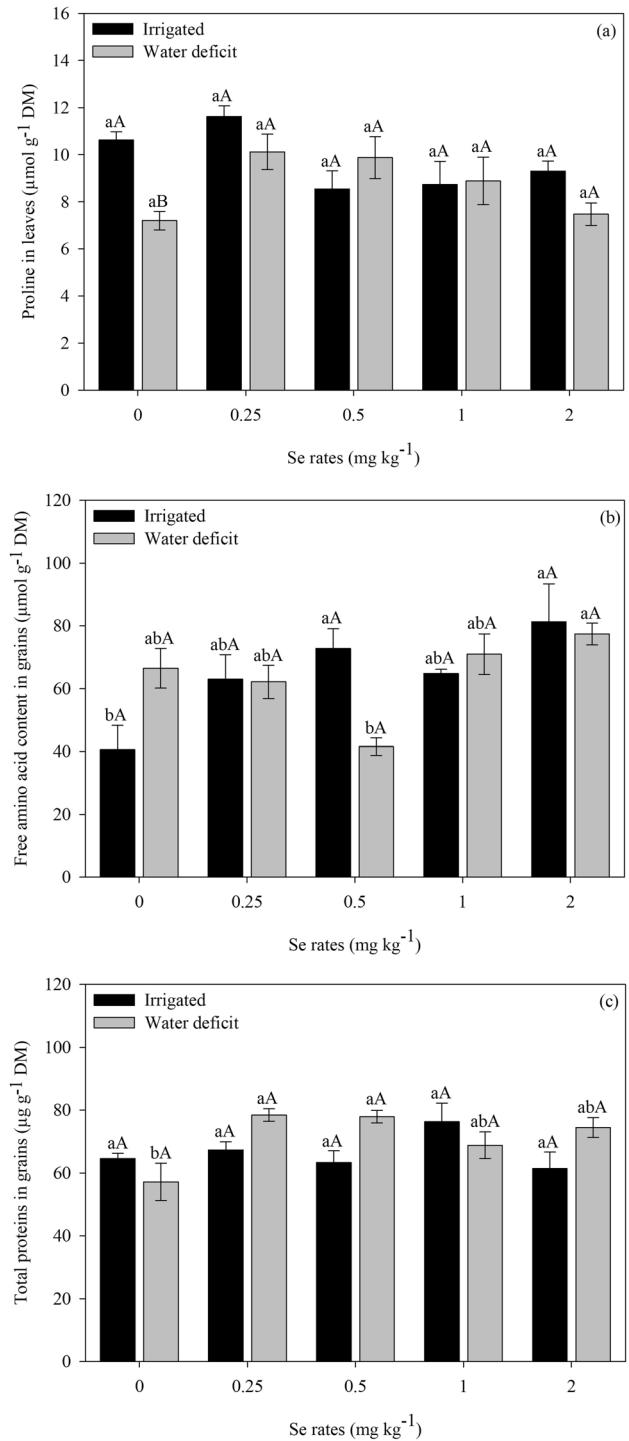


Fig. 3 Proline content in dry mass (DM) of quinoa leaves (a), free amino acid (b) and total protein (c) contents in dry mass (DM) of quinoa grains. Uppercase letters compare the means of soil water conditions at each Se rate, and lowercase letters compare the means of Se rates at each soil water condition, according to Tukey’s test (at 5% probability). Vertical bars indicate standard errors of average values ($n=4$)

At irrigated treatments, Se addition enhanced free amino acid content in grains, reaching their maximum values at Se rates of 0.5 and 2 mg kg⁻¹ (Fig. 3b); however, it did not modify total protein content in grains (Fig. 3c). Under water deficit treatments, the highest free amino acid content in grains was found at the highest Se rate (2 mg kg⁻¹) (Fig. 3b); while protein formation in grains was favored by Se rates of 0.25 and 0.5 mg kg⁻¹, slightly decreasing at Se rates of 1 and 2 mg kg⁻¹ (Fig. 3c).

3.4 Selenium Content and Accumulation, and Se Recovery Percentage

Selenium content in grains (Fig. 4a), Se accumulation, and Se-recovery by grains (Fig. 5) were significantly affected

($p \leq 0.05$) by the interaction of soil water conditions and Se rates; whereas, Se content in leaves was only influenced ($p \leq 0.05$) by Se rates (Fig. 4b).

