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Comparative Physiological and Biochemical Mechanisms of Salt Tolerance in Four Quinoa Cultivars Under Varying Salinity and Sodicity Levels

Asma Zafar[1,3] · Ghulam Murtaza[1] · Irfan Afzal[2] · Zia Ur Rahman Farooqi[1] · Weibo Shen[3] · Ali Raza[2]

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Abstract

Salinization and sodication present significant threats to crop productivity in many parts of the world including Pakistan. Cultivating halophytes like quinoa presents a viable solution for the profitable use of salt-affected lands. This study specifically examines the performance and salt tolerance mechanism of four quinoa accessions under varying salinity and sodicity levels. In addition to a control group, different combinations of electrical conductivity and sodium adsorption ratio (ECe dS m^{-1} SAR levels) were established: 10:20, 10:40, 20:20, and 20:40, achieved by using a mixture of salts. Most of the quinoa cultivars exhibited robust growth, with the exception of GLN-22, which proved unable to withstand high levels of salinity and sodicity, resulting in a 78% reduction in yield. GLN-29, on the other hand, demonstrated superior performance across all levels of salinity and sodicity. UAF-Q7 excelled under conditions of high salinity and low sodicity compared to equivalent salinity levels but elevated sodicity. Meanwhile, GLN-33 exhibited enhanced growth under elevated sodicity levels but struggled in the face of high salinity stress. In terms of nutrient uptake, GLN-29 displayed a higher accumulation of Na^+ (32%) in older leaves compared to younger ones, alongside elevated levels of antioxidant activity at all salinity and sodicity levels. Notably, GLN-29 exhibited excellent adaptation to both high salinity and sodicity levels, resulting in the highest grain yield (14.75 g/pot) and the salt tolerance mechanism was associated with highly efficient K^+ retention and transport of Na^+ to older leaves. This underscores the necessity for further comprehensive field studies to ascertain its suitability for the sustainable utilization of salt-affected soils.

Keywords Quinoa · Salt tolerance · Salt-affected soils · Yield performance

Introduction

The uncontrolled increase in the global population in recent decades has posed serious threat to sustainable agriculture and food security. Land resources are shrinking progressively due to land-degradation. Poor soil fertility, soil salinity, water logging, soil erosion, soil pollution, deficiency of essential minerals, and steady reduction of organic matter content are key features of soil degradation. Among these, soil salinity and sodicity is considered as the most critical issue of agriculture sector particularly in countries with arid to semi-arid climatic conditions (Akram et al. 2021). The salt-affected area of semi-arid and arid regions occupies about 1 billion hectares (Syed et al. 2021) and in spite all the efforts put forward by scinetific community, it is incerasing with variable rates across the world. The total area of 831 Mha in the world is salt-affected of which 397 Mha comprises saline soils and 434 Mha have sodic soils (Hasanuzzaman et al. 2014). Approximately 6.30 Mha area of Pakistan is salt-affected and out of which 1.89, 1.85, 1.02 and 0.028 Mha are saline, permeable saline-sodic, impermeable saline-sodic and sodic, respectively (Hussain et al. 2020).

Handling Author: Vijay Pratap Singh.

✉ Irfan Afzal
iafzal@uaf.edu.pk

[1] Institute of Soil and Environmental Sciences, University of Agriculture, Faisalabad 38040, Pakistan

[2] Department of Agronomy, University of Agriculture, Faisalabad 38040, Pakistan

[3] College of Natural Resources and Environment, Northwest A&F University, Yangling 712100, Shaanxi, People's Republic of China

Salt stress affects 20% of total farm land and 50% of irrigated regions around the world. Growth and productivity of crops are negatively affected on salt-affected soils. The crop growth and yield in salt-affected soils is mainly affected due to osmotic stress, ionic toxicity, nutrient deficiency and poor physical conditions of soils (Munns and Tester 2008; Abbas et al. 2015). Leaf gas exchange, chlorophyll and relative water contents are severely decreased due to high levels of salts in soil solution (Flowers and Colmer 2015; Abbas et al. 2017). Plants growing in salt-affected soils also suffer from oxidative stress due to the over production of several reactive oxygen species (ROS) (Abbas et al. 2017). Macromolecules such as carbohydrates, lipids, protein, and cell membranes are damaged due to cytotoxic nature of ROS. Due to lipid peroxidation, cell membranes are ruptured and results in plant death (Abbas et al. 2017). To overcome the ROS actions, antioxidant enzymes activities are increased such as superoxide dismutase, peroxidase, and catalase in plants (Parvez et al. 2020; Rehman et al. 2019). Under salinity stress, the accumulation of sugars and other compatible solutes (e.g., proline) allows plants to maintain their cellular turgor pressure necessary for cell expansion and growth under stress conditions; they also act as osmo-protectants. Proline is also considered the only osmolyte able to scavenge free radicals thereby ensuring membrane stabilization and preventing protein denaturation during severe osmotic stress (Szabados and Savouré 2010).

The productive utilization of degraded salt-affected soils is crucial to meet the needs of expanding population of the world. Depending upon type of salt-affected soils and availability of management package, salt-affected soils can be reclaimed using different physical, chemical, and biological methods. One option for counteracting the salt stress is the enhancement of salt tolerance potential of glycophytes through genetic engineering or plant breeding (Negrão et al. 2017). However, this option is time consuming and little success has been reported in developing salt tolerance and growing such corps at large areas. Another approach is to utilize such soils by cultivating halophytes (Panta et al. 2014). According to Adolf et al. (2013), the second option is the most promising approach. However, halophytes have great genetic variability regarding their salt tolerance potential (Ruiz et al. 2016). For examples, Dicotyledonous halophytes have shown maximum growth around 150 mM NaCl concentration, whereas monocotyledonous halophytes have maximum growth around 50 mM NaCl (Adolf et al. 2013).

The most promising example of dicotyledonous halophytes is quinoa (*Chenopodium quinoa* Willd. L.). It has the capacity to grow even at 400 mM salt concentration (Riaz et al. 2020) and can produce highly nutritious food grains (Afzal et al. 2023). Moreover, it can grow well in highly salt-affected soils with limited water supply and has potential as supplementer/alternative human food source with high nutritional value (Jacobsen 2017). In light of the current changing climate scenario and also due to extraordinary nutritional profile, and adaptability to adverse climate, quinoa has recently received a considerable attention of the progressive farmers and researchers from the arid and semi-arid regions to be used as an alternative food crop for ensuring the issue of food security and also to efficiently utilizing the saline-sodic soils (Adolf et al. 2013; Afzal et al. 2023).

Intensive research has been done on quinoa to evaluate its growth and yield potential on saline soils however to best of our knowledge, limited information is available regarding its cultivation on soils with varying levels of salinity and sodicity. Therefore, the current study was designed to address this research gap and to explore the comparative growth, yield, phenological responses, and potential salt tolerance mechanisms of different available quinoa genotypes under saline-sodic conditions. We hypothesize that genotypic variations may be a feasible approach to reduce the salinity and sodicity levels.

Materials and Methods

Experimental Design

Present study was conducted at the Wire House at Institute of Soil and Environmental Sciences, University of Agriculture Faisalabad (UAF), Pakistan during the months of November to May 2020–2021 to test the performance of three genotypes (GLN-22, GLN-29, GLN-33) and one variety UAF-Q7 of quinoa crop under saline-sodic conditions. The soil used in the study was collected from student experimental area of Institute of Soil and Environmental Sciences, UAF and characterized using methods described by U.S. Salinity Laboratory Staff (1954) and Bottomley et al. (2020) for various physico-chemical properties before start of the experiment (Table 1). The sieved soil (10 kg) was filled in each ceramic pot lined internally with polythene sheet before filling with soil and the hole at bottom was also plugged with cork to prevent leaching. Using quadratic equation, required salt concentrations were calculated to develop different salinity: sodicity (ECe:SAR) levels i.e., 10:20; 10:40; 20:20; and 20:40 (dS m^{-1}:mmol $L^{-1})^{1/2}$ along with control and each with three replications (Haider and Ghafoor 1992). The pots were saturated to soil saturation percentage using distilled water along with calculated amounts of salts and incubated for one month. After incubation, 10 seeds of quinoa in each pot were sown at the depth of 2.50 cm. Each pot was supplemented with P and K at 60 kg ha^{-1} as basal dose using diammonium phosphate (DAP) and sulphate of potash (SOP) fertilizers, while N dose was applied at 75 kg ha^{-1}

Table 1 Physico-chemical characteristics of experimental soil and irrigation water used in the experiment

Characteristics	Soil		Canal water
	Units	Values	
Sand	%	35	–
Silt	%	30	–
Clay	%	35	–
Textural class	–	Clay loam	–
Saturation percentage (%)	%	35	–
EC_e	dS m^{-1}	2.74	0.3
pH_s	–	7.50	7.3
CO_3^{2-}	$mmol_c$ L^{-1}	0	0
HCO_3^-	$mmol_c$ L^{-1}	15	1
Cl^-	$mmol_c$ L^{-1}	6	4
SO_4^{2-}	$mmol_c$ L^{-1}	6.4	–
$Ca^{2+} + Mg^{2+}$	$mmol_c$ L^{-1}	23	2
Na^+	$mmol_c$ L^{-1}	4.5	–
SAR	$(mmol_c\ L^{-1})^{1/2}$	1.30	–
Organic matter	%	0.82	–

using urea (half dose at sowing and half along with 2nd irrigation). Each pot was irrigated with canal water throughout the experiment. After seed emergence, only 3 plants in each pot were retained till maturity.

