



Silicon Supplement Improves Growth and Yield Under Salt Stress by Modulating Ionic Homeostasis and Some Physiological Indices in *Hordeum vulgare* L

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Abstract

The application of silicon through external means has been proved to accelerate stress tolerance in different plant species. In this regard, we conducted an experiment to evaluate the role of silicon applied through rooting media on growth and yield of barley (*Hordeum vulgare* L.) under salinity stress. Silicon (200 ppm) was applied through rooting media to barley (*Hordeum vulgare* L.) genotypes [salt tolerant-B10008 and salt sensitive-B14011] subjected to 200 mM NaCl stress. A remarkable decline in growth (shoot and root lengths and biomass accumulation), leaf relative water contents (LRWC), chlorophyll constituents, and ionic concentrations (K^+ , Ca^{2+} , P, and Si), with a substantial increase in total soluble proteins (TSP) and concentrations of Na^+ and Cl^- , was observed under salt stressed compared to control plants. Salinity stress lowered the efficiency of Photosystem II (PSII) by hindering absorption/transport of electrons through thylakoid membranes; decrease in size of reaction centers (Fv/Fo) and delayed electron transport from PSII to ETC (Fm/F_o) further confirmed by the appearance of K- and L-bands. Alternatively, the fertigation of silicon (Si) through rooting media significantly ($P < 0.001$) enhanced the uptake of essential nutrients i.e., Ca^{2+} , P, K^+ , and Si, while lowered the uptake and/or accumulation of Na^+ and Cl^- concentration in salt-stressed barley plants. Similarly, the PSII efficiency was enhanced by maintaining photosynthetic apparatus intact under salt-stressed plants. The yield response was also lowered in salt-stressed barley plants, whereas Si application improved yield-related attributes (grains weight, number of tillers, and number of grains). Salinity (200 mM NaCl) stress reduced growth (26–58%) and biomass accumulation (25–34%) while application of silicon through rooting media enhanced growth (29–36%) and biomass (16–19%) in barley (B-10008, B-14011) genotypes as compared to salt-stressed plants. This boost in growth after silicon supplement showed improved chlorophyll contents, photosynthetic efficiency, ionic balance, and ultimately better yield (26–55%). Although the tolerant genotype (B-10008) showed better salt tolerance, still the response of sensitive genotype (B-14011) was outstanding after silicon application in saline environment.

Keywords Barley · Chlorine · Sodium · Silicon · K-band · PSII efficiency · Yield

1 Introduction

Soil salinity is a major global problem affecting almost 50% of the world's irrigated land, and is a key constraint in achieving maximum agricultural goals (Fita et al. 2015; Thorne et al. 2020). Soils having elevated levels of salts disturb cellular processes in plants via experience oxidative stress, nutrient imbalance, disturbance in the synthesis of hormones, modifications in antioxidant response, and interruption in signaling pathway and gene expression (Khan et al. 2020a; Zhao et al. 2020). Under such circumstances, the excessive accumulation of reactive oxygen species (ROS) is an inevitable process that can potentially

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damage photosynthetic pigments that are the backbone of photosynthetic processes (Betzen et al. 2019). The excessive production and accumulation of ROS under salinity-induced oxidative stress normally reduce the repair of D1 protein (a sign of PSII damage), which under low stress has a potential to be repaired automatically (Huihui et al. 2020a; Bose et al. 2017).

Similarly, the concentrations of light harvesting antenna complexes (LHCs) in photosystem I and II (PSI and PSII) are also damaged that reduces absorption of light and transport of electron through thylakoid membranes thus lowering efficiency of photosynthetic apparatus (Majeed and Muhammad 2019). This decrease in LHCs results in reduction in size of reaction centers (RCs) (Fv/Fo), mounting the number of non-functional (closed) reaction centers (VJ and VI), and lowering electron transport through PSII (Fm/Fo) (Akhter et al. 2021b). All these events are responsible for lowering performance index (PI) and efficiency of PSII (Fv/Fm) of photosynthetic apparatus (Lima et al. 2018; Yildiztugay et al. 2020).

Tolerance to salinity in different plant species depends on their ability to maintain adequate water and nutrient status in response to increased salinity (Khan et al. 2019b). The efficiency by which the antioxidants can detoxify excessive ROS under saline environment is also an important indicator of stress tolerance in many plants species (Khan et al. 2020a). The plants have internal mechanism to tolerate salinity either by reducing Na^+ uptake, enhancing its efflux from roots, or compartmentalizing extra Na^+ in that vacuole to minimize cytoplasmic ionic toxicity. The plant's internal stress-induced defense can only counter these stresses up to a certain limits, which is normally mitigated by application of materials like silicon (Si) that has gained much attention in improving salinity tolerance in crops during recent years (Meng et al. 2020).

Silicon is absorbed by roots as $\text{Si}(\text{OH})_4$ by the action of specific aquaporin and is transported to aerial parts (leaves) via transpiration stream (Chaiwong and Prom-u-thai 2022; Exley et al. 2020). Si fertigation through external means improves the growth and yield of plants subjected to drought and salinity (Coskun et al. 2016; Guerriero et al. 2016). However, Si application through external means under saline media has the ability to enhance plant growth through modulating metabolic, physiological, and molecular processes (Khan et al. 2019a), maintaining nutrient balance, reducing ion toxicity, and enhancing ROS scavenging system (Abdelaal et al. 2020). Si application on one the hand reduces Na^+ concentration while on the other hand increases K^+ concentration (Meng et al. 2020) through enhanced activity of H^+ -ATPase on plasma membranes and H^+ -PPase in saline media (Soleimannejad et al. 2019). This upregulation of H^+ -ATPase and H^+ -PPase is involved in exclusion of Na^+

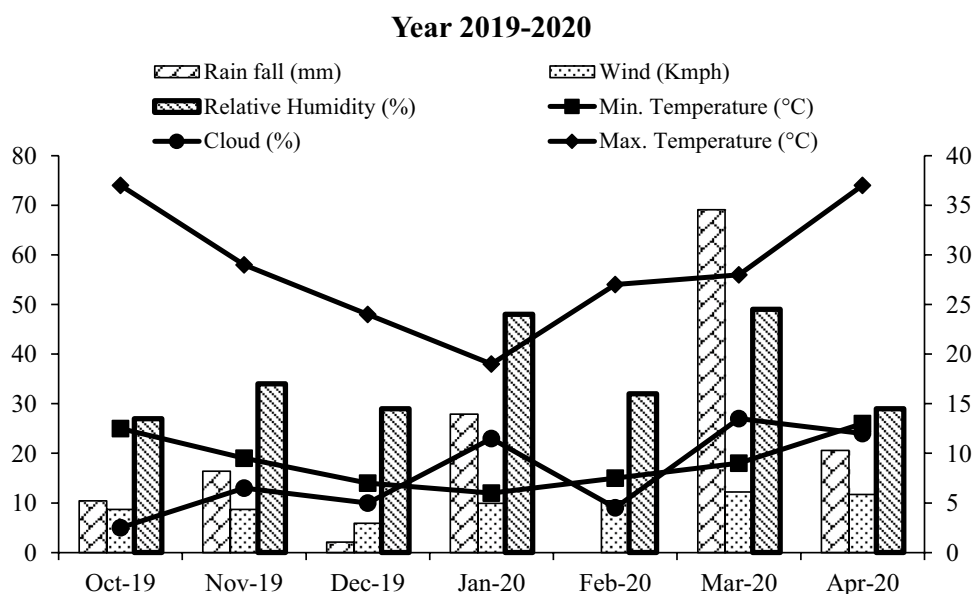
out of cell and compartmentalization of Na^+ into vacuole to reduce Na^+ toxicity caused by salt stress (Assaha et al. 2017). Similarly, the constituents of P, Ca^{2+} , Mg, and Fe are reported to be boosted through application of Si which leads to optimal growth under stress (Li et al. 2015; Khoshgoftarmansh et al. 2014). The Si-mediated enhancement in growth has potential to considerably improve yield of crops grown under saline stress (Kumar et al. 2020; Martin et al. 2017; Saleh et al. 2017). Therefore, it is necessary to comprehend the means for yield improvement of barley crop by adopting mitigation approaches to salt stress. The principal objective of this study was to evaluate the role of Si against negative impacts of salinity stress in barley crop. Thus, we evaluated the role of application Si through rooting media in maintaining growth, ionic homeostasis, improving photosynthetic efficiency, and enhancing yield of barley genotypes under salinity stress.