Selenium content in grains and leaves (Fig. 4) and Se accumulation by grains (Fig. 5a) were linearly increased upon increasing Se rates in both soil water conditions. In contrast, the percentage of Se-recovery by grains as a function of Se addition followed different patterns depending on soil water conditions. Under irrigated treatments, this variable also increased with the addition of ascending Se rates. However, at water deficit, Se-recovery by grains fitted to a quadratic model. In this case, the maximum value for Se-recovery by grains was obtained with Se addition at 1.44 mg kg⁻¹ and was 2%, with this value being decreased afterwards at higher Se rates (Fig. 5b).

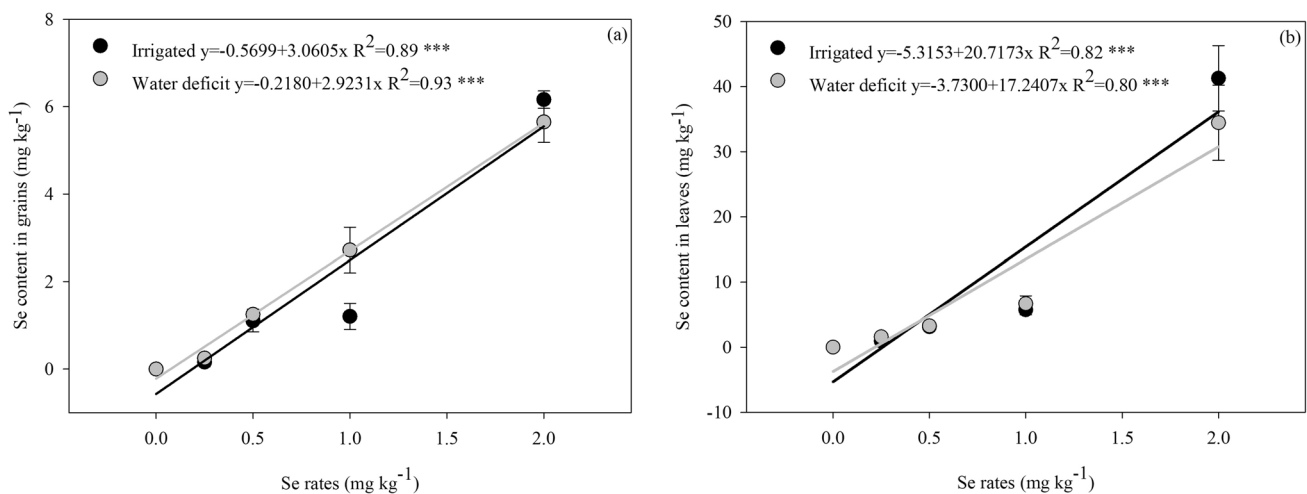


Fig. 4 Selenium content in grains (a) and leaves (b) of quinoa in response to Se rates and soil water conditions. The vertical bars indicate standard errors of average values ($n = 4$). Statistically significant differences are indicated: ***, $p \leq 0.001$