Phenological and Physiological Attributes

The phenological data (emergence of cotyledon and true leaves, visible floral bud, anthesis, end of flowering, physiological maturity) were recorded as and when needed. For recording of data, a specific phenological stage is considered completed when half of the plant population completed that stage (Stanschewski et al. 2021).The leaf area of the quinoa plant during the vegetative growth stage was measured using a LICOR LI-3000 leaf area meter (Hunt 1978). Physiological parameters like Transpiration and photosynthetic rates were recorded using an infrared gas analyzer (IRGA) (Analytical development company, Hoddeson, UK) in the morning during the vegetative growth stage. Chlorophyll content was assessed at the vegetative stage using a chlorophyll meter (Minolta SPAD-502 DL meter Japan).

Fully expanded top 2nd leaf of the plant was used to determine the relative water content (RWC) of the quinoa plant. 0.5 g of fresh leaf sample was immediately immersed in Petri plates filled with distilled water (DW) for 4 h. Subsequently, leaves were removed from the Petri plates, dried with tissue paper, and their turgid weights were recorded. The samples were then placed in an oven at 70 °C for 48 h until a constant weight was achieved. The dry weights were measured using weighing balance (OHAUS digital weighing balance PX233). The RWC was determined in leaf samples using the equation (Tahjib-Ul-Arif et al. 2018).

The membrane stability index (MSI) was determined using fully expanded younger leaves. The fresh weight of these leaves was measured after rinsing them with distilled water. In a test tube containing fresh leaf cuttings of equal size (0.2 g), 10 mL of distilled water was added. After 30 min, these test tubes were placed in a water bath at 40 °C. The first electrical conductivity (EC1) reading was taken after 30 min. EC_2 was noted 15 min after placing the samples back in the water bath at a temperature of 100 °C, and the MSI was calculated according to the method outlined by Sairam et al. (2002).

Ionic Analysis

Each quinoa genotype's fully expanded younger and older leaves as well as their respective roots samples were taken from each salt-treated and non-treated pots. Roots and shoots were ground separately. The ground plant samples (0.5 g) were acid digested with a diacid mixture (HNO_3 and $HClO_4$ in 2:1 ratio). The digestates were cooled, filtered, and diluted up to 50 mL using distilled water. The ionic concentrations (Na^+ and K^+) of leaf and root samples were measured using a flame photometer (Sherwood, Japan, Model 410) (Shavrukov et al. 2009).

Antioxidants Assay

Fully expanded younger leaves (60 days after emergence) were removed from each pot. Leaf samples were collected in the morning before 5:00 am, and enveloped in aluminum foil and stored in plastic zipper-bags, then placed in ice box and subsequently frozen till analysis. Within two days of leaves collection, antioxidants were determined. In a pre-chilled pestle and mortar, leaf samples (0.1 g) were grounded in 1 mL phosphate buffer (50 mM; pH 7.8). Grounded material was transferred into pre-chilled Eppendorf tubes, which were centrifuged (Clandon, T53, England) for 20 min at 15,000 rpm and the supernatant was collected to measure the activities of antioxidant enzymes, superoxide dismutase (SOD) (Giannopolitis and Ries 1977), peroxidase (POD) and catalase (CAT) (Chance and Maehly 1955) by taking absorbance at 560 and 240 nm, correspondingly. Proline contents in fresh leaves were also determined using the method described by Bates et al. (1973).

Yield and Yield-Related Attributes

Crop was harvested at maturity and plant tissue samples were collected for ionic composition and biochemical analyses. Filter paper was used to dry inflorescences and

other parts of plants were dried out at 25–30 °C. The seeds were threshed manually after drying. The remaining plant parts were dried at 65 °C till constant weight was achieved and the dry matter was given. Plant height, main panicle length, width, no. of branches per plant, total dry biomass per plant and given yield/plant, total grain yield and thousand seeds weight was recorded. Panicle shape of quinoa plant was also recorded according to the protocol given by Bertero et al. (1996). Harvest index was also calculated after harvesting of crop by using standard procedures.

Statistical Analysis

Data obtained from the experiment were analyzed statistically using 2-way analysis of variance (ANOVA), while significance of treatments was compared at 5% probability level using least significant difference (LSD) test using XLSTAT v2019, USA (Steel 1997).

Results

Phenological Responses

The statistical analysis of growth stage data revealed significant effects of salinity and sodicity on quinoa growth. Genotypes GLN-29 and GLN-33 exhibited the shortest duration to reach each growth stage, closely followed by UAF-Q7. In contrast, GLN-22 took the longest time from cotyledon emergence to maturity due to the imposed salinity and sodicity stress (Table 2).

The data in Table 2 illustrates the influence of varying salinity and sodicity levels on the germination percentage (%) of quinoa genotypes in both the control (normal soil) and saline-sodic soils. As salinity and sodicity levels increased, germination of all tested genotypes significantly decreased (i.e., up to 43% in GLN-22 at ECO20:SAR40) compared to the control treatment. Notably, GLN-29 exhibited the highest germination percentage (56.6%).

Table 2 Effects of different EC:SAR ratios on phenological attributes of quinoa cultivars

Cultivars	Emergence percentage (%)	Days to emergence of true leaves	Days to visible floral bud	Days to branching stage	Days to anthesis	Days to end of flowering	Days to physiological maturity
CONTROL							
UAF-Q7	96.66 ± 0.33a	23 ± 1.00f	61 ± 0.67e	70 ± 0.00k	93 ± 0.00l	99 ± 0.33k	143.00 ± 0.33n
GLN-22	83.33 ± 0.33bc	25 ± 1.73c–e	65 ± 1.20bc	71 ± 0.33ij	98 ± 0.33j	103 ± 0.57ij	151.00 ± 0.57jk
GLN-29	86.66 ± 0.33bc	24 ± 1.00d–f	61 ± 0.67e	70 ± 0.33jk	92 ± 0.33l	98 ± 0.33k	142.00 ± 0.57o
GLN-33	90 ± 0ab	23 ± 1.33ef	64 ± 0.88cd	71 ± 0.58i-k	95 ± 0.33k	101 ± 0.33j	145.33 ± 0.33m
EC10:SAR20							
UAF-Q7	80 ± 0cd	22 ± 0.00f	64 ± 0.00cd	72 ± 0.58i	100 ± 0.58i	105 ± 0.33h	146.67 ± 0.33m
GLN-22	80 ± 0cd	26 ± 0.88a-d	65 ± 1.33bc	76 ± 0.33g	103 ± 0.33g	111 ± 0.57e	156.00 ± 0.57g
GLN-29	80 ± 0.57cd	24 ± 1.20d–f	62 ± 0.88de	73 ± 0.33h	98 ± 0.33j	104 ± 0.33hi	146.00 ± 0.57m
GLN-33	83.3 ± 0.33bc	23 ± 1.00ef	64 ± 0.33cd	73 ± 0.33h	99 ± 0.00j	107 ± 0.33g	150.00 ± 0.00kl
EC10:SAR40							
UAF-Q7	73.33 ± 0.33de	24 ± 1.00d–f	64 ± 1.20cd	75 ± 0.88g	106 ± 0.58e	110 ± 0.33ef	153.00 ± 0.57hi
GLN-22	66.66 ± 0.33ef	24 ± 1.00d–f	65 ± 0.33bc	78 ± 0.33f	109 ± 0.33c	113 ± 0.33d	167.00 ± 1.15c
GLN-29	73.3 ± 0.33de	24 ± 1.00de	62 ± 0.88ab	75 ± 0.33g	102 ± 0.33h	107 ± 0.33g	149.00 ± 0.33l
GLN-33	70 ± 0ef	24 ± 1.00d–f	64 ± 0.33cd	75 ± 0.33g	103 ± 0.33g	109 ± 0.00fg	153.00 ± 0.57hi
EC20:SAR20							
UAF-Q7	56.6 ± 0.33gh	25 ± 0.33b–e	67 ± 0.33ab	80 ± 0.33e	106 ± 0.33e	113 ± 1.20d	154.00 ± 0.66h
GLN-22	50 ± 0hi	27 ± 0.58a–c	69 ± 0.33a	83 ± 0.33c	110 ± 0.33bc	118 ± 0.33b	170.00 ± 0.33b
GLN-29	63.3 ± 0.33fg	28 ± 0.00a	67 ± 0.33ab	78 ± 0.33f	104 ± 0.33f	111 ± 0.33e	151.00 ± 0.33ij
GLN-33	63 ± 0.33fg	27.00 ± 0.67a–c	67 ± 0.33ab	81 ± 0.33d	108 ± 0.33d	115 ± 0.33e	157.00 ± 0.33f
EC20:SAR40							
UAF-Q7	50 ± 0hi	27 ± 0.33ab	67 ± 1.53b	86 ± 0.00b	110 ± 0.33b	119 ± 0.33b	161 ± 0.33b
GLN-22	43.3 ± 0.34i	28 ± 0.00a	69 ± 1.20a	90 ± 0.00a	113 ± 0.33a	123 ± 0.88a	173 ± 0.33a
GLN-29	56.6 ± 0.33gh	27 ± 0.33ab	67 ± 0.41ab	85 ± 0.00b	106 ± 0.33e	113 ± 0.33d	156 ± 0.57d
GLN-33	53.3 ± 0.35h	28 ± 0.33a	69 ± 0.33a	86 ± 0.00b	108 ± 0.33d	118 ± 0.33b	159 ± 0.33b