2 Materials and Methods

The study was conducted at Botanic Garden, Institute of Pure and Applied Biology, Bahauddin Zakariya University Multan, Pakistan (latitude 30.26° and longitude 31.50°) from October 2019 to April 2020. The seeds of six rowed barley genotypes, viz B-10008 (RHN-03//ARAR/LIGNEE527) and B-14011 (Rhn-03/7/Giza121/CI06248/4/Apm/1B65//11012-2/3/Api/CM-ICB05-0998-0AP-4AP-0AP), were obtained from Wheat Research Institute, Ayub Agriculture Research Institute Faisalabad, Pakistan. The meteorological data (Fig. 1) presents the monthly average rain fall (mm), wind (Kmph), relative humidity (%), clouds (%), and maximum and minimum temperature for 2019–2020 growing period. The barley genotype B-10008 was screened as salt-tolerant while B-14011 was screened as salt-sensitive genotype in our earlier experiment (Akhter et al. 2021b).

The pots filled with 8 kg of river sand (Stoughton 1953) for each genotype were divided into two groups: (a) control (with no salinity) and (b) saline (200 mM NaCl); however, each group, a and b, was further divided into two sub-groups: (i) control with no Si application ($-\text{Si}$) and (ii) 200 ppm Si application ($+\text{Si}$). Ten healthy seeds of each genotype were sown in respective pots arranged in factorial Completely Randomized Design (CRD) with four replicates for each treatment. After complete germination, two plants per pot were maintained to grow and harvested at maturity. One plant was used for morphological, physiological, and biochemical analysis while the second one used to record yield attributes. Salinity (200 mM NaCl) was applied to barley plants at 3rd week of germination. The salinity levels were developed by adding NaCl (national refined salt 99% pure) in distilled water, while EC of leached water was monitored by portable EC meter (AD 31 EC/TDS)

Fig. 1 Meteorological data presenting monthly average rain fall (mm), wind (Kmph), relative humidity (%), clouds (%), and maximum and minimum temperature for 2019–2020 growing period



to ensure that desired concentration of salt was developed in each pot. Salt levels in aliquots were increased step wise, with gap of 1 day, from 50 to final 200 mM NaCl concentration. The salt level at 200 mM NaCl was maintained after every week. The first application of Si (200 ppm) through rooting media was done when the barley plants were 28 days old, while 2nd Si application (similar dose) was done 15 days after 1st Si application. The required Si solutions were prepared by adding measured volume of liquid $K_2SiO_3 \cdot 2H_2O$ (Daejung) in distilled water and pH = 8 was maintained by adding few drops of HCl. The plants were regularly irrigated with tap water while Hoagland and Arnon (1950)'s nutrient solution (Table 1) was applied once a week to fulfill nutrient requirements of plants. The data for following attributes was recorded at 4th week of 1st

Si treatments, while yield attributes were recorded at maturity of barley crop.

2.1 Morphological Attributes

Four plants from each treatment were uprooted carefully, washed with water, and cut into roots and shoots. The root and shoot lengths were measured using measuring rod, while their fresh and dry (after oven drying at for 48 h at 75 °C) weights were recorded using digital balance.

2.2 Chlorophyll Concentration

The chlorophyll contents were extracted with acetone (C_3H_6O) using Arnon (1949) methodology. For this purpose,

Table 1 The compositions of Hoagland and Arnon nutrient solution

Chemicals	Molecular weight (g mol ⁻¹)	Concentration in stock solution	Volume of stock solution per liter of final solution (water)
Macronutrients			
KNO ₃	101.10	101.10 g L ⁻¹	6 mL
Ca(NO ₃) ₂ ·4H ₂ O	236.16	236.16 g L ⁻¹	4 mL
NH ₄ H ₂ PO ₄	115.08	115.08 g L ⁻¹	2 mL
MgSO ₄ ·7H ₂ O	246.48	246.48 g L ⁻¹	1 mL
Micronutrients			
KCl	74.55	1.864 g L ⁻¹	2 mL
H ₃ BO ₃	61.83	0.773 g L ⁻¹	
MnSO ₄ ·H ₂ O	169.01	0.169 g L ⁻¹	
ZnSO ₄ ·7H ₂ O	287.54	0.288 g L ⁻¹	
CuSO ₄ ·5H ₂ O	249.68	0.062 g L ⁻¹	
H ₂ MoO ₄ (85% MoO ₃)	161.97	0.040 g L ⁻¹	
Na.Fe EDTA (10%Fe)	558.5	8.03 g L ⁻¹	1 mL

0.1 g of mid-rib free flag leaves from each replicates was grinded in 5 mL 80% acetone using pestle and mortar and filtered with Whatman filter paper. The absorbance was noted at 663 nm and 645 nm using spectrophotometer and concentrations of chlorophyll-a (C_a), chlorophyll-b (C_b), and total chlorophyll (C_t) were calculated using the following formulas.

$$C_a = (12.7A_{663} - 2.69A_{645}) \times V / (1000 \times W)$$

$$C_b = (22.9A_{645} + 8.02A_{663}) \times V / (1000 \times W)$$

$$C_t = (20.2A_{645} + 8.02A_{663}) \times V / (1000 \times W)$$

where C: concentration of (a) chlorophyll-a, (b) chlorophyll-b, and (t) total chlorophyll; V: volume of buffer; W: weight of leaf sample; A: absorbance at specific wavelength

2.3 Leaf Relative Water Contents (LRWC)

The LRW contents were measured by the Smart and Bingham (1974) method. A mature flag leaf from each replicate was trimmed at 9 a.m. and fresh weights (FW) were recorded immediately. The leaf samples were submerged in distilled water from their cut side and turgid weights (TW) were recorded after 10 h. These leaves were then oven dried, and dry weights (DW) were recorded. Following formula was used for measuring LRWC.

$$LRWC = \frac{FW - DW}{TW - DW} \times 100$$

2.4 Total Soluble Proteins (TSP)

The fresh flag leaf samples (0.5 g) from each replicate were homogenized in sodium phosphate buffer (8 mL, pH 7.8) and centrifuged at 15,000 rpm for 12 min at 4 °C. The 0.1 mL of supernatant thus removed was poured in test tubes containing 5 mL Bradford reagent. The reading was taken at 595 nm using a spectrophotometer after 15 min of incubation at room temperature (Bradford 1976). TSP contents were determined using the standard curve.

2.5 Chlorophyll-a Fluorescence

The response of dark adapted leaves (covered with aluminum foil for 30 min) was recorded by using fluorescence meter (FP-100MX-LM, Photon International). Different attributes like accumulation of close reaction centers (V_j and V_1), the efficiency of water splitting complex on donor side of PSII (F_v/F_o), electron transport rate through PSII (F_m/F_o), the physiological state of photosynthetic apparatus

(baseline quantum yield) (F_0/F_m), and maximum quantum yield of PSII (F_v/F_m) were recorded in barley plants (Strasser et al. 2000; Umar et al. 2019).

The chlorophyll-a fluorescence curves were double normalized between F_o (maximum fluorescence at 20 μ s) and F_K (maximum fluorescence at 300 μ s) and were expressed as $\Delta VOK = [VOK = \left\{ \frac{F_t - F_o}{F_k - F_o} \right\}]$ to understand the probability of fluorescence rise at K step (300 μ s), while the kinetic differences between saline and non-saline curves of this phase were expressed as ΔVOK or L-band (ΔVOK). The curves were double normalized between F_o (20 μ s) and F_J (maximum fluorescence at 2000 μ s) and were expressed as $\Delta VOJ = [VOJ = \left\{ \frac{F_t - F_o}{F_j - F_o} \right\}]$ and the kinetic difference between saline and non-saline curves were expressed as K-band (ΔVOJ) (Strasser et al. 2004; Kalaji et al. 2018).

2.6 Quantum Yield (QY)

Quantum yield (QY) was recorded from middle of the fully expanded flag leaf at midday by FluorPen (FP-100 MX-LM, Photon International). The mean of three readings from each replicate was taken.

2.7 Ion Estimation

For estimation of ionic contents (Na^+ , K^+ , Ca^{2+} , P, Cl^- , and Si) in dried leaf and root samples, digestion mixture was prepared. The mixture of 14 g $LiSO_4 \cdot 2H_2O$ (lithium sulfate) and 0.42 g Se (selenium) mixed in 350 mL of dH_2O_2 was slowly poured in ice bathed flask containing 420 mL of concentrated H_2SO_4 (sulfuric acid). The digestion mixture so formed was used for digestion of plant samples. Leaf and root samples (0.1 g) were taken in digestion flasks containing 2 mL of digestion mixture and were kept overnight at 25 °C. Afterwards, the flasks were transferred to hot plate set at 250 °C for 30 min. Samples were heated till fume formation. Flasks were removed; 0.5 mL of $HClO_4$ (perchloric acid) was added in each flask and again transferred these flasks to hot plate at 250 °C for almost 2 h until discoloration of samples. After filtration of these samples, the volume was raised to 50 mL with dH_2O and was used for estimation of ionic concentration (Allen et al. 1985).