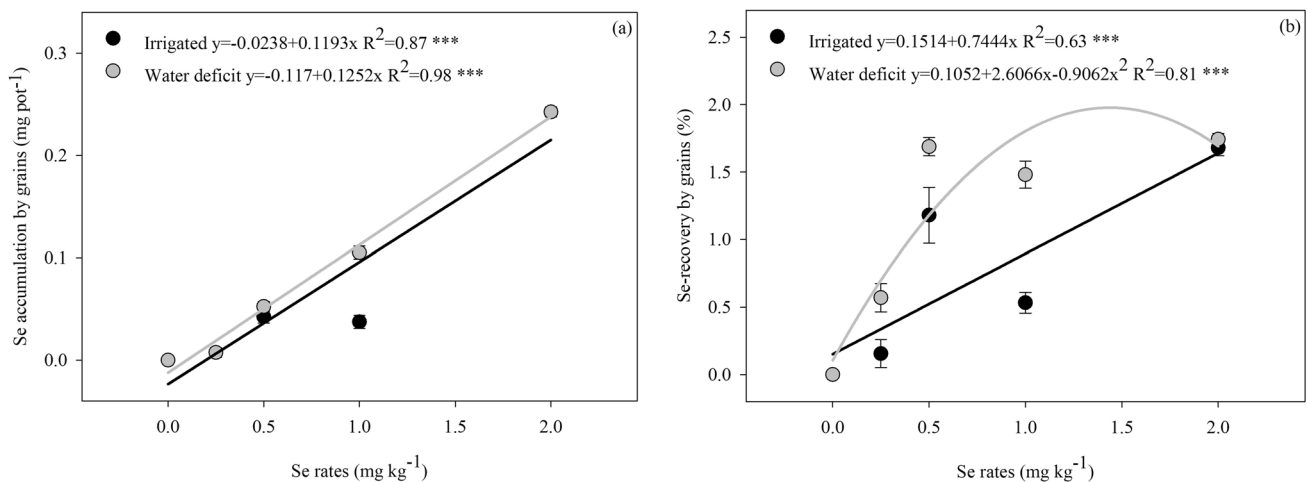


Fig. 5 Selenium accumulation by grains (a) and selenium recovery by grains (b) of quinoa in response to Se rates and soil water conditions. Vertical bars indicate standard errors of average values ($n = 4$). Statistically significant differences are indicated: ***, $p \leq 0.001$

3.5 Nutrient Accumulation

Nitrogen, P, and K accumulation by grains was modified ($p \leq 0.05$) by the interaction of Se rates and soil water conditions (Fig. 6). Data of N, P, and K accumulation by grains as a function of Se rates were fitted to quadratic models under the two assessed soil water conditions. As a general trend, in the models for irrigated treatments, the accumulations of these three nutrients increased, reaching their maximum values at rates very close to 1 mg kg⁻¹ Se. Selenium applications above these Se rates gradually decreased their nutrient accumulations in the grain. At the water deficit models, N, P, and K accumulations decreased until values were slightly above 1 mg kg⁻¹ Se; after these rates, their accumulations grew (Fig. 6).

Regarding Se addition, quinoa grains in irrigated treatments contained higher amounts of N at 0.25 to 1 mg kg⁻¹ Se (Fig. 6a) and of P and K at 0.25 mg kg⁻¹ Se (Fig. 6b, c). At the same time, 0.25 mg kg⁻¹ Se promoted the highest accumulations of these nutrients in water deficit (Fig. 6).

At water deficit treatments, when their controls were compared with the irrigated treatment controls, accumulation of N was 20% higher (Fig. 6a), P was similar (Fig. 6b), K was 15% lower (Fig. 6c). Nitrogen and K accumulation maintained the levels of their irrigated treatments at 0.25 and 2 mg kg⁻¹ Se (Fig. 6a and c). Nitrogen at Se rates of 0.5 and 1 mg kg⁻¹ decreased 12 and 18%, respectively, compared with their irrigated treatments (Fig. 6a), while K had more drastic drops, 36 and 29%, respectively (Fig. 6c). Concerning P accumulation, it was 15% higher, 15 and 13% lower, and similar to their irrigated treatments at Se rates of 0.25, 0.5, 1, and 2 mg kg⁻¹, respectively (Fig. 6b).

3.6 Principal Component Analysis (PCA) of Individuals

Principal component analysis (PCA) for individual revealed that two principal components were representative of the interaction among evaluated variables and accounted for 54.6% of the total variance (Fig. 7). The first component (Dim1) explained 30.7% variation, while the second component (Dim2) explained 23.9%. In Dim1 ($|cor| > 0.5$), major variance was contributed by A , g_s , E , E_iC , grain dry mass, Se content in grains and leaves, Se accumulation and Se-recovery by grains, P and K accumulation by grains, and proline content in leaves. In Dim2 ($|cor| > 0.5$), major variance was contributed by A , g_s , E , WUE , E_iC , shoot dry mass, Se content in grains and leaves, and Se and N accumulation by grains.

The effect of treatments on variables distinguished six groups by confidence regions at a 95% confidence level. At the same time, the distance among the ellipses allowed the identification of two completely different groups among the