Values after ± denotes standard error, while the values sharing same letters are not statistically different at $p \leq 0.05$

Physiological Responses

The physiological parameters of quinoa plants exhibited adverse effects at different ECe:SAR levels compared to the control. Among these, the maximum decrease in relative water content (RWC) was observed in GLN-22 at EC:SAR 20:40 (78% reduction compared to the control), followed by decreases of 59, 36, and 10% at ECe:SAR levels 20:20, 10:40, and 10:20, respectively (Fig. 1b). Similarly, the maximum reduction in membrane stability index was recorded in genotype GLN-22 at ECe:SAR 20:20 (20% decrease), followed by decreases of 9, 7, and 1% at ECe:SAR levels 10:20, 10:40, and 20:40, respectively (Fig. 1c). In terms of photosynthetic rate, the most significant decrease was observed in GLN-22 at ECe:SAR 20:40 (83% reduction compared to the respective control), followed by decreases of 60, 39, and 15% at ECe:SAR levels 20:20, 10:40, and 10:20. Notably, GLN-29 experienced a 2% increase in photosynthetic rate at ECe:SAR 20:40 (Fig. 2a). The transpiration rate exhibited the maximum reduction in GLN-22 at ECe:SAR 20:40 (86% decrease), followed by decreases of 66, 63, and 53% at ECe:SAR levels 20:20, 10:40, and 10:20, respectively (Fig. 2b). Furthermore, the SPAD value saw the most significant reduction in UAF-Q7 (94%) at ECe:SAR 20:40, followed by decreases of 19, 17, and 4% at ECe:SAR levels 20:20, 10:40, and 10:20, respectively. Interestingly, no reduction in SPAD value was recorded in genotype GLN-33 at EC:SAR 10:20 (Fig. 2c).

Ionic Analysis

The concentration of Na^+ in both older and younger leaves, as well as roots, of quinoa genotypes exhibited an increase, while the concentration of K^+ showed a decrease with rising ECe:SAR levels. In older leaves, generally GLN-29 accumulate higher amount of Na^+ in its older leaves at ECe:SAR(20:40) but if we talk about % age increase of Na^+ accumulation with the increment in salinity and sodicity among all quinoa genotypes then, the most significant rise in Na^+ concentration (49% relative to the control) was observed in GLN-33 at ECe:SAR (20:40), followed by increases of 19, 19, and 8% at ECe:SAR levels 20:20, 10:40, and 10:20, respectively (Fig. 3a). Conversely, the most substantial decrease in K^+ concentration (49% compared to the control) was recorded in older leaves of UAF-Q7 at ECe:SAR (20:40) (Fig. 3b). For younger leaves, the same case was observed as older leaves i.e. GLN-22 accumulate highest quantity of Na^+ in younger leaves but according to % age increase with the increasing salinity and sodicity levels, the highest increase in Na^+ concentration was noted in UAF-Q7, showing a 56% rise compared to the respective control, at ECe:SAR (20:40). This was followed by increases of 28, 26, and 14% at ECe:SAR levels 20:20, 10:40, and 10:20, respectively (Fig. 4a). Meanwhile, the concentration of K^+ in younger leaves of UAF-Q7 significantly decreased (− 63% compared to its control) (Fig. 4b). In terms of Na^+/K^+ ratio, the highest value was recorded in older leaves of GLN-29 at the highest ECe:SAR level. In the case of younger leaves, the highest Na^+/K^+ ratio was found in GLN-22 at ECe:SAR level of 20:40 (Figs. 3c, 4c). It's worth noting that the roots of all genotypes exhibited lower Na^+ levels and higher K^+ levels. According to % age increase in Na^+ concentration with increasing salinity and sodicity (ECe:SAR), UAF-Q7 showed the highest Na^+ levels, reaching 82% at ECe:SAR (20:40) compared to its control, followed by EC_e:SAR (10:20, 10:40, and 20:20) with corresponding increases of 63, 35, and 1% (Fig. 5a). Overall GLN-22 showed maximum accumulation of Na^+ at highest ECe:SAR level i.e., 20:40. The concentration of K^+ was most significantly decreased in the roots of GLN-22, which were 59% lower than the respective control at ECe:SAR (20:40) (Fig. 5b). Na^+/K^+ ratio was highest in the roots of GLN-22 at ECe:SAR (20:40) (Fig. 5c).

Biochemical Attributes

The biochemical responses of quinoa showed improvements under saline-sodic conditions, indicating an enhanced antioxidant activity with increasing ECe:SAR levels. The highest % age increase in SOD activity was observed in genotype GLN-22, showing a 60% rise compared to its respective control at ECe:SAR (20:20). This was followed by increases of 54, 43, and 36% at control and ECe:SAR (10:40, 20:40, and 10:20). (Fig. 6a).

Maximum % age enhancement in POD activity was recorded in GLN-33 at ECe:SAR (20:40), which exhibited a remarkable 584% increase compared to its respective control. This was followed by increases of 281, 258, and 105% at ECe:SAR (20:20, 10:40, and 10:20) (Fig. 6b). Regarding CAT activity, the highest increase was observed in GLN-22 (37%) at ECe:SAR (20:40), followed by 21, 20, and 12% increases at ECe:SAR (10:40, 20:20, and 10:20) respectively (Fig. 6c). In terms of organic osmolyte proline concentration, the maximum % age increase was observed in UAF-Q7 (46% increase compared to the control) at ECe:SAR (20:20), followed by 44, 19, and 13% increases at ECe:SAR (10:20, 20:40, and 10:40). Interestingly, proline concentration decreased to 9% at EC_e:SAR (20:20) in GLN-33 (Fig. 1a). But generally, among all the quinoa genotypes, GLN-29 showed a remarkable increase in activity of antioxidant enzymes, and proline contents at highest ECe:SAR level (Figs. 1a, 6a–c).

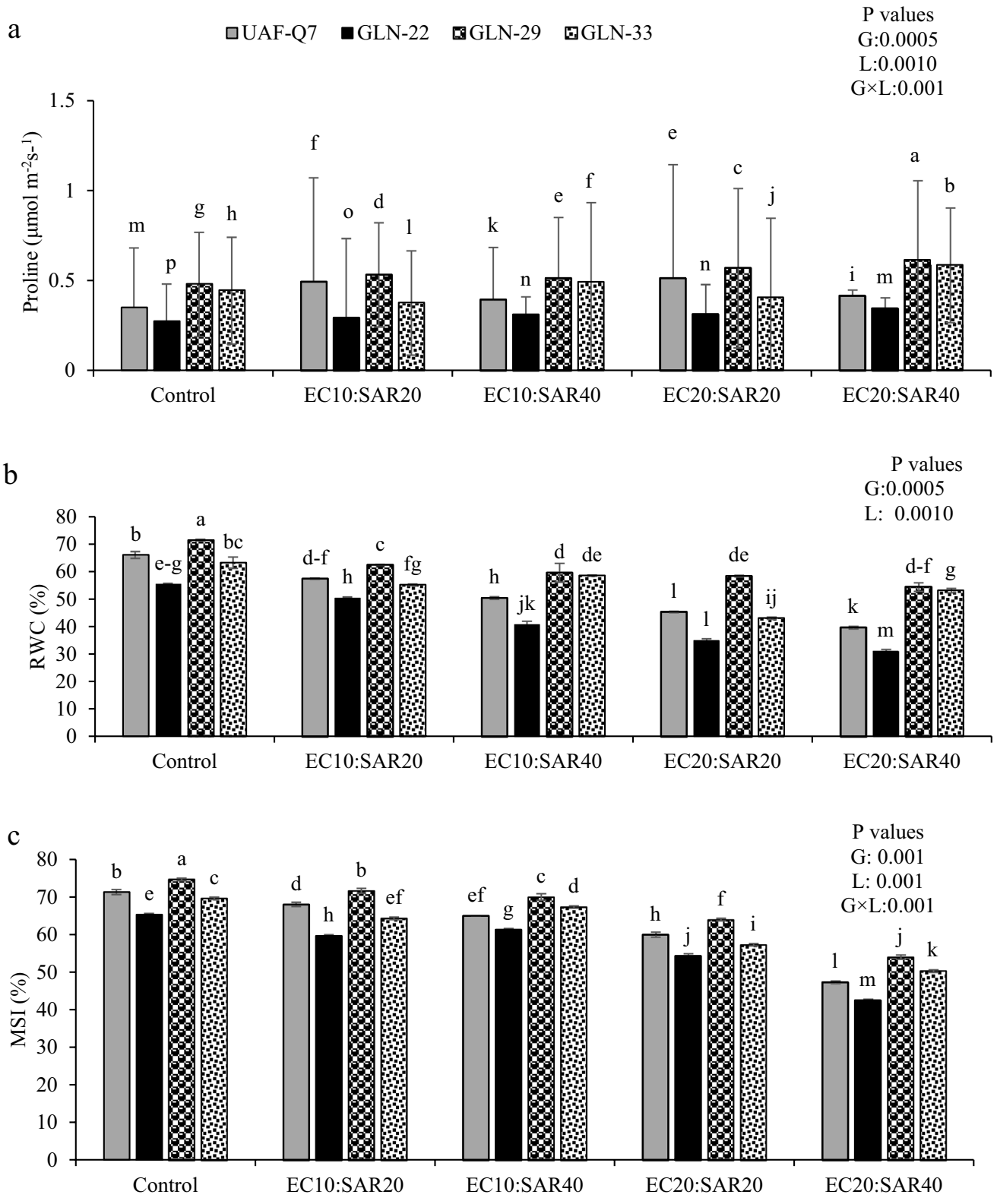


Fig. 1 Effects of different salinity and sodicity levels (EC:SAR ratios) on **a** proline, **b** relative water contents (RWC), **c** membrane stability index (MSI) of four quinoa genotypes. Different letters indicating level of significance at $p < 0.05$