The Na^+ , K^+ , and Ca^{2+} concentrations in plant samples were estimated using flame photometer (Jenway-PFP7, UK) while Cl^- concentration was recorded by chlorine analyzer (CLH 1740) (Munns et al. 2010; Schrenk et al. 1951). The concentration of Si in leaves and roots was measured by $(NH_4)_6Mo_7O_{24}$ methodology devised by (Weimin et al. 2005) at 650 nm with UV-Vis spectrophotometer (Hitachi U-2900, Hitachi High Technologies America, Inc.), while Barton's reagent was used to determine phosphorous concentrations in leaves and roots (Jackson 1973).

2.8 Flag Leaf Area

The flag leaf area (FLA) is a characteristic feature of cereal crop plants. Owing to its physiological significance for in important metabolic processes and economic yield, FLA was used as predictor. FLA was measured as mean of three flag leaves from each pot. The length and width was multiplied for measuring FLA (Muller 1991).

2.9 Yield

At maturity, all spikes were removed from each plant and data for different yield attributes were recorded including no. of tillers plant⁻¹; number of grains spike plant⁻¹; grain weight spike⁻¹, grain weight plant plant⁻¹, and 100 grain weight. Three spikes from each plant/replicate were crushed, seeds were removed, and the mean number and weight of grains correspond to number of grains spike plant⁻¹ and grain weight spike⁻¹ respectively. Similarly, all the spikes/plant/replicate were cured and weight was recorded for grain weight plant⁻¹.

2.10 Statistical Analysis

Experimentation was done in factorial Complete Randomize Design (CRD) with three factors (genotype, salinity, and silicon) and four replications for each treatment.

Three-way analysis of variance (ANOVA) was performed using SPSS-20 (SPSS Inc. Chicago, IL, USA). Means were compared using Duncan's multiple range test (DMRT) at $P \leq 0.05$ significance level. Graphs were developed using Origin (v.2021) and R-studio (v 4.0.4) was used to draw principal component analysis and correlation with the help of "ggplot2" package.

3 Results

3.1 Biomass Accumulations

Salt stress (200 mM NaCl) resulted in substantial ($P < 0.001$) differences in biomass accumulation, i.e., fresh and dry weights of shoot and root, while application of 200 ppm silicon (Si) through rooting media enhanced the accumulation biomass either under control or saline conditions (Table 2). It was observed that under control conditions, the application of Si enhanced shoot fresh weight (12%, B-1008; 18%, B-14011), shoot dry weight (33%, B-1008; 20%, B-14011), root fresh weight (22%, B-1008; 43%, B-14011), and root dry weights (20%, B-1008; 21%, B-14011). On the other hand, salinity stress reduced shoot fresh weights (20%, B-10008; 56%, B-14011), shoot dry weights (19%, B-10008; 52%, B-14011), root fresh weights (16%, B-10008; 65%, B-14011), and root

Table 2 Influence of rooting media fertigation of 200 ppm Si on shoot and root fresh weights, shoot and root dry weights, and shoot and root lengths of barley genotypes B-10008 and B-14011 grown under non-saline and saline (200 mM NaCl) conditions

Genotypes	Treatments	Shoot fresh weight (g plant ⁻¹)	Shoot dry weight (g plant ⁻¹)	Root fresh weight (g plant ⁻¹)	Root dry weight (g plant ⁻¹)	Shoot length (cm)	Root length (cm)
B-10008	Control	124.1 ± 1.65 ^b	15.7 ± 0.72 ^a	70.9 ± 3.49 ^{ab}	7.53 ± 0.11 ^{ab}	106.59 ± 2.16 ^b	35.64 ± 1.57 ^b
	200 ppm Si	146.8 ± 2.63 ^a	19.3 ± 0.54 ^a	77.9 ± 1.85 ^a	8.34 ± 0.48 ^a	130.70 ± 3.97 ^a	46.52 ± 0.91 ^a
	200 mM NaCl	86.51 ± 2.43 ^e	9.73 ± 0.73 ^d	49.6 ± 1.69 ^c	5.12 ± 0.32 ^e	78.47 ± 1.07 ^{cd}	27.93 ± 1.46 ^c
	200 mM NaCl + 200 ppm Si	105.3 ± 3.10 ^c	14.5 ± 1.14 ^{cd}	67.6 ± 2.35 ^b	6.99 ± 0.25 ^{bc}	101.33 ± 1.53 ^b	35.01 ± 0.80 ^b
	Control	96.0 ± 2.10 ^d	10.7 ± 0.91 ^{cd}	53.2 ± 3.71 ^c	5.74 ± 0.35 ^{de}	72.97 ± 1.86 ^d	18.21 ± 1.13 ^d
B-14011	200 ppm Si	107.6 ± 2.05 ^c	12.7 ± 0.46 ^c	62.4 ± 2.13 ^b	6.32 ± 0.22 ^{cd}	81.73 ± 2.71 ^c	20.81 ± 0.97 ^d
	200 mM NaCl	25.5 ± 1.26 ^g	2.93 ± 0.40 ^e	25.1 ± 1.56 ^d	2.73 ± 0.09 ^f	29.96 ± 1.65 ^f	7.26 ± 0.59 ^e
	200 mM NaCl + 200 ppm Si	34.0 ± 1.65 ^f	4.35 ± 0.034 ^e	30.3 ± 1.77 ^d	3.37 ± 0.11 ^f	40.63 ± 2.68 ^e	9.84 ± 0.70 ^e
	Control	***	***	***	***	***	***
	Salinity	***	***	***	***	***	***
ANOVA	Silicon	***	***	**	***	***	***
	Genotype × salinity	***	*	*	ns	***	ns
	Genotype × silicon	*	**	ns	**	***	***
	Salinity × silicon	ns	ns	ns	ns	ns	ns
	Genotype × salinity × silicon	ns	ns	**	*	ns	ns

Data are means ± SE ($n=4$). Different letters (a–g) represent significant difference at $P \leq 0.05$ (Duncan's multiple range test). ***, **, * = significance at 0.001, 0.01, 0.05 respectively; ns, non-significant

Value in the bold indicates the parameter studied and plant parts

dry weights (25%, B-10008; 64%, B-14011). However, the application of Si caused enhancement in shoot fresh weights (25%, B-10008; 34%, B-14011), shoot dry weights (25%, B-10008; 28%, B-14011), root fresh weights (24%, B-10008; 65%, B-14011), and root dry weights (47%, B-10008; 59%, B-14011) as compared to salt treatment. The results showed that the increase in biomass accumulation was more prominent in B-14011 (salt-sensitive genotype) after application of Si under salinity stress (Table 2).

3.2 Shoot and Root Length

Both barley genotypes experienced a notable drop in length (shoot and root) after being exposed to salt stress; however, the application of Si showed positive impact of height of barley plants either under control or saline conditions (Table 2). Salinity stress caused a significant reduction in shoot (26% and 58%) and root lengths (22% and 60%) in B-10008 and B-14011, respectively, compared to control, while the application of Si enhanced shoot and root length of both genotypes under salinity stress. However, the enhancement in shoot and root length was prominent on B-14011 (37% and 35%) as compared to B-10008 (29% and 25%) after Si application under salinity stress (Table 2).

3.3 Chlorophyll Contents

Results displayed that the effect of Si was significant on chl.-a and total chl. contents while non-significant on chl.-b under salinity stress (Table 3). When silicon was applied under saline conditions, the genotype B-14011 accumulated higher chl.-b and total chlorophyll contents, whereas genotype B-10008 accumulated maximum chl.-a contents at this treatment (Table 1). The maximum decrease in chl.-a (43%), chl.-b (44%), and total chl. (44%) contents was noted in genotype B-14011 at 200 mM NaCl stress. However, using 200 ppm Si under saline environment caused highest improvement in chl.-a (36%), chl.-b (48%), and total chl. (40%) contents in same genotypes (Table 3).

3.4 Leaf Relative Water Contents

A significant variation in LRWC was observed among barley genotypes subjected to salt stress. The impact of Si was also prominent (Table 3). As compared to control plants, maximum reduction (19%) in LRWC under salinity stress was observed in B-14011, while the same genotype showed higher (18%) improvement in LRWC after application of Si through rooting media under saline environment, while the LRWC of B-10008 showed non-significant effect of either salinity stress or Si application (Table 3).