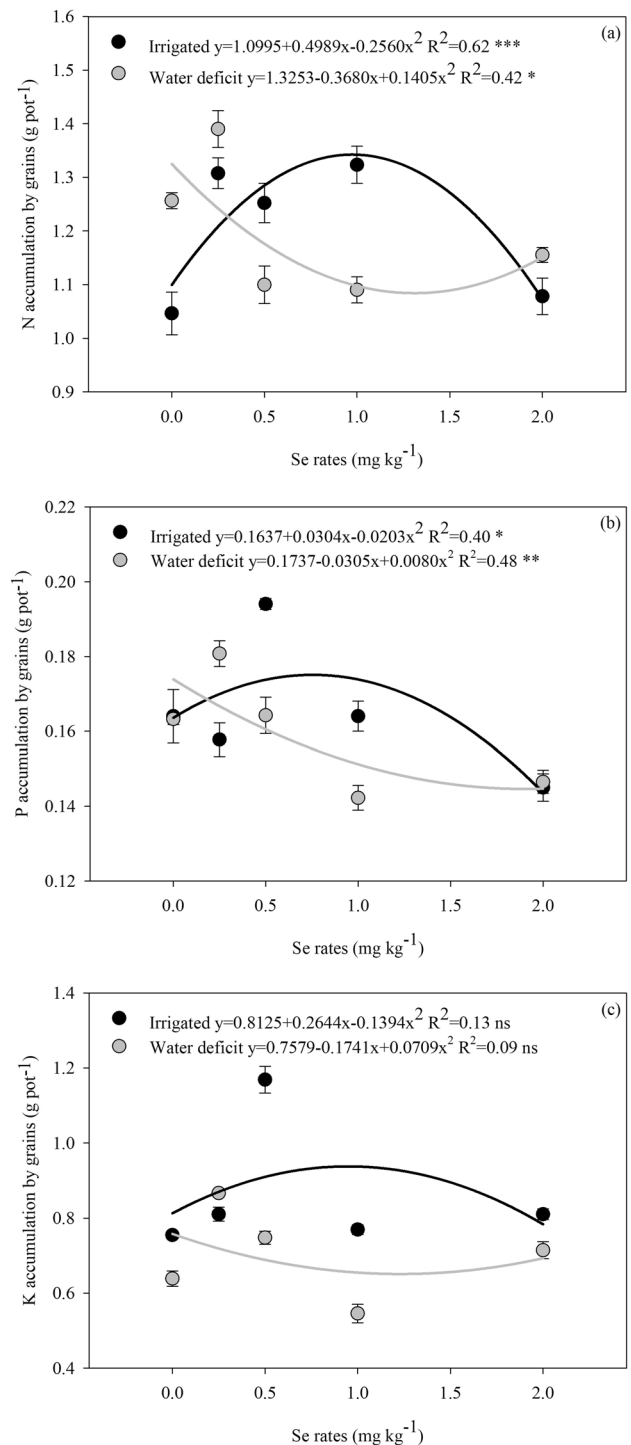
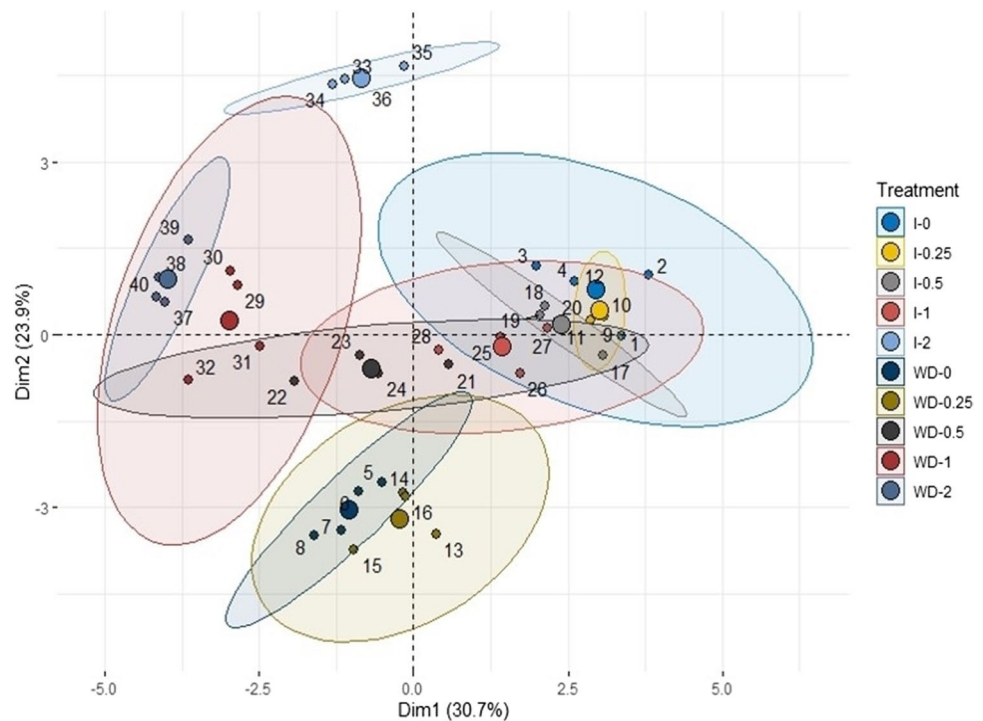