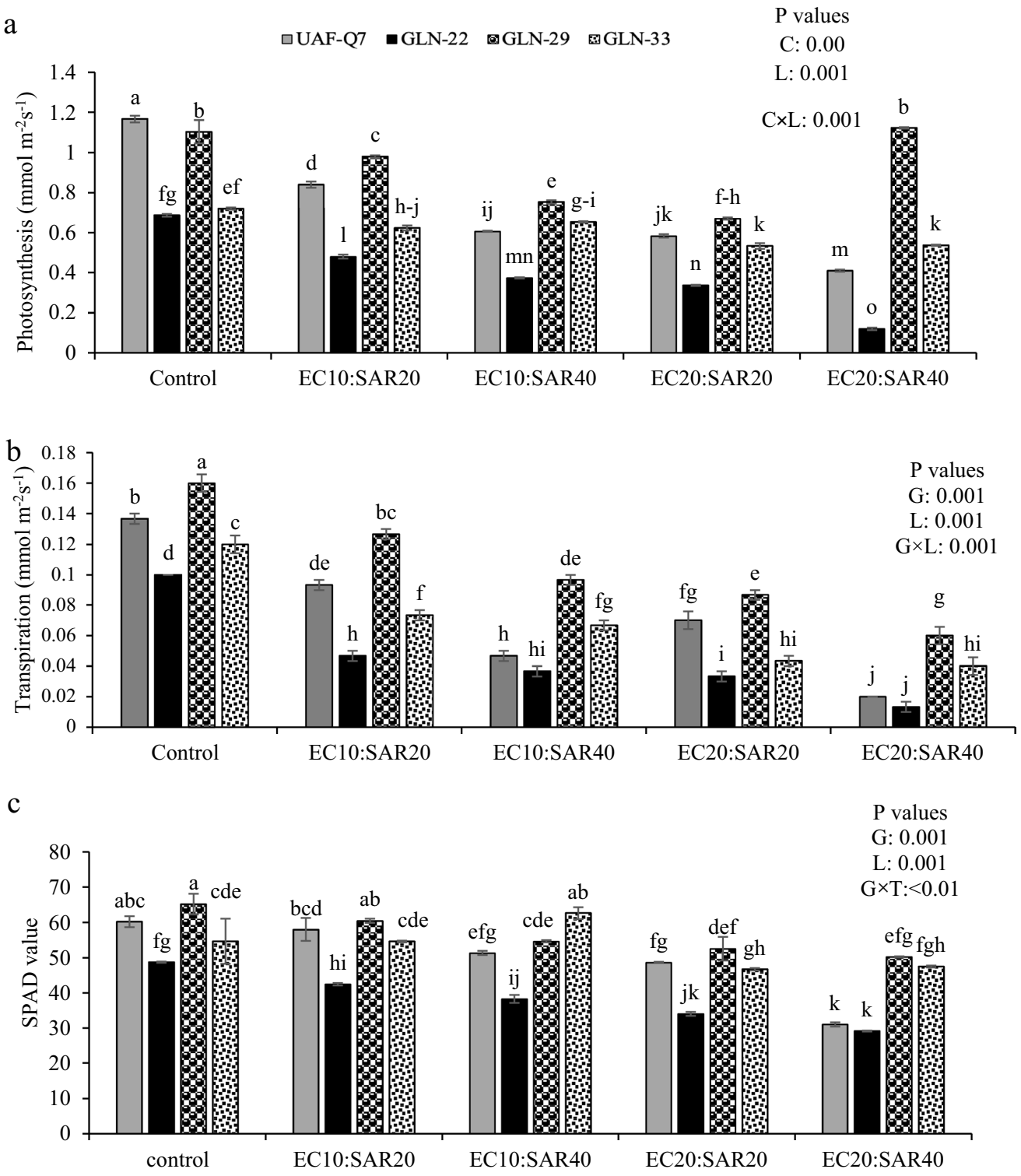


Fig. 2 Effects of different salinity and sodicity levels (EC:SAR ratios) on **a** photosynthesis rate, **b** transpiration rate, and **c** SPAD value of four quinoa genotypes. Different letters indicating level of significance at $p < 0.05$

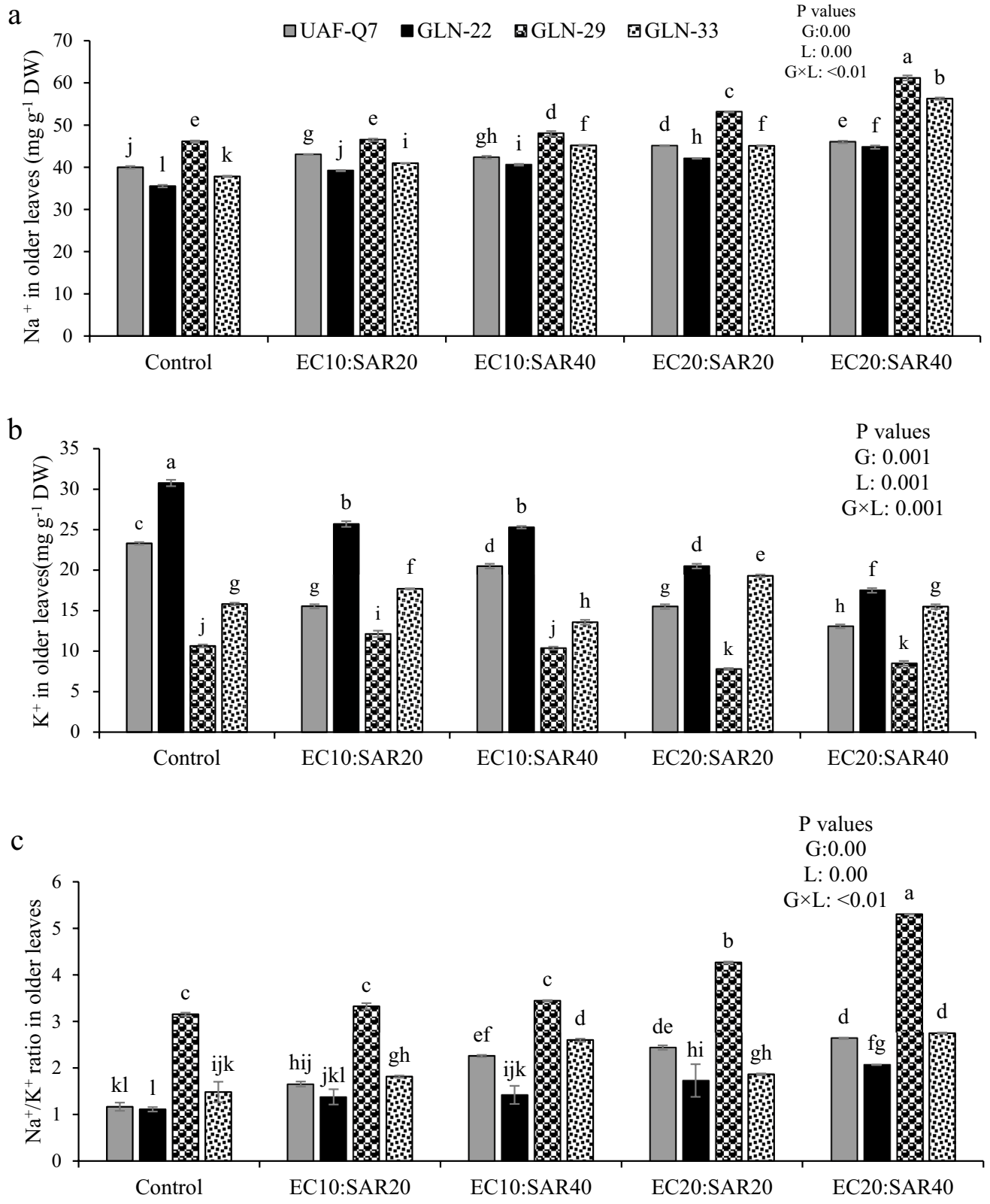


Fig. 3 Effects of different salinity and sodicity levels (EC:SAR ratios) on **a** Na^+, **b** K^+, and **c** Na^+/K^+ ratio in older leaves of four quinoa genotypes. Different letters indicating level of significance at $p < 0.05$