Table 3 Influence of rooting media fertigation of 200 ppm Si on chlorophyll-a, chlorophyll-b, and total chlorophyll, total soluble proteins, leaf relative water contents (LRWC), and quantum yield (QY) of

barley genotypes B-10008 and B-14011 grown under non-saline and saline (200 mM NaCl) conditions

Genotypes	Treatments	Chlorophyll-a (mg g ⁻¹ f.wt)	Chlorophyll-b (mg g ⁻¹ f.wt)	Total chlorophyll (mg g ⁻¹ f.wt)	Total soluble proteins (mg g ⁻¹ f.wt)	LRWC (%)	Quantum yield
B-10008	Control	1.34 ± 0.053 ^b	0.49 ± 0.011 ^b	1.83 ± 0.045 ^b	6.64 ± 0.19 ^c	92 ± 2.35 ^{bc}	0.83 ± 0.006 ^b
	200 ppm Si	1.45 ± 0.053 ^a	0.55 ± 0.018 ^a	2.00 ± 0.034 ^a	7.59 ± 0.45 ^b	95 ± 2.02 ^a	0.86 ± 0.003 ^a
	200 mM NaCl	1.13 ± 0.019 ^c	0.44 ± 0.012 ^{cd}	1.58 ± 0.027 ^c	8.17 ± 0.25 ^b	90 ± 2.85 ^{cd}	0.76 ± 0.004 ^c
	200 mM NaCl + 200 ppm Si	1.29 ± 0.030 ^b	0.48 ± 0.018 ^{bc}	1.77 ± 0.019 ^b	10.5 ± 0.32 ^a	93 ± 2.84 ^{ab}	0.81 ± 0.003 ^{bc}
B-14011	Control	1.04 ± 0.015 ^c	0.43 ± 0.014 ^d	1.47 ± 0.018 ^d	1.84 ± 0.28 ^f	90 ± 1.16 ^d	0.82 ± 0.015 ^b
	200 ppm Si	1.11 ± 0.025 ^c	0.44 ± 0.016 ^{cd}	1.55 ± 0.018 ^c	2.01 ± 0.16 ^f	92 ± 2.38 ^{cd}	0.83 ± 0.012 ^b
	200 mM NaCl	0.59 ± 0.006 ^e	0.24 ± 0.013 ^f	0.83 ± 0.008 ^f	3.25 ± 0.24 ^e	73 ± 1.58 ^f	0.70 ± 0.009 ^d
	200 mM NaCl + 200 ppm Si	0.80 ± 0.032 ^d	0.35 ± 0.013 ^e	1.16 ± 0.026 ^e	4.50 ± 0.42 ^d	86 ± 2.84 ^e	0.78 ± 0.011 ^{cd}
ANOVA	Genotype	***	***	***	***	***	***
	Salinity	***	***	***	***	***	***
	Silicon	***	***	***	***	***	***
	Genotype × salinity	***	***	ns	ns	ns	*
	Genotype × silicon	ns	ns	***	*	ns	ns
	Salinity × silicon	*	ns	**	**	ns	***
	Genotype × salinity × silicon	ns	**	**	ns	ns	*

Data are means ± SE ($n=4$). Different letters (a–g) represent significant difference at $P \leq 0.05$ (Duncan's multiple range test). ***, **, * = significance at 0.001, 0.01, 0.05 respectively; ns, non-significant

Value in the bold indicates the parameter studied and plant parts

3.5 Total Soluble Protein Contents

In both genotypes, a significant ($P < 0.001$) accumulation of TSP content was observed after saline stress or Si application (Table 3). The accumulation of TSP was 23% in B-10008 and 76% in B-14011 under saline stress as associated to control barley plants, while after application of Si under salinity stress, this enhancement was further accelerated to 29% in B-10008 and 38% in B-14011 (Table 3).

3.6 Leaf and Root Sodium (Na^+) and Chlorine (Cl^-) Concentrations

At 200 mM NaCl stress, the concentration of Na^+ and Cl^- in the roots and leaves of barley plants was considerably ($P < 0.001$) increased. Similarly, the response of genotypes and Si application also showed significant ($P < 0.001$) response (Table 4). A significant interaction of genotype \times salinity showed that the impact of salt on the buildup of Na^+ and Cl^- in roots and leaves was different in both genotypes. Similarly, a significant ($P < 0.001$) interaction between salinity \times Si showed that application of Si under saline stress posed a prominent effect on lowering the accumulation/uptake of these elements in both barley genotypes (Table 4).

Data revealed that behavior of Na^+ and Cl^- accumulation in barley plant parts was remarkably similar, with maximum accumulation of leaf Na^+ (1092%), root Na^+ (263%), leaf Cl^- (1595%), and root Cl^- (923%) contents in B-14011 in salt-stressed plants as compared to control. However, the genotype B-10008 relatively accumulated lower leaf and root Na^+ (427% and 227%) and leaf and root Cl^- (1007% and 517%) contents under saline media (Fig. 2a, b). The application of Si to salt barley-stressed plants lowered leaf and root Na^+ (742% and 428%) and Cl^- (1399% and 742%)

contents more prominently in genotype B-14011 as compared to leaf and root Na^+ (294% and 144%), Cl^- (90% and 125%) contents of B-10008 (Fig. 2a, b).

3.7 Leaf and Root Potassium (K^+) and Calcium (Ca^{2+}) Concentration

It has also been observed from ANOVA that application of Si under saline stress (salt \times Silicon) showed significant ($P < 0.001$) interaction (Table 4), while salinity-induced decrease in K^+ and Ca^{2+} concentration in barley plants was enhanced with the application of 200 ppm Si through external means. As compared to control, the application of Si to non-saline barley genotypes enhanced leaf and root K^+ (39% and 21% in B-10008; 10% and 6% in B-14011) and Ca^{2+} (17% and 23% in B-10008; 11% and 19% in B-14011) contents respectively (Fig. 2c, d).

Salt application decreased the concentrations of K^+ and Ca^{2+} in leaves and roots in both genotypes while Si application with salt treatment decreased the effect of salinity stress by enhancing the uptake and accumulation of these elements in both barley genotypes. When Si was applied under saline conditions, maximum enhancement in leaf K^+ (from 32 to 8%), root K^+ (29 to 12%), leaf Ca^{2+} (39 to 27%), and root Ca^{2+} (64 to 27%) concentrations was observed in salt-sensitive genotype B-14011 (Fig. 2c, d).

3.8 Leaf and Root Phosphorus (P) Concentration

The leaf and root P concentrations were lowered under salinity stress. A significant interaction (salt \times silicon) showed that the presence of Si positively affected leaf and root P concentration in salt stress growing media (Table 4). Under salinity stress, this decrease was 10% and 20% in leaves and

Table 4 Three-way ANOVA summary for significance for different parameters studied in barley genotypes B-10008 and B-14011 grown under non-saline and saline (200 mM NaCl) conditions, after 200 ppm Si application

Parameters		G	S	Si	G \times S	G \times Si	S \times Si	G \times S \times Si
Na^+	Leaf	***	***	***	***	ns	**	ns
	Root	***	***	***	*	*	***	*
Cl^-	Leaf	***	***	***	***	ns	***	ns
	Root	*	***	***	***	ns	***	ns
K^+	Leaf	***	***	***	*	ns	*	ns
	Root	***	***	***	ns	ns	**	*
Ca^{2+}	Leaf	***	***	***	***	***	*	ns
	Root	***	***	***	***	ns	*	ns
P	Leaf	***	***	*	ns	ns	*	ns
	Root	**	**	***	ns	ns	*	*
Si	Leaf	***	***	***	**	***	ns	ns
	Root	***	***	***	ns	ns	*	***

***, **, * = significance at 0.001, 0.01, 0.05 respectively; ns, non-significant; Na^+ , sodium; Cl^- , chlorine; K^+ , potassium; Ca^{2+} , calcium; P, phosphorous; Si, silicon; G, genotypes; S, salinity