Fig. 6 Nitrogen accumulation (a), phosphorus accumulation (b), and potassium accumulation (c) by quinoa grains in response to Se rates and soil water conditions. Vertical bars indicate standard errors of average values ($n=4$). Statistically significant differences are indicated: ns, *, **, ***, $p \leq 0.001$

irrigated treatments (from I-0 to I-1 and I-2 mg kg⁻¹ Se) and two more groups among the water deficit treatments (from WD-0 to WD-0.25 and from WD-1 to WD-2 mg kg⁻¹ Se).

Fig. 7 PCA graph of individuals. Circles of the same color represent the treatments of soil water conditions (irrigated (I) and water deficit (WD)) in each Se rate (0.00, 0.25, 0.50, 1.00, and 2.00 mg kg⁻¹)



On the other hand, the interception of the ellipses indicated similarity in the behavior of the water deficit treatment at 0.5 mg kg⁻¹ Se with the groups composed by the irrigated treatments from 0 to 1 mg kg⁻¹ Se and water deficit treatments from 0 to 0.25 and from 1 to 2 mg kg⁻¹ Se. Also, irrigated treatment at 1 mg kg⁻¹ Se exhibited the same behavior, except with the water deficit treatment at 2 mg kg⁻¹ Se because they are mutually exclusive.

4 Discussions

The tissue elasticity and growth plasticity of quinoa permit it to tolerate water deficit (Hinojosa et al. 2018). In our study, the decrease in g_s (Fig. 1a), E (Fig. 1b), A (Fig. 1c), and EiC (Fig. 1d) reflected moderate (0.5 mg kg⁻¹ Se) and severe (0, 0.25, 1, and 2 mg kg⁻¹ Se) water deficits (Flexas and Medrano 2002) and the sensitivity of quinoa leaf gas exchange to water deficit which suggests an accumulation of abscisic acid (ABA) as a promoter to rapid stomata closure (Jacobsen et al. 2009). This is a feature of isohydric properties of quinoa used to maintain its leaf hydric potential (Killi and Haworth 2017). Likewise, inhibition of photosynthesis expressed in the drop of A (Fig. 1c) and lower shoot dry mass formation (Fig. 2c) at low water availability involved the reduction of WUE (Fig. 1e) since moderate and severe water deficits obtained have reduced the contribution of photosynthesis and photorespiration, as indicated by Flexas and Medrano (2002).

Despite this adverse condition, the beneficial effects of the presence of low Se rates play important roles on the efficiency of the plant's photosynthetic metabolism since Se acts as an antioxidant (Adnan 2020; Hawrylak-Nowak et al. 2018; Lanza and Reis 2021; Raina et al. 2021; Sarwar et al. 2020) in quinoa plants (Khalofah et al. 2021). Our results have shown that low Se rates (0.25 and 0.5 mg kg⁻¹) regulated quinoa photosynthesis under water deficit to mitigate the impact of fixing less carbon. Carbon dioxide input tended to increase in quinoa leaves, and g_s reached its maximum concentration at 0.5 mg kg⁻¹ Se (Fig. 1a) since this Se rate enhanced its water deficit status, turning it into a moderate water deficit. This suggested that higher carbon was available, and EiC (Fig. 1d) was greater to enhance A (Fig. 1c) by increasing chlorophyll, as pointed out by Khalofah et al. (2021). In contrast, higher Se rates (1 and 2 mg kg⁻¹) modified the beneficial trend of lower Se rates since it behaved as a pro-oxidant, as referred by Khalofah et al. (2021). The toxic Se effect could be increasing the oxidative stress that altered the physiological and metabolic processes in the plant, such as the gas exchange reduction.

In addition, Se rate of 0.5 mg kg⁻¹ enhanced WUE (Fig. 1e) since the higher photosynthetic activity increased shoot dry mass production (Fig. 2c) with lower water availability. This influence extends at the Se rate of 1 mg kg⁻¹, where WUE is maximum. Although the shoot dry mass produced is slightly lower at this rate (Fig. 2c), the biomass per unit of water is higher. This behavior is similar to that of the genotypes tolerant to water deficit (Saddiq et al. 2021).