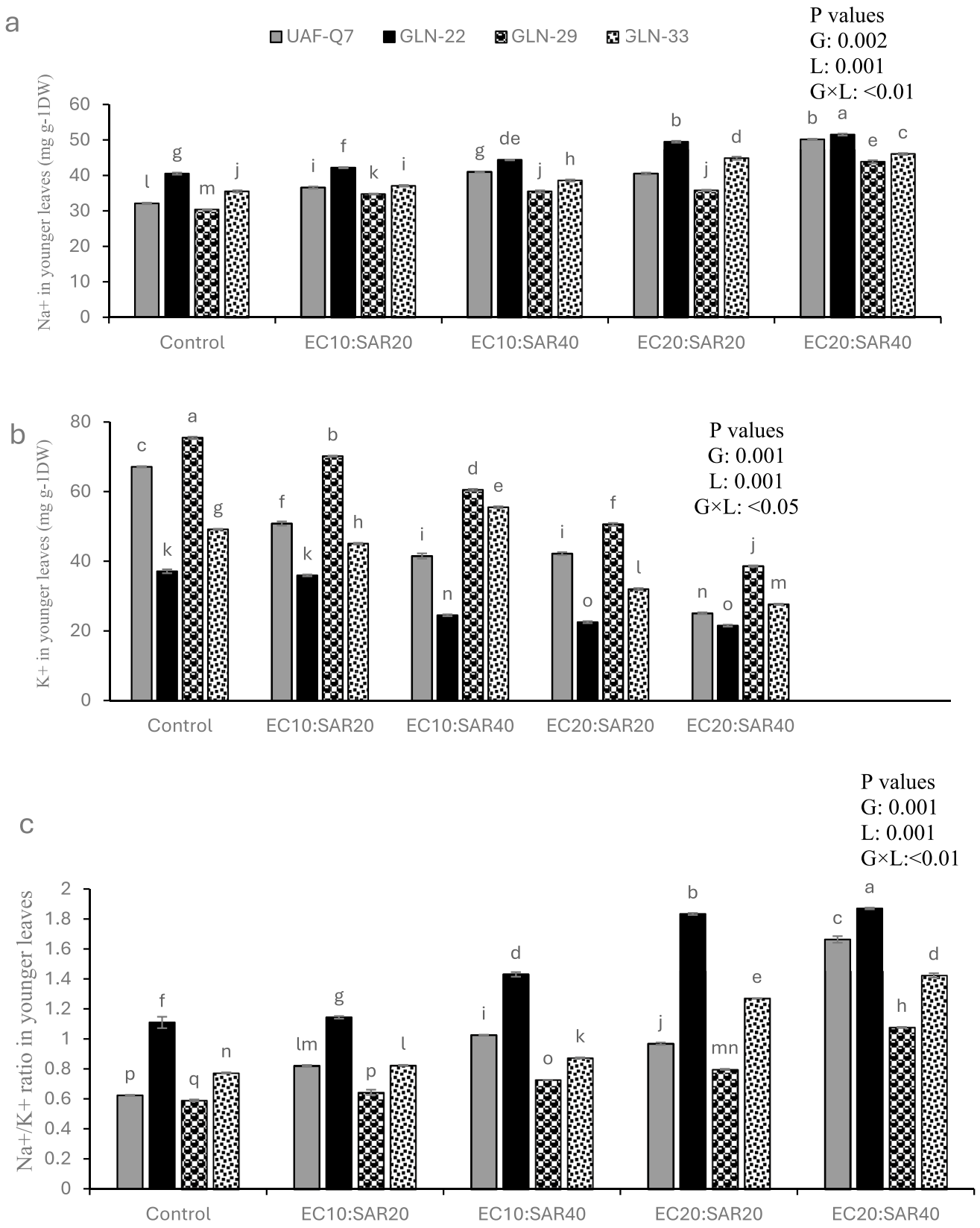
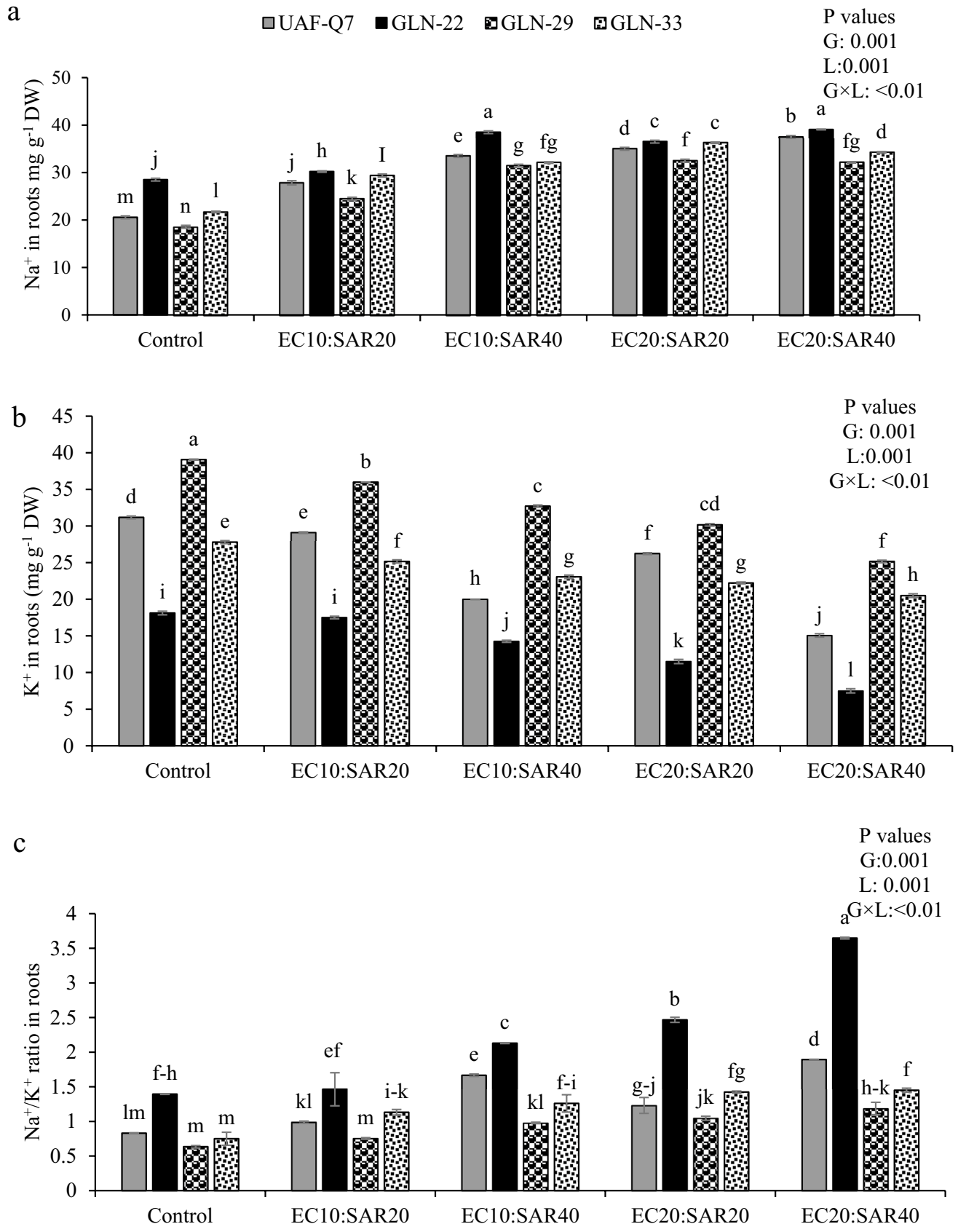


Fig. 4 Effects of different salinity and sodicity levels (EC:SAR ratios) on **a** Na^+, **b** K^+, and Na^+/K^+ ratio in younger leaves of four quinoa genotypes. Different letters indicating level of significance at $p < 0.05$


a
UAF-Q7
GLN-22
GLN-29
GLN-33
P values
G: 0.001
L:0.001
G×L: <0.01
Na+ in roots mg g-1 DW)
Control
EC10:SAR20
EC10:SAR40
EC20:SAR20
EC20:SAR40
b
P values
G: 0.001
L:0.001
G×L: <0.01
K+ in roots (mg g-1 DW)
Control
EC10:SAR20
EC10:SAR40
EC20:SAR20
EC20:SAR40
c
P values
G:0.001
L: 0.001
G×L:<0.01
Na+/K+ ratio in roots
Control
EC10:SAR20
EC10:SAR40
EC20:SAR20
EC20:SAR40

◂**Fig. 5** Effects of different salinity and sodicity levels (EC:SAR ratios) on **a** Na^+, **b** K^+, and Na^+/K^+ ratios in roots of four quinoa genotypes. Different letters indicating level of significance at $p < 0.05$