Value in the bold indicates the parameter studied and plant parts

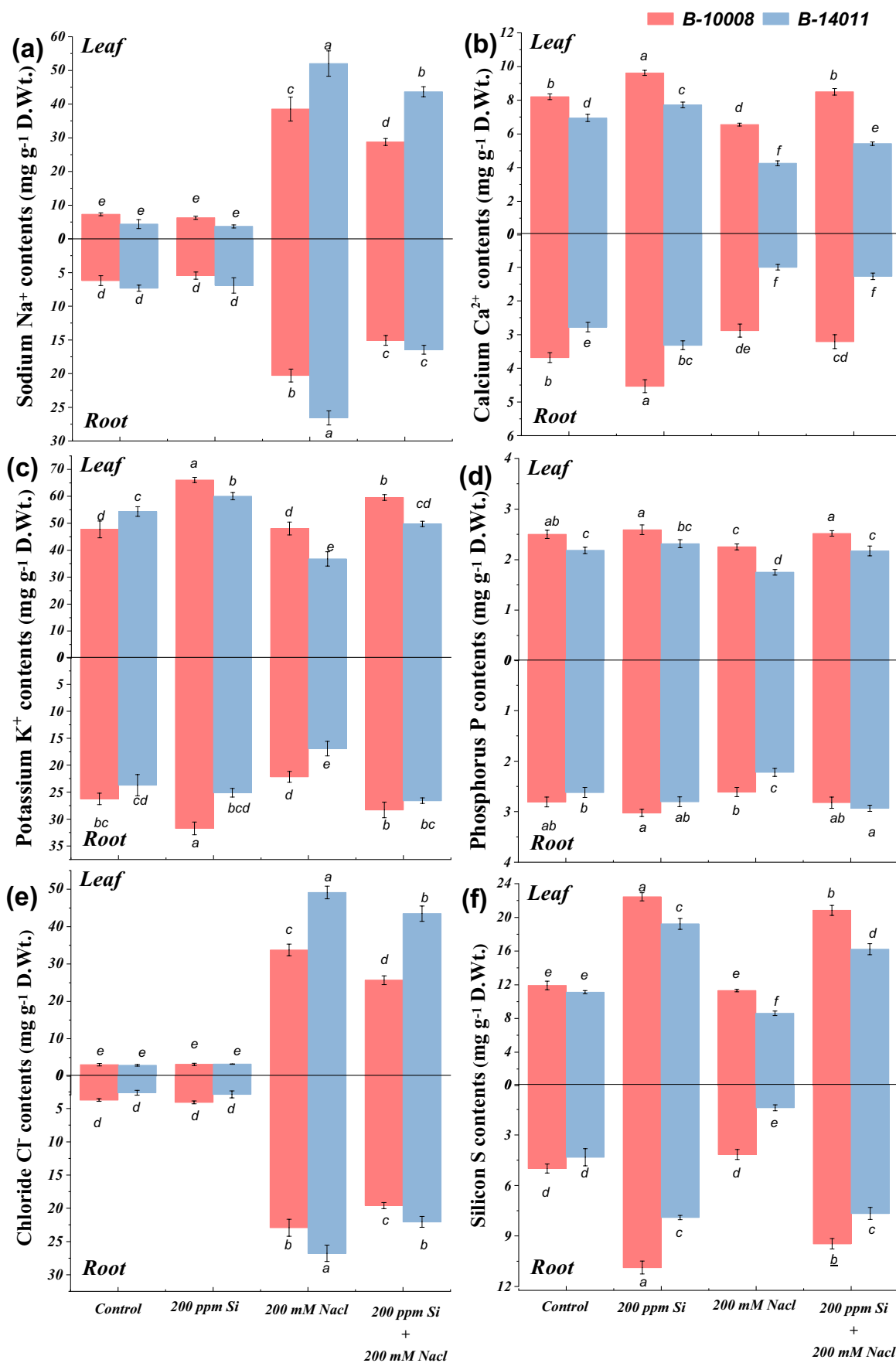


Fig. 2 Influence of rooting media fertigation of 200 ppm Si on leaf and root Na⁺ (a), Ca²⁺, (b), K⁺ (c), P (d), Cl⁻ (e), and Si (f) contents (mg g⁻¹ D.wt.) of barley genotypes (B-10008 and B-14011) grown at 200 mM NaCl stress. Data (bars) are means ± SE (*n*=4). Different letters (a–f) above and below bars represent significant difference at *P* ≤ 0.05 (Duncan's multiple range test)

7% and 15% in roots of B-10008 and B-14011 respectively compared with control plants, while P concentration under salinity stress with the application of Si the P contents was enhanced to 12% and 24% in leaves and 8% and 32% in roots of B-10008 and B-14011 respectively as compared to their respective salt-treated plants (Fig. 2e).

3.9 Leaf and Root Silicon (Si) Concentration

The contents of Si were declined in leaves and root tissues of barley plants under saline environment, while the Si application reduced the effect of salinity by improving Si concentration in barley plants under salinity stress (Table 4). It was observed from data that the accumulation of leaf and root Si concentration was 89% and 118% in B-10008 and 73% and 81% in B-14011, respectively, after Si application through rooting media in comparison to control plants. The salt stress reduced leaf Si concentration to 5% and 23% and root Si concentration to 16% and 68% in B-10008 and B-14011 respectively, while the application of Si through rooting media to plants experiencing salinity stress significantly enhanced Si concentration in leaf (84% and 88%) and root (126% and 453%) of B-10008 and B-14011 respectively (Fig. 2f).

3.10 Quantum Yield

As compared to control plants, genotype B-14011 showed maximum reduction (15%) in QY under salt treatment, while after application of Si through rooting media under saline environment, the same genotype showed 11% higher QY as compared to B-10008 (7%) (Table 3).

3.11 Performance of PSII

The performance of PSII (probed by chlorophyll-*a* fluorescence) was lowered under salinity stress in barley plants; on the other hand, Si application reduced the toxic effects of salinity by maintaining the PSII efficiency. The data revealed that accumulation of closed reaction centers at PSII (represented by V_J and V_I) was improved under salinity stress. However, Si application reduced the number of closed reaction (V_J and V_I) especially under saline conditions (Fig. 3). A considerable reduction in state of photosynthetic apparatus (F_O/F_m); efficiency of water splitting complex on donor end of PSII (F_v/F_o) and the electron transport rate through

PSII (F_m/F_O) were observed under salinity stress. Reduction in these parameters also lowered quantum yield of PSII (F_v/F_m) in barley plants subjected to salt treatment. However, this depression was more prominent in B-14011 as compared to B-10008 under stress. Conversely, Si application enhanced the health of PSII by improving F_v/F_o, F_m/F_o, F_o/F_m, and F_v/F_m under salinity stress. Salinity stress significantly increased dissipation energy flux (DI_o/RC) to protect PSII from photo-damage, which was further escalated with Si application under salinity stress (Fig. 3).

Further examination of OJIP data demonstrated that K- and L-bands developed in both barley genotypes under salinity stress. The K- and L-bands were more prominent in B-14011 than B-10008 under salinity (Fig. 4). As compared to control plants, a positive K-band was observed in B-14011 than B-10008 where it showed a negative value for this parameter under salinity stress. A negative L-band was observed in B-14011 under salinity stress. In B-10008, the L-band was positive till 100 μs then it becomes negative. On the other hand, the Si application through external means reduced the damages of NaCl to PSII and OEC by restoring the connections of LHCs to PSII and maintained structural stability of PSII (K- and L-band) under salinity stress (Fig. 4).

3.12 Yield Attributes

All studied yield attributes [(flag leaf area (FLA), no. of tiller (NOT), no. of grains/spike (NOG/S), grain weight/spike (GW/S), grain weight/plant (GW/P), and 100 grain weight (HGW)] showed an evident effect of salinity and Si application. Maximum decrease in FLA (33%), NOT (48%), NOG/S (34%), GW/S (46%), GW/P (72%), and HGW (39%) was noted in salt-sensitive genotype B-14011 under salinity (200 mM NaCl) stress which was reduced to 28% (FLA), 40% (NOT), 27% (GW/S), 26% (NOG/S), 55% (NOG/P), and 26% (HGW) in same genotypes after application of 200 ppm Si under saline environment (Fig. 5).

3.13 Correlations

The correlation analysis (Pearson's) depicted a positive correlation among chlorophyll constituents, ionic concentrations, and yield attributes of barley plants; however, Na⁺ and Cl⁻ concentrations in leaves and roots of barley plants posed significantly negative effect on all studied parameters (Fig. 4). Although Na⁺ and Cl⁻ caused drastic effect on all studied parameters, still the negative effect of these elements was more prominent on F_v/F_m, root and leaf Ca²⁺ concentration, HGW, NOT, and GW/P of barley genotypes. The data showed that Si concentrations in barley tissues showed a positive relationship with chlorophyll constituents, F_v/