Water deficit increases oxidative stress which affects chlorophyll synthesis (Farooqi et al. 2020; Hussain et al. 2019). In contrast to our expectations, quinoa leaves under water deficit exhibited better SPAD chlorophyll index status, which could be attributed to a concentration effect (Bocchini et al. 2018) (Fig. 1f).

Quinoa grains accumulated lower dry mass in water deficit (Fig. 2a) than the grains from irrigated treatments. This observation might be in response to reduced photosynthetic activity, which was expressed in low gas exchange. On the other hand, dual role of Se indicated by Khalofah et al. (2021) was observed in the production of grain dry mass and shoot dry mass. The accumulation of grain dry mass in response to Se rates (Fig. 2b) was correlated with the gas exchange; at low Se rates, grain dry mass production was enhanced up to a Se rate of 0.5 mg kg^{-1} , after its accumulation was detrimental. Probably, low Se rates promote activities of antioxidant enzymes and non-enzymatic antioxidants to scavenge ROS and protect the integrity of cell membranes and ensure the continuity of photosynthesis, while high rates contribute to oxidation, as found by Khalofah et al. (2021).

Unlike the behavior of the accumulation of grain dry mass concerning Se rates, the production of shoot dry mass at water deficit increased at all Se rates (Fig. 2c), suggesting that high Se rates would not be phytotoxic to accumulation of dry mass in quinoa leaves and stems, as reported by Vega-Ravello et al. (2022).

Quinoa is an inherent water deficit-tolerant species that has morphological, physiological, and molecular mechanisms to respond against low water availability (Hinojosa et al. 2018). Moreover, proline accumulation is a mechanism that has a dual role as osmoprotectant and an osmolyte (Sadiq et al. 2021). Nevertheless, when comparing irrigated and water-deficient plant controls (Fig. 3a), the proline content found in leaves suggested that quinoa var INIA Salcedo does not use proline accumulation as the primary mechanism of water deficit tolerance, as reported by Hinojosa et al. (2018) for other quinoa varieties. On the other hand, proline content in quinoa leaves in response to soil Se addition did not vary markedly (Fig. 3a), opposite behavior to that found in maize (Bocchini et al. 2018) and in other study involving quinoa plants (Khalofah et al. 2021). Although no notable differences were found, the tendency to accumulate more proline at 0.25 and 0.5 mg kg^{-1} Se under water deficit (Fig. 3a) suggests that lower Se rates promote its increase and other mechanisms to cope with water deficit. Likewise, the increase of proteins by Se rates at water deficit (Fig. 3c) was indicative that proline contributed to maintain their integrity (Chauhan et al. 2019; Hawrylak-Nowak et al. 2018; Hayat et al. 2012; Khalofah et al. 2021; Lanza and Reis 2021; Nahar et al. 2016; Sarwar et al. 2020; Wrobel et al. 2020).

The increase of free amino acid content in quinoa grains in the treatment Se at 2 mg kg^{-1} rate (Fig. 3b), suggests that

the Se applied was incorporated by the plant and used in the formation of selenomethionine and selenocystine (Hossain et al. 2021; Sarwar et al. 2020). As we known, amino acids are precursors of proteins which maintain their vital functions in living species. However, under water deficit, the content of free amino acid was not strictly associated to total proteins as amino acids can also act individually as compatible solutes (Farooqi et al. 2020; Hussain et al. 2019). Thus, although the highest amount of amino acids (Fig. 3b) was found at the highest Se rate (2 mg kg^{-1}), the water deficit does not ensure that total amino acids are directed toward protein formation. On the contrary, the lowest Se rates (0.25 and 0.5 mg kg^{-1}) were the most efficient in protecting proteins, which is reflected in their higher amount of total proteins (Fig. 3c).

Even though proline and protein contents did not show notable differences concerning Se rates at water deficit, if there was an increase concerning the control, they could reflect their participation as osmolytes in the osmotic adjustment of quinoa. This behavior could also have enhanced gas exchange by maintaining the cell membranes' integrity.