Yield and Yield-Related Attributes

Data regarding yield and yield-related attributes is provided in Table 3. Salinity and sodicity levels had a relatively less significant influence on plant height, main panicle lengths, and width for all quinoa genotypes (UAF-Q7, GLN-22, GLN-29, and GLN-33). Notably, even the ECe:SAR (10:20) stress had a significant negative effect on plant height, main panicle length, and panicle width across all genotypes. Furthermore, increased levels had even more pronounced negative effects. The most substantial decrease in plant height and main panicle length was observed in UAF-Q7 (15 and 39%) at the highest salinity and sodicity levels, i.e., ECe:SAR (20:40), followed by decreases of 11, 8, and 2% in plant height and 20, 18 and 7% in panicle length at ECe:SAR (20:20, 10:40, and 10:20). Plant height of GLN-33 increased by up to 2% at ECe:SAR (10:20). Additionally, the maximum decrease in panicle width was recorded in GLN-22 (18%) at ECe:SAR (20:40) compared to the control. Total dry biomass (TDB) of quinoa genotypes was also negatively influenced by increasing salinity and sodicity levels. But even at all salinity and sodicity levels, GLN-22 had attained the highest TDB. Meanwhile, the maximum decrease in TDB was noted in UAF-Q7 (40%) at ECe:SAR (20:40) compared to the control, followed by reductions of 14, 10, and 4% at ECe:SAR (10:40, 20:20, and 10:20). Seed yield, 1000 seeds weight, and harvest index (HI) were also adversely affected by increasing salinity and sodicity levels, with GLN-29 showing the minimum effects of ECe:SAR. The most significant decrease in seed yield, 1000 seeds weight, and HI was observed in GLN-22 (78, 76, and 58% compared to the control) at ECe:SAR (20:20, 10:20, and 10:40), respectively. The highest decrease in number of branches per plant were recorded in GLN-33, at 22% at ECe:SAR (20:40), while an increase of 2% was observed in UAF-Q7 at ECe:SAR (10:20). Leaf area reduced with increasing salinity and sodicity, with UAF-Q7 experiencing the highest reduction at the highest ECe:SAR level (69% compared to the control), followed by decreases of 41, 17, and 7% at ECe:SAR (20:20, 10:40, and 10:20) according to percentage decrease but in general, GLN-29's leaf area was reduced significantly (Table 3).

Soil Analysis After Harvest

The EC_e, pH, and SAR levels exhibited significant decreases in the soil where quinoa genotype GLN-22 was cultivated, whereas the smallest reduction was observed in the soil where GLN-29 was grown. The highest pH was noted in the soil with ECe:SAR (20:40) where GLN-29 was cultivated, while the maximum EC_e was observed in the soil with ECe:SAR (20:40) where GLN-33 was grown. The highest SAR value was recorded at ECe:SAR (10:40) where GLN-29 was grown, while the lowest EC_e, pH, and SAR values were noted in the soil where GLN-22 was cultivated at all salinity and sodicity levels (Table 4).

Correlation Analysis

A strong negative correlation was observed between yield attributes and increasing salt stress. Conversely, a positive correlation was noted in the accumulation of Na^+ ions in older leaves under stress. Moreover, there was a significant positive correlation observed between biochemical attributes (SOD, POD, CAT, Proline) and salt stress. Seed yield and harvest index exhibited a strong correlation with all physiological, biochemical parameters, and yield-related attributes, except for plant height, potassium levels in older leaves, sodium levels in younger leaves, and roots (Fig. 7).

Discussion

All genotypes exhibited a typical halophytic nature, displaying higher growth and biomass and a shorter time to complete each phenological stage under moderate salinity and sodicity levels (ECe10:SAR20). However, high salinity and sodicity levels led to a significant decrease in biomass compared to the control treatment (Table 3). These results differ from the findings of Hariadi et al. (2011), who reported an increase in growth of different quinoa genotypes under 150 mM salinity level. Survival of quinoa even at 500 mM salinity level was also observed in a Peruvian variety (Koyro and Eisa 2008). Salinity and sodicity induced physiological drought and hydrolysis of stored foods, resulting in a slight loss in dry biomass yield. Overall, GLN-29 recorded less yield reduction under all saline-sodic conditions (Table 3). ECe:SAR level (10:20) was considered optimum for the growth of tested quinoa cultivars. These results are consistent with previous studies (Koyro and Eisa 2008; Hariadi et al. 2011; Iqbal et al. 2019) that reported decreased biomass production and yield of quinoa due to higher levels of soil sodicity. The lower 1000-seed weight of all genotypes at high levels of salinity (30 and 40 dS m^{-1}) could be attributed to higher protein concentration in seeds than carbohydrates (Koyro and Eisa 2008). Panicle length and width of all tested genotypes were affected by increasing salinity and sodicity, while the maximum reduction in panicle width and number of branches per plant might be due to the maximum plant height of quinoa plants. Our findings support the study of Beyrami et al. (2020) who reported that soil salinity has adverse effects on different phenological and yield-related

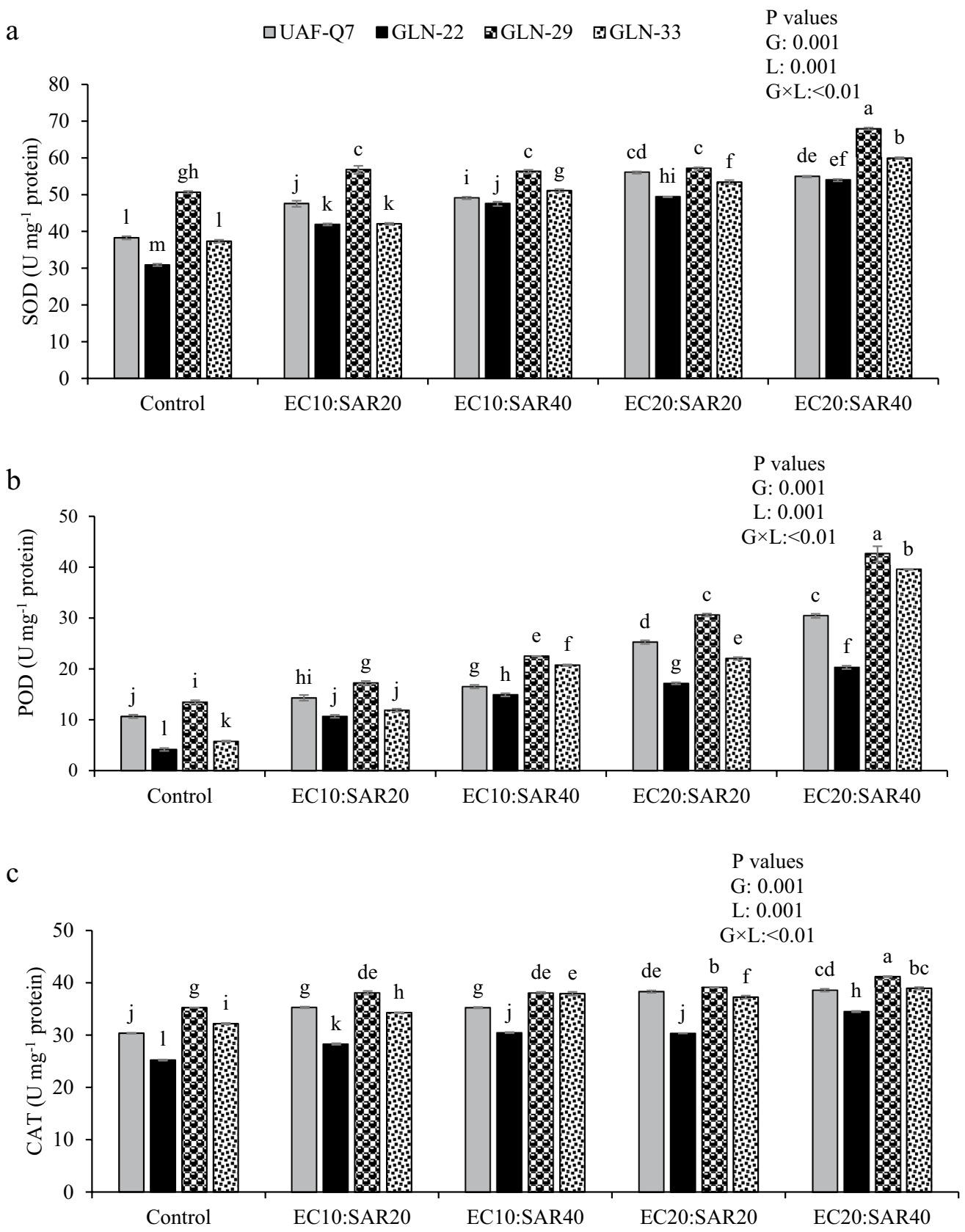


Fig. 6 Effects of different salinity and sodicity levels (EC:SAR) on **a** superoxide dismutase (SOD), **b** peroxidase (POD), and **c** catalase (CAT) of four quinoa genotypes. Different letters indicating level of significance at $p < 0.05$

Table 3 Effects of different EC:SAR ratios on different agronomic attributes of quinoa cultivars