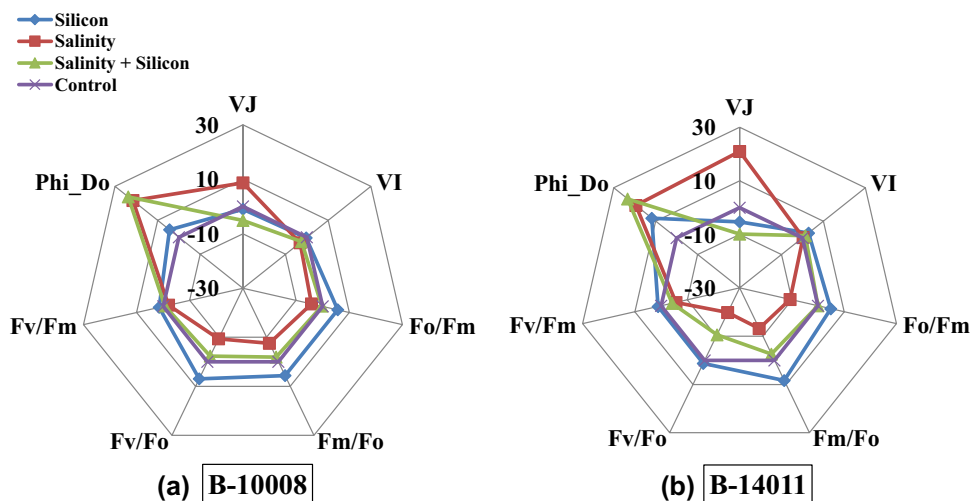
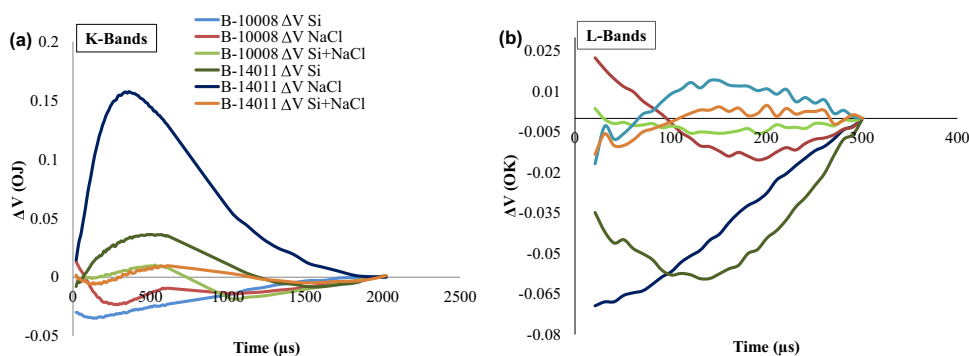


Fig. 3 Effect of rooting application of 200 ppm Si on some chlorophyll fluorescence parameters (V_j , V_i , F_o/F_m , F_m/F_o , F_v/F_o , F_v/F_m , and Φ_{iDo}) of barley genotype B-10008 (a) and B-14011 (b) grown at 200 mM NaCl stress. V_j : variable fluorescence at J step; V_i : variable fluorescence at I step; F_o : maximum fluorescence at 20 μ s; F_m :

maximum fluorescence at 2 ms; F_v : variable fluorescence ($F_m - F_o$); F_o/F_m : quantum yield of baseline; F_m/F_o : rate of electron transport through PSII; F_v/F_o : size and number of active reaction centers of photosynthetic apparatus; F_v/F_m : maximum quantum yield of PSII; Φ_{iDo} : dissipation energy flux

Fig. 4 Influence of rooting media fertigation of 200 ppm Si on K-Band (a) and L-Bands (b) of barley genotypes (B-10008 and B-14011) grown at 200 mM NaCl stress



F_m , yield attributes and ionic concentrations except for Na^+ and Cl^- concentrations where a negative interaction was observed (Fig. 6).

3.14 Principal Component Analysis (PCA)

The PCA-Biplot (Fig. 7A–C) was drawn to figure out the effect of salt and Si on chlorophyll concentration, chlorophyll fluorescence attributes, ionic concentrations, and yield attributes of two barley genotypes. Results demonstrated that majority of the variables lie in first four Dims while the contribution of Dim. 5–7 was very low (Fig. 7C). The PC1 accounts for 68.4% and PC2 for 10.3% for stress (200 NaCl) and application (200 ppm Si). The PCA (Fig. 5a) for stress displayed that the impact of 200 mM NaCl concentrations was more prominent on R_{Na} , L_{Na} , L_{Cl} , R_{Cl} , F_o/F_v , and F_o/F_m . This PCA also demonstrated a strong negative correlation among leaf and Na^+ and Cl^- concentrations and growth

attributes, chlorophyll constituents, ionic elements, and yield attributes of both barley genotypes. The PCA for Si application showed that 200 ppm Si level caused more prominent effect on barley plants as most of traits representing ionic constituents (LP, RP, LK, RK, LSi, RSi) are present in the area of 200 ppm Si (Fig. 7B).

4 Discussion

Salinity has been a global agricultural concern, reducing crop development and productivity throughout the world (Kramer and Mau 2020). This salinity-induced growth reduction is mainly caused by hyper ionic and hyper osmotic conditions (Naheed et al. 2022; Zeeshan et al. 2020). These conditions disturb photosynthetic process, interfere with the osmotic and ionic equilibrium, and produce extreme ROS (Ahanger and Agarwal 2017; Sarker and Oba 2020;

Thorne et al. 2020) results in stunted growth and low yield (Mahmoud et al. 2020). In response, plants counter salinity-induced damages by a cascade of physio-biochemical and molecular signaling. But persistent exposure to salinity stress may weaken the defense system resulting in cell death and collapse of plant tissues (Akhter et al. 2022; Majeed and Muhammad 2019). In this aspect, exogenous Si treatment can aid the plant to upregulate its defensive system, hence increasing growth and yield (Akhter et al. 2021a; Arif et al. 2020).

The growth response of plants to saline environment gives a complete picture about salinity tolerance of crop as it is an indicator for stress tolerance (Liu et al. 2018). The present study revealed that saline stress caused a significant decline in the growth (fresh and dry weights and lengths) attributes. The basic processes of salinity-induced growth loss include excessive Na^+ and Cl^- buildup in plant cellular systems, a decrease in critical nutrient intake (N, P, K^+ , Ca^{2+} , etc.), and a decline in LRWC (Acosta-Motos et al. 2017). The reduction in accumulation of biomass and shorter shoots and roots length under salinity stress has been previously reported in various plant species like in canola (Naheed et al. 2021), mung bean (Abbasi et al. 2020), wheat (McDonald et al. 2020), barley (Laifa et al. 2020), and maize (Raza et al. 2019). However, Si fertigation reversed the toxic effect of NaCl stress resulting into prominent increase in growth-related attributes (lengths and weights) in barley plants.

The application of Si enhanced deposition of extra Si in leaf cuticle, which helped plant to reduce the evapotranspiration process and conserved more water. These modifications resulted in enhancing photosynthetic process especially under stressful conditions. Similarly, the uptake of Na^+ and Cl^- was declined and redox-homeostasis mechanism was modified after application of Si in salt affect soils (Shi et al. 2013). These favorable alterations following exogenous Si application allow barley plants retain better development under salt stress than salinity stress alone. Similarly, the positive effect of rooting application of 1 mM Si under saline stress (120 mM NaCl) has been demonstrated by Chen et al. (2014) in 31-day-old wheat plants. They found that using Si increased growth characteristics under saline stress significantly.

The optimum growth is directly related to photosynthetic efficiency of the plants which provides essential energy for developmental processes. The photosynthetic process is generally based on photosynthetic pigments (chlorophyll pigments and assessor pigments) which absorb light energy and initiate light reaction, i.e., transfer of light-driven electrons from reaction centers (RC) to electron transport chain (ETC) of thylakoid membrane (Fromme et al. 2003). So, a direct relationship exists between chlorophyll molecules and ETC during photosynthesis (Messedi et al. 2016; Çiçek et al. 2020). But salinity-induced accumulation of Na^+ and Cl^- to toxic levels may reduce photosynthetic activity (Khan

et al. 2019a) through decrease in photosynthetic pigments (Najar et al. 2019; Abbas et al. 2015) and photochemical reactions (Bose et al. 2017). A saline-induced reduction in chlorophyll concentration (chl.-a, chl.-b, and total chl.) was observed in barley plants. However, compared to their respective controls, a greater degree of reduce was observed in B-14011 (salt sensitive) rather than B-10008 (salt tolerant). The salinity-induced increase chlorophyllase activity was the reason behind reduction of these pigments as this activity decreased the synthesis of chlorophyll molecules (Mihailovic et al. 1997).

Si application, on the other hand, increases chlorophyll content in both barley genotypes under control and saline environments. This Si-mediated increment in chlorophyll contents is previously documented in plant species; alfalfa (Zhu et al. 2019), lettuce (Meng et al. 2020), and mulberry (Huihui et al. 2020b). A restoration of chlorophyll concentration was observed in salt-stressed wheat by Parveen and Ashraf (2010). Similarly, the external application of Si for 10 days to salt-stressed tomato plants enhanced chlorophyll concentration (Hoffmann et al. 2020). The enhancement of 22.2% in chlorophyll concentration was observed by Rehman et al. (2020) after application of Si in 2-month-old maize plants under saline stress.