We observed that the quinoa biofortification has increased in response to the Se application on the soil (Fig. 4). In this study, quinoa was grown in alkaline Peruvian soil ($\text{pH} = 8.09$), which enhanced the availability of selenate in the soil. However, the results obtained from the Se content in grains and leaves (Fig. 4) as well as the Se accumulation in grains (Fig. 5a), and the Se recovery percentage in grains (Fig. 5b) differ from results reported by other authors in similar experiments performed in rice (Andrade et al. 2018), potato (de Oliveira et al. 2019), common bean (Vega-Ravello et al. 2022), and radish (Cipriano et al. 2022b). The content of Se in the quinoa grains var INIA Salcedo was significantly higher than those reported by Nascimento et al. (2014) and Ruales and Nair (1993) and was lower than the study published by Al-anbari and Al-taweel (2019). Still, we must consider that it was a pot experiment. Prauchner (2014) highlighted that Se availability in soil, Se uptake, and the inorganic and organic flow of Se within the plant are influenced by plant species, plant morphology and phenology, chemical Se forms, soil conditions, and crop management. Ahmad et al. (2021) found that selenate was the most efficient inorganic form to increase Se in wheat grains in calcareous soil. Selenate is more water-soluble, predominates in neutral to higher pH soils, and enhances Se uptake and Se translocation using the same sulfate transporters (Hossain et al. 2021; Sarwar et al. 2020; Trippe and Pilon-Smits 2021).

Nitrogen, P, and K accumulations by quinoa grains (Fig. 6) reflected the impact of soil water conditions on plant metabolic and physiologic processes. Water deficit lessened the accumulation of N, P, and K in quinoa grains since low soil water content diminishes root activity and nutrient and water uptake, as reported by Farooqi et al. (2020). In addition, the reduction of gas exchange in leaves intensified oxidative

stress in quinoa which disturbed photosynthesis, reducing photosynthate formation and its redistribution to grains.

It is well known that adequate water supply promotes nutrient availability and uptake, and plant growth, while water deficit disturbed them. The lowest Se rate (0.25 mg kg^{-1}) increased the accumulation of N, P, and K in quinoa grains subjected to water deficit (Fig. 6). Selenium promotes antioxidant non-enzyme mechanisms to eliminate free radicals and maintain cell membrane integrity in water deficit by the production of proline and proteins. These mechanisms may explain our findings because we had high levels of proline and proteins under water deficit (Fig. 3a and c) as well. The expression of such mechanisms would enhance the photosynthetic process of quinoa. According to Zhou et al. (2020), plants uptake essential nutrients to increase their biomass and take up Se. Also, Schiavon et al. (2020) reported that Se promotes N assimilation in horticultural crops, and Bocchini et al. (2018) referred that Se increases K content in maize due to increased N metabolism.

Groups delimited by the ellipses (Fig. 7) allowed to consolidate the understanding of factor effects under study. Principal component analysis of individuals indicated that most of the variables from irrigated treatments at Se rates of 0, 0.25, 0.5, and 1 mg kg^{-1} (I-0, I-0.25, I-0.5, and I-1) presented similar behaviors. Likewise, water deficit treatment at 0.5 mg kg^{-1} Se (WD-0.5) may be considered as the most favorable rate to mitigate water deficit since its effect on quinoa showed similar behavior than quinoa subjected to irrigated treatments at rates of Se less than 2 mg kg^{-1} (I-2).

5 Conclusions

Our study found that Se biofortification enriches quinoa grains. The antioxidant non-enzyme activity mediated by the accumulation of proline and proteins seems to be one of the mechanisms involved for enhancing the tolerance effect of quinoa var INIA Salcedo. This effect was clearly observed at low rates of Se application under water deficit; the activation of the mechanism mentioned above may allow for regulating gas exchange, provide continuity to photosynthesis, and increase biomass production. The Se rate at 0.5 mg kg^{-1} seems to be the most promising for improving photosynthetic rate (*A*), instantaneous carboxylation efficiency (*EiC*), and shoot dry mass, whereas the addition of 0.25 mg kg^{-1} Se has shown to be favorable for increasing the accumulation of N, P, and K in grains.

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Author Contribution R Vega-Ravello: conceptualization, methodology, validation, formal analysis, investigation, data curation, writing—original draft, writing—review and editing. M Romero-Poma: methodology, validation, formal analysis, investigation, writing—original draft. C de Oliveira: supervision, writing—review and editing. L Guilherme: resources, supervision, writing—review and editing. G Lopes was the project advisor, planned, and supervised all phases of this research.

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Declarations

Conflict of Interest The authors declare no competing interests.

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