	Plant height (cm)	Panicle length (cm)	Panicle width (cm)	No. of branches/plant	Leaf area/plant (cm^2)	Total dry biomass (g)	1000-seed weight (g)	Harvest index (%)	Seed yield per plant (g)
CONTROL									
UAF-Q7	93.66 ± 0.88bc	15.2 ± 0.12bc	3.72 ± 0.06b	28.33 ± 0.33b–d	173 ± 0.58c	51.54 ± 1.42b–d	2.43 ± 0.03bc	25.25 ± 0.25a–c	13.17 ± 0.72a–d
GLN-22	106.66 ± 0.88a	16.16 ± 0.17a	3.28 ± 0.04ef	31.5 ± 0.29a	125.67 ± 0.33a	58.73 ± 0.15a	1.78 ± 0.01hi	12.74 ± 0.03g	7.5 ± 0.00h
GLN-29	87.2 ± 0.61c–f	15.53 ± 0.27b	4.1 ± 0.06a	28 ± 0.58b–e	181.67 ± 0.88j	57.37 ± 0.41a	2.78 ± 0.01a	30 ± 0.00cd	14.75 ± 0.25a
GLN-33	84.13 ± 0.47c–h	15.16 ± 0.12bc	3.58 ± 0.01b–d	25.67 ± 0.33c–e	170.43 ± 0.30b	48.13 ± 1.16d–f	2.17 ± 0.04de	23.25 ± 0.25cd	12.75 ± 0.25b–d
EC10:SAR20									
UAF-Q7	85.26 ± 0.15c–g	14.1 ± 0.17ef	3.66 ± 0.02bc	28.67 ± 0.33a–c	163 ± 0.58e	49.21 ± 0.35c–e	2.26 ± 0.10cd	24.76 ± 0.28b–d	12.25 ± 0.25b–e
GLN-22	101.10 ± 0.29ab	15.46 ± 0.29bc	3.15 ± 0.00f	29 ± 0.00ab	110.95 ± 0.25b	55.13 ± 0.47ab	1.33 ± 0.12l	13.07 ± 0.57fg	7.25 ± 0.25h
GLN-29	86.66 ± 1.20c–f	14.54 ± 0.14de	3.72 ± 0.02b	26.67 ± 0.33b–e	173.33 ± 0.88k	51.33 ± 0.88b–d	2.51 ± 0.01b	27.75 ± 2.26a	14 ± 1.00b
GLN-33	80.5 ± 0.29d–i	13.74 ± 0.13fg	3.51 ± 0.02cd	25 ± 0.00e	155.19 ± 0.26d	41.55 ± 0.29hi	1.79 ± 0.05hi	22.91 ± 1.49cd	9.5 ± 0.50g
EC10:SAR40									
UAF-Q7	74.38 ± 0.20hi	12.4 ± 0.21hi	3.45 ± 0.02de	18.33 ± 0.33gh	143.43 ± 0.30g	43.87 ± 0.68gh	1.93 ± 0.02f–h	24.15 ± 0.29b–d	10.75 ± 0.25e–g
GLN-22	90.11 ± 5.53cd	14.97 ± 0.03cd	3.1 ± 0.06f	25.33 ± 0.33df	101.47 ± 0.29f	52.17 ± 0.12bc	1.34 ± 007l	7.27 ± 2.47h	3.8 ± 1.30i
GLN-29	80.8 ± 0.42d–i	14 ± 0.00f	3.61 ± 0.02b–d	20 ± 0.58f-h	152.8 ± 1.11l	48.99 ± 0.18c–e	2.22 ± 0.12d	28.03 ± 0.65a	13.775 ± 0.28a–c
GLN-33	75.83 ± 0.44g–i	13.47 ± 0.26g	3.55 ± 0.00b–d	19.33 ± 1.33f–h	150 ± 0.58h	46.10 ± 0.59e–g	2.09 ± 0.09d–f	27.85 ± 1.94a	13 ± 1.00a–d
EC20:SAR20									
UAF-Q7	82.83 ± 0.44i	12.17 ± 0.12hi	3.46 ± 0.01de	20.33 ± 0.33fg	100.43 ± 0.38n	46.37 ± 0.32e–g	1.87 ± 0.08g–i	22.5 ± 0.50cd	11.75 ± 0.25de
GLN-22	88.83 ± 0.44c–e	13.23 ± 0.12g	2.81 ± 0.24g	21 ± 0.58fg	71 ± 0.58i	47.63 ± 0.20d–g	0.8 ± 0.06m	5.00 ± 0.02hi	2.39 ± 0.00ij
GLN-29	73.66 ± 0.84i	12.67 ± 0.09h	3.51 ± 0.01cd	20 ± 2.08f–h	130.77 ± 0.39o	44.5 ± 0.29f–h	2.02 ± 0.09e–g	26.5 ± 0.50ab	12.75 ± 0.25b–d
GLN-33	74.83 ± 0.42hi	12.33 ± 0.33ij	3.42 ± 0.02de	17.67 ± 1.20h	90.5 ± 0.29l	33.65 ± 1.78jk	1.59 ± 0.05jk	15.75 ± 0.25ef	9.57 ± 1.08fg
EC20:SAR40									
UAF-Q7	80.31 ± 0.16e–i	9.27 ± 0.15l	3.11 ± 0.06f	21 ± 3.22fg	52 ± 0.58m	30.63 ± 0.45k	1.48 ± 0.02kl	16.5 ± 0.50e	10.5 ± 0.50e–g
GLN-22	83.44 ± 14d–h	12.13 ± 0.09i	2.70 ± 0.04g	21.67 ± 0.33f	46.95 ± 0.04l	44.5 ± 5.44f–h	0.74 ± 0.03m	3.07 ± 0.28i	1.43 ± 0.41j
GLN-29	77.93 ± 0.52f–i	11.57 ± 0.43j	3.51 ± 0.01cd	20.67 ± 1.47f–h	101 ± 0.58q	39.5 ± 0.29i	1.98 ± 0.01fg	23.35 ± 0.35cd	11.92 ± 0.92c–e
GLN-33	77.66 ± 0.33f–i	10.63 ± 0.19k	3.27 ± 0.12ef	20 ± 1.16f–h	95.5 ± 0.29p	35.27 ± 0.15j	1.69 ± 0.01ij	22.25 ± 0.25d	11.41 ± 0.91d–f

Values after ± denotes standard error, while the values sharing same letters are not statistically different at $p \leq 0.05$

attributes such as dry biomass yield, seed yield and harvest index, plant height, panicle length, panicle width, number of branches, number of panicles per plant, and 1000-seed weight. GLN-22 prolonged its vegetative stage and utilized all nutrients from the soil in gaining maximum height and total dry biomass, thus reaching maturity late with a drastic reduction in seed yield.

The physiological traits, such as relative water contents (RWC) of leaves, were not significantly affected by salinity stress in UAF-Q7, GLN-29, and GLN-33, confirming their salt-tolerant nature. However, in saline-sodic soil with ECe:SAR level (20:40), RWC was reduced, validating prior research on quinoa under salt stress conditions (Takagi and Yamada 2013; Amjad et al. 2015). Significant declines in RWC, proline, and membrane stability index were found in genotype GLN-22 because of oxidative stress (Fig. 1). Similar results were also reported by Abbas et al. (2021) who concluded that soil salinity and sodicity decreased the membrane stability index of quinoa. Leaf chlorophyll contents (SPAD value) were decreased at the lower salinity and sodicity level ECe:SAR (10:20), but increased in GLN-33 at ECe:SAR (10:40), confirming the salt tolerance nature of quinoa genotype GLN-33 (Fig. 2c). Reduction in chlorophyll contents of quinoa at higher salinity levels might be due to degradation of chlorophyll structure (Rangani et al. 2016). Riaz et al. (2020) also reported the decrease in chlorophyll contents and RWC to a greater extent in genotype Puno than A-1, indicating higher stability of chlorophyll structure in A-1 than Puno. In our study, the reduction in transpiration and photosynthesis was observed with the increasing salinity and sodicity levels in all studied genotypes, especially in GLN-22 (Fig. 2a, b), which might be due to reduced leaf area because of which the plant decreased transpiration to avoid water loss from its leaf surface. Leaf area of the plant is an imperative morphological attribute that illustrates the photo-assimilation in plants. Higher photosynthesis rate in salt-tolerant quinoa genotypes was due to increased chlorophyll contents and stomatal closure under salt stress (Qureshi and Daba 2020).

An increasing trend of Na^+ concentration in quinoa plant tissues of all cultivars was recorded with increasing ECe:SAR levels in the medium (Fig. 3). Shabala et al. (2013) explored the genotypic differences regarding salt tolerance among fourteen quinoa genotypes based on shoot Na^+ uptake and found that exclusion as well as sequestration of Na^+ into vacuoles are important traits for salt tolerance of crop plants. Similar to this, in our study, we observed that the tolerant genotypes i.e., GLN-29 and GLN-33

Table 4 Physico-chemical properties of soil quinoa harvest

Cultivars	pH_s	EC_e (dS m^{-1})	TSS (me L^{-1})	SAR (mmol $L^{-1})^{1/2}$
Control				
UAF-Q7	7.25m	2.04o	20.27o	1.83l
GLN-22	7.01o	2.69n	26.93n	1.40l
GLN-29	7.31m	2.72n	27.17n	1.25l
GLN-33	7.31m	2.72n	27.23n	1.31l
EC10:SAR20				
UAF-Q7	7.75i	8.10k	92.0k	17.67gh
GLN-22	7.93g	8.97j	109.67i	16.0ij
GLN-29	7.70ij	6.50m	74.33m	17.33hi
GLN-33	7.83h	8.01k	96.33j	13.67k
EC10:SAR40				
UAF-Q7	8.17f	9.07j	111.33i	34.33cd
GLN-22	7.73i	9.48i	116.33h	33.33de
GLN-29	8.53e	6.50m	74.0m	37.80a
GLN-33	8.23f	8.01l	83.67l	36.37b
EC20:SAR20				
UAF-Q7	8.65d	16.33c	202.33c	18.54gh
GLN-22	7.55l	15.50e	195.0d	15.58j
GLN-29	8.81c	17.47b	239.67b	18.94g
GLN-33	7.66jk	13.30g	162.67f	17.23hi
EC20:SAR40				
UAF-Q7	7.63k	14.40f	176.0e	32.67e
GLN-22	7.12n	11.50h	125.0g	29.33f
GLN-29	9.01a	15.80d	199.0cd	35.33bc
GLN-33	8.93b	18.93a	248.0a	35.67bc