Salinity-induced accumulation of elements (Na^+ and Cl^-) to toxic levels not only degrades chlorophyll molecules but also disturbs the ionization and effectiveness of different protein complexes (PSII and PSI) and electron carriers located on thylakoid membranes (Bose et al. 2017). The results also confirm that under saline stress, the physiological state of PSII (F_o/F_m), considered indicator of stress, was reduced (Umar et al. 2019). The increase value of F_o/F_m under salinity stress specifies that the rate of decrease of (primary quinone electron acceptor of PSII) Q_A was much higher than the rate of oxidation of (secondary quinone electron acceptor of PSII) Q_B, which might be due to accumulation of closed reaction centers at PSII (high V_J and V_I values under stress). The quantum efficiency of water splitting complex on donor end of PSII (F_v/F_o) and the transport of excited electron through PSII (F_m/F_o) were also lowered in NaCl-treated barley plants as compared to control ones. F_v/F_o is one of the most sensitive components of ETC (Fricke and Peters 2002); therefore, any change in the efficiency of this component may reduce the donation of electron from water splitting complex to PSII (Pereira et al. 2000). The presence of K- and L-bands in salt-stressed barley plants also supported the fact that LHCs were damaged and efficiency of OEC was also reduced under saline stress as was detected by Rastogi et al. (2020) in sweet sorghum.

Salinity stress lowered the values of F_v/F_o and F_m/F_o indicating that accumulation of inactive RCs in PSII significantly reduced the electron accepting capacity of PSII from water splitting complex (Sun et al. 2016). These events

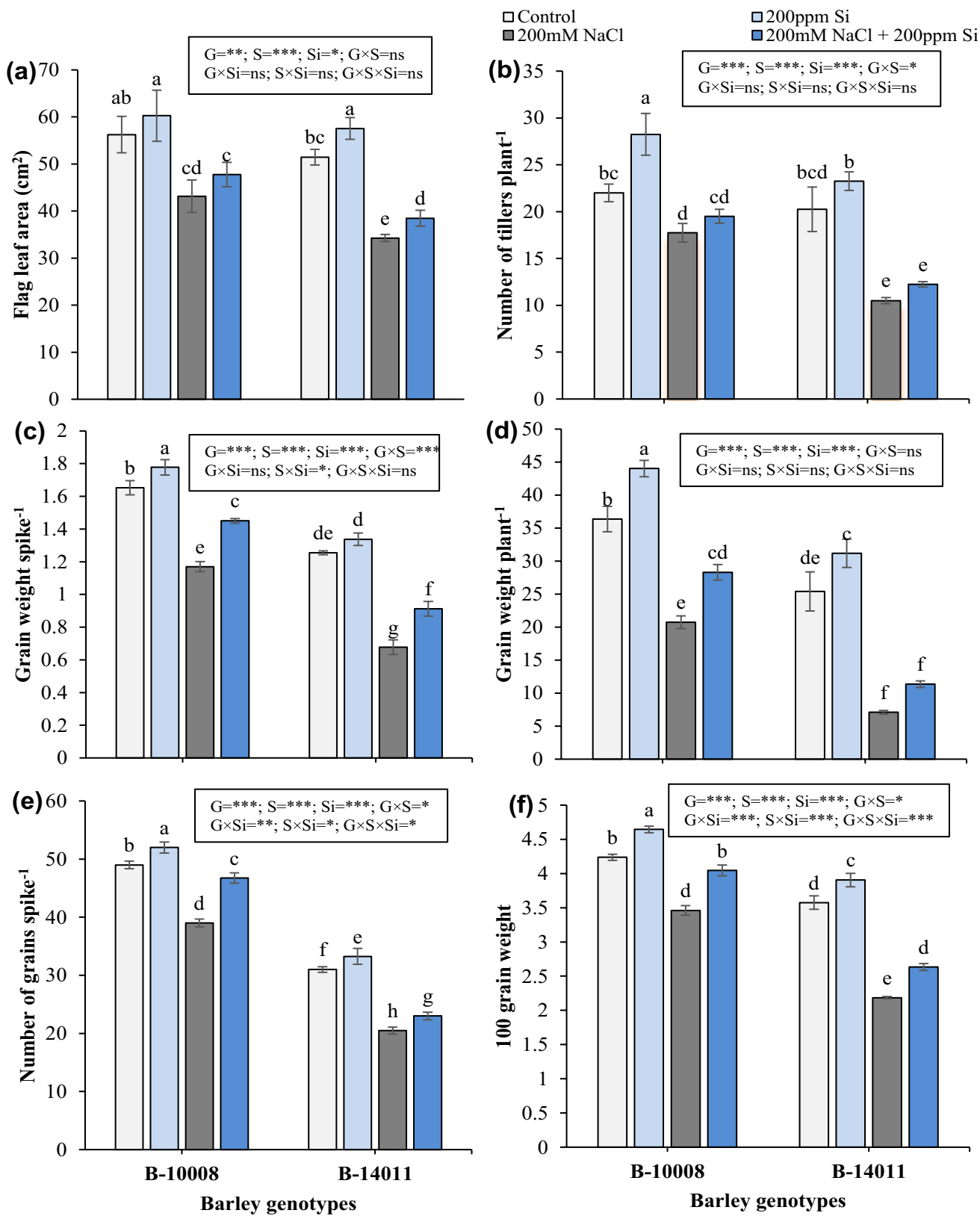


Fig. 5 Influence of rooting media fertigation of 200 ppm Si on flag leaf area (cm²) (a), no. of tillers/plant (b), no. of grains/spike (c), grain weight/plant (g) (d), grain weight/spike (g) (e), and 100 grain weight (g) (f) of barley genotypes (B-10008 and B-14011) grown at 200 mM NaCl stress. Data (bars) are means \pm SE ($n=4$). Different letters (a–g) on bars represent significant difference at $P \leq 0.05$ (Duncan's multiple range test). ***, **, * = significance at 0.001, 0.01, and 0.05 respectively; ns, non-significant; df, degree of freedom, G, genotypes; S, salinity; Si, silicon

eventually reduce maximum quantum yield of PSII (Fv/Fm) in barley plants subjected to salinity stress. The reason behind low Fv/Fm is that the RCs of PSII were either damaged or photo chemically inactive, further aided by low electron capacity from water splitting complex to ETC around PSII under stress (Mahdiah et al. 2015). The salinity-induced decline/blockage of electron transfer through ETC may cause photo-oxidation of thylakoid membrane's protein complexes; consequently, the barley plants modified its photosynthetic apparatus to dissipate excessive energy (DfO/RC) in order to protect its molecules from photo-damage.

These adverse effects of NaCl to photosynthetic apparatus can be reversed by Si application through external means (Hoffmann et al. 2020). The efficiency of PSII (Fv/Fm) of stressed barley plants was enhanced by reducing the number of inactive reaction centers (VJ and VI) and enhancing the physical health of PSII (Fo/Fm), electron transport rate through ETC (Fm/Fo), and efficiency of water splitting complex (Fv/Fo). The elevation in dissipation of excessive excitation energy (DfO/RC) in salt-stressed barley plants worked to protect the photosynthetic machinery from photo-oxidative damage. Salinity-induced enhancement of efficiencies of PSII indicators were previously observed in sunflower (Umar et al. 2019), mustard (Wani et al. 2019), canola (Iqbal et al. 2019), and barley (Ulfaat et al. 2020).

Salinity-induced increase in Na⁺ concentration in soils reduces the ability of plants to uptake other nutrients like Ca²⁺, K⁺, P, Mg, and Si by roots epidermis (Hnilíčková et al. 2019; Phogat et al. 2020). It has been observed in this experiment that salinity stress caused a remarked increase in leaf and root sodium (Na⁺) and chlorine (Cl⁻) concentrations in barley plants; however, this increase was substantially greater in B-14011 compared to B-10008, whereas potassium (K⁺), calcium (Ca²⁺), phosphorous (P), and silicon (Si) uptake and accumulation were decreased under salinity stress. The disruption in uptake and accumulation of these elements under salinity stress has been previously reported by various researchers in different plant species (Akhter et al. 2021b; Safdar et al. 2019). Due to the similar cationic nature of Na⁺ and K⁺, various K⁺ transporters take Na⁺ into the cell instead of K⁺ which leads to the accumulation of Na⁺ in plants' cellular systems to toxic levels (Xu et al. 2015). This excessive buildup of Na⁺ hinders the absorption and transport of important nutrients into and within

the plants (Munns et al. 2020). Similarly, the toxic effects of Cl⁻ are more significant than Na⁺ as plants are better adopted to exclude Na⁺ from leaf blades as compared to Cl⁻ (Munns and Gilliam 2015; Arif et al. 2020). It has been observed in citrus leaves that increase in Cl⁻ contents stimulates the production of (1-aminocyclopropane-1-carboxylic acid) ACC which is eventually converted into ethylene hence triggering leaf abscission (Acosta-Motos et al. 2017).