Values sharing same letters are not statistically different at $p \leq 0.05$

accumulated higher Na^+ in shoots than roots, so they probably sequestered the excessive Na^+ into their leaf vacuoles. It suggests that the most prominent mechanism of salinity tolerance in quinoa is vacuolar Na^+ compartmentalization rather than root exclusion (Maughan et al. 2009; Shabala et al. 2013). We found that K^+:Na^+ ratio was decreased in genotypes GLN-29 and UAF-Q7 with increasing levels of salinity only and in GLN-29 and GLN-33 with increasing sodicity. This ratio is an important element elucidating the salt tolerance potential of quinoa (Adolf et al. 2013). The higher cytoplasmic concentration of Na^+ leads to a lower K^+:Na^+ ratio, which ultimately affects plant metabolism. Moreover, loss of K^+ from leaf mesophyll cells under salinity causes the activation of many proteases which initiate the programmed cell death (Shabala et al. 2005; Shabala 2009). Hence, the capability of the plants to limit K^+ loss and maintenance of high ionic ratio (K^+:Na^+) in cytoplasm is an indication of their salt tolerance potential (Adolf et al. 2012) which was proved in the current study.

A lower degree of Na^+ accumulation was observed in younger leaves of GLN-29 and UAF-Q7 at ECe:SAR (10:20 and 20:20) and in GLN-29 and GLN-33 at ECe:SAR (10:40 and 20:40). These cultivars responded to salt by translocating Na^+ in older leaves (Fig. 3a). This strategy of low accumulation of Na^+ might be linked with preferential K^+ uptake at root parenchyma and translocation to leaf, as leaf K^+ concentration was also higher in UAF-Q7 and GLN-33 along with GLN-29. Quinoa plants accumulate more K^+ in leaves under salt stress (Adolf et al. 2013) which was confirmed in this study. Both osmotically induced stomatal closure and excessive Na^+ accumulation in the cytosol under

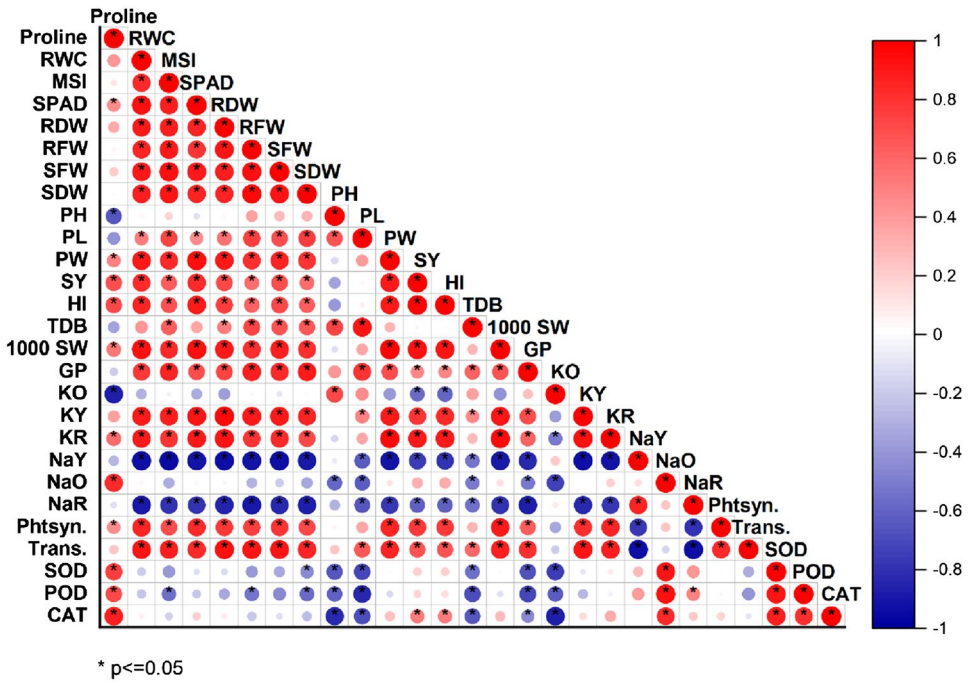


Fig. 7 Correlation analysis between the plant attributes under study. *RWC* relative water contents, *MSI* membrane stability index, *SPAD* chlorophyll content taken by SPAD meter, *RDW* root dry weight, *RFW* root fresh weight, *SFW* shoot fresh weight, *SDW* shoot dry weight, *PH* plant height, *PL* panicle length, *PW* panicle width, *SY* seed yield, *TDB* total dry biomass, *GP* germination percentage, *KO* K in older leaves, *KY* K in younger leaves, *KR* K in roots, *NaO* Na in older leaves, *NaY* Na in younger leaves, *NaR* Na in roots, *Photosyn* photosynthesis, *Trans* transpiration, *SOD* super oxide dismutase, *POD* peroxidase, *CAT* catalase

saline-sodic regimes decrease the plant's capability to utilize light absorbed by photosynthetic pigments and lead to the generation of reactive ROS (Tavakkoli et al. 2011; Shabala et al. 2012, 2013). The antioxidant defense system operates in plant cells to limit the excessive accumulation of ROS in cell (Adolf et al. 2013; Waqas et al. 2017; Iqbal et al. 2018). Such a defensive system was found operative in leaves of all tested quinoa cultivars (Figs. 1a, 6).

Quinoa, like other halophytes, appears to have an unusual ability to use superoxide dismutase (SOD) to protect cell machinery (Ismail et al. 2015). The end product of SOD activity is H_2O_2 that can either operate as a signal to stimulate adaptive reaction in response to adversative environmental conditions (Bose et al. 2014) or cause cell membrane damage, therefore over-produced H_2O_2 is detoxified by catalase (CAT) and scavenged by peroxidase (POD) (Mittler 2002). In the present study, both CAT and POD remained stable under normal and salt stress regimes in all quinoa cultivars and found functioning to safeguard from ROS. Moreover, the strong correlation between all antioxidative enzymes and sodium uptake in older leaves is an indication of the protective role of antioxidant enzymes against salt stress (Fig. 7). The increased activities of SOD in quinoa are necessary for rapid induction of H_2O_2 "signature" for the sake of triggering adaptive responses cascade and role of other antioxidant enzymes might be for decreasing H_2O_2 basal levels, once triggering signals of H_2O_2. Furthermore, the role of non-enzymatic antioxidants seems to be osmo-protection, ROS scavenging or quenching and preventing K^+ loss, an indirect role. In the non-enzymatic strategy proline production and accumulation in response to various abiotic stimuli, particularly salt stress, is generally recognized as a biochemical sign of tolerance to stress; their function as an osmoprotectant, suitable solute for adjustment of osmolytes and antioxidants or ROS suppressor is well established. According to the results of the current study, the level of proline was increased under salinity and sodicity stress in all the genotypes especially in GLN-29 (Fig. 1a). Moreover, there is a strong correlation between proline and antioxidant enzymes (Fig. 7).

According to post-quinoa harvest soil results, salinity and sodicity exhibited significant influence on soil properties (Table 4). At the soil ECe:SAR (10:20 and 20:20) levels, along with GLN-29 grown soil, UAF-Q7 grown soil and at ECe:SAR (10:40 and 20:40) GLN-33 grown soil had higher pH_s, EC_e and SAR values which might be due to their resistivity to saline-sodic conditions so they uptake less amount of salt in their cells thus leaving a higher quantity of salts in the root zone. While the soil where GLN-22 was grown had the lowest values of pH_s, EC_e, and SAR which might be due to its sensitivity to saline-sodic condition as GLN-22 accumulated a higher concentration of salts in it thus absorbing much quantity of salts from the root zone that's why its yield was reduced. However, quinoa post-harvest soil characteristics are not well documented, therefore further studies must be conducted for conclusive findings.

Conclusion

The findings of this study provide compelling evidence that quinoa not only survive in saline-sodic conditions but also produce significant seed yield that confirms the halophytic nature of quinoa. The tested quinoa genotypes demonstrated significant potential to withstand salinity and sodicity stress. Among all the tested quinoa genotypes, UAF-Q7 interestingly exhibited its best performance under moderately saline-sodic conditions, while GLN-33 excelled at the highest salinity-sodicity levels. Notably, GLN-29 consistently outperformed at all salinity and sodicity levels. On the other hand, GLN-22 showed poor performance with a substantial 78% yield reduction. The salt tolerance in quinoa genotype GLN-29 appears to be associated with maintaining low Na^+ levels and high K^+ concentrations, along with elevated activities of antioxidant enzymes. These findings have significant implications for utilizing quinoa genotypes in the sustainable management of salt-affected soils across a wide range of salinity and sodicity levels.

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Declarations

Conflict of interest The authors declare that he/she has no conflict of interest.

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