The rooting application of Si through rooting media reduced Na⁺ and Cl⁻ concentrations, with a subsequent increase in the uptake and accumulation of K⁺, Ca²⁺, P, and Si in both barley genotypes. Si-mediated enhancement in these elements in different plant species has been discussed by Pavlovic et al. (2021). Under salinity stress, Si in rooting media inhibited Na⁺ absorption from roots and decreased its translocation to leaves through transpiration stream (Tahir et al. 2012). Si-mediated suberization of exodermis and endodermis of root cell is the main reason for lowering Na⁺ toxicity in plants and enhancing uptake of essential elements (Gong et al. 2006; Ibrahim et al. 2016; Li et al. 2017) as lower levels of Na⁺ in plant cellular system is important for optimal growth and development of plants (Keisham et al. 2018). Similarly, salinity tolerance in plants is normally linked to low Na⁺ absorption and a consequent reduced Na⁺ translocation to aerial parts and/or accumulation of extra Na⁺ in vacuole in order to protect cellular compartments from ionic injury (Mahmood 2011; Munns and Tester 2008) by making complexes with Na⁺. The presence of silicon through rooting media resulted lowering of Na⁺ contents in barley plants which supports our hypothesis that Si supplement can ameliorate Na⁺ toxicity by lowering Na⁺ accumulation.

K⁺ being vital and essential element is required for proper plant growth, because it is a component of numerous enzymes. It is also involved in maintaining membrane potential. The cytoplasmic K⁺ determines the response of plants to different environmental constrains (Aqeel et al. 2021; Shabala et al. 2016). Salinity-induced K⁺ deficiency is enhanced by Si application by replacing Na⁺ uptake with K⁺ as was observed in wheat (Marschner 2012; Krishnasamy et al. 2014). The upregulation in the expression of SKOP channel and downregulation of HAK5 and AKT1 transporters also maintained higher K⁺ contents in xylem (Chen et al. 2016). Calcium (Ca²⁺) is an important element that plays a structural role in holding plant cell walls together and preserves membrane intactness for better growth (Vafadar et al. 2020); however, its deficiency can lead to stunted growth due to tissue damage and lead to reduction in dry weights (Yeh et al. 2000). The Si application through rooting media enhances Ca²⁺ contents in barley tissues under salinity stress. The increased uptake of Ca²⁺ may be ascribed to Si-mediated restoration of plasma membrane due to high H⁺-ATPase activity (Kaya et al. 2006).

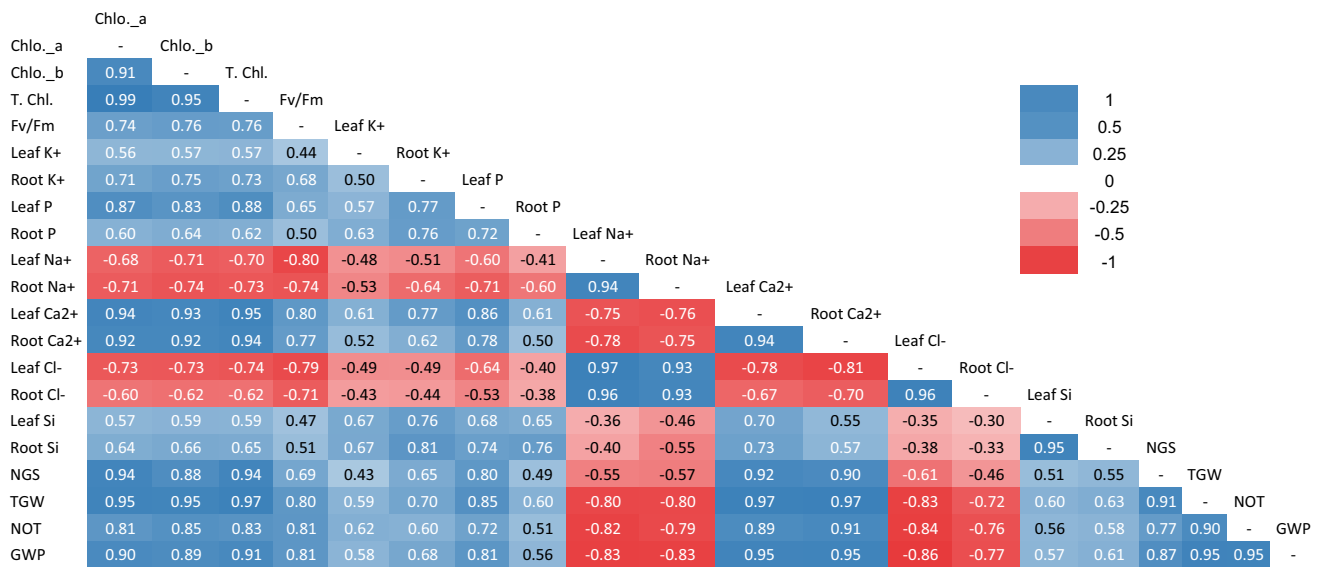


Fig. 6 Pearson's correlation analysis showing the effect of application of Si through rooting media among different ionic concentrations in leaves and roots, chlorophyll contents, and yield attributes of barley genotypes B-10008 and B-14011 grown under 200 mM NaCl stress. Chl-a, chlorophyll-*a*; Chl-b, chlorophyll-*b*; T-Chl., total chlorophyll; Fv/Fm, maximum quantum yield of PSII; LNa, leaf sodium; RNa,

root sodium; LCl, leaf chlorine; RCl, root chlorine; LK, leaf potassium; RK, root potassium; LCa, leaf calcium; RCa, root calcium; LP, leaf phosphorous; RP, root phosphorous; LSi, leaf silicon; RSi, root silicon; NGS, number of grains/spike; GW/P, grain weight/plant; HGW, hundred grain weight; NOT, number of tillers

Phosphorous (P) is an important element for plant growth as it is a structural constituent of nucleic acid, lipids, and sugar. In plants, P plays a central role in key processes like seed germination, respiration, photosynthesis, nitrogen fixation, and flower and seed development (Malhotra et al. 2018). The reduction in P under salinity stress was enhanced in barley genotypes after Si application through rooting media probably due to increased activity of genes related to P uptake as was observed by Kostic et al. (2017) in wheat. Si-mediated enhancement in P contents was previously observed in tomato (Zhang et al. 2019). Similarly, applying Si through rooting media under salinity stress significantly enhanced Si contents in leaves and roots of both barley genotypes which is attributed to enhanced activity of *LSi1*, *LSi2*, and *LSi6*, the Si transporters in barley (Mandlik et al. 2020). Similar results that Si can enhance nutrient contents under salt stress were observed in alfalfa (Meng et al. 2020) and wheat (Ibrahim et al. 2016), sunflower (Hurtado et al. 2019), aloe (Xu et al. 2015), and barley (Akhter et al. 2021a).

The yield of barley plants was lowered by salt stress, which was improved by applying Si externally. Qados and Moftah (2015) reported that exogenous application of Si increased yield of faba bean (pod number, seed/pod, number of seeds/plant) when grown in saline environment. The Si-mediated increase in yield of mung bean has been observed under salt stress through exogenous application of Si (Mahmood et al. 2016). Furthermore, field condition

enhancement in number of tillers, grain yield/spike/plant was increased with Si application in wheat under salinity stress (Mahmoud et al. 2020). Bybordi (2015) found that fertigation with potassium silicate enhanced growth and seed yield of salinity stressed wheat plants. Previously, similar studies on Si-induced increases in yield under salt stress were published in sweet pepper (Abdelaal et al. 2020), wheat (Khan et al. 2020b), maize (Sirisuntornlak et al. 2020), tomato (Haghighi and Pessaraki 2013), and barley (Laifa et al. 2020).

5 Conclusions

The current work revealed that exogenous Si application through rooting media minimized the negative impacts of salinity stress on barley plants. Salinity stress reduced barley plant development significantly, owing to excessive buildup of Na⁺ and Cl⁻ in plant tissues, which damaged chlorophyll pigments and PSII and disrupted electron transport across the ETC of the thylakoid membrane. The uptake and accumulation of essential elements (K⁺, Ca²⁺, P, Si) were reduced with concurrent accumulation Na⁺ and Cl⁻ to toxic levels in cellular compartments of barley leaves and roots under salinity stress. However, application of 200 ppm Si through rooting media caused a considerable improvement in growth-related attributes, chlorophyll concentrations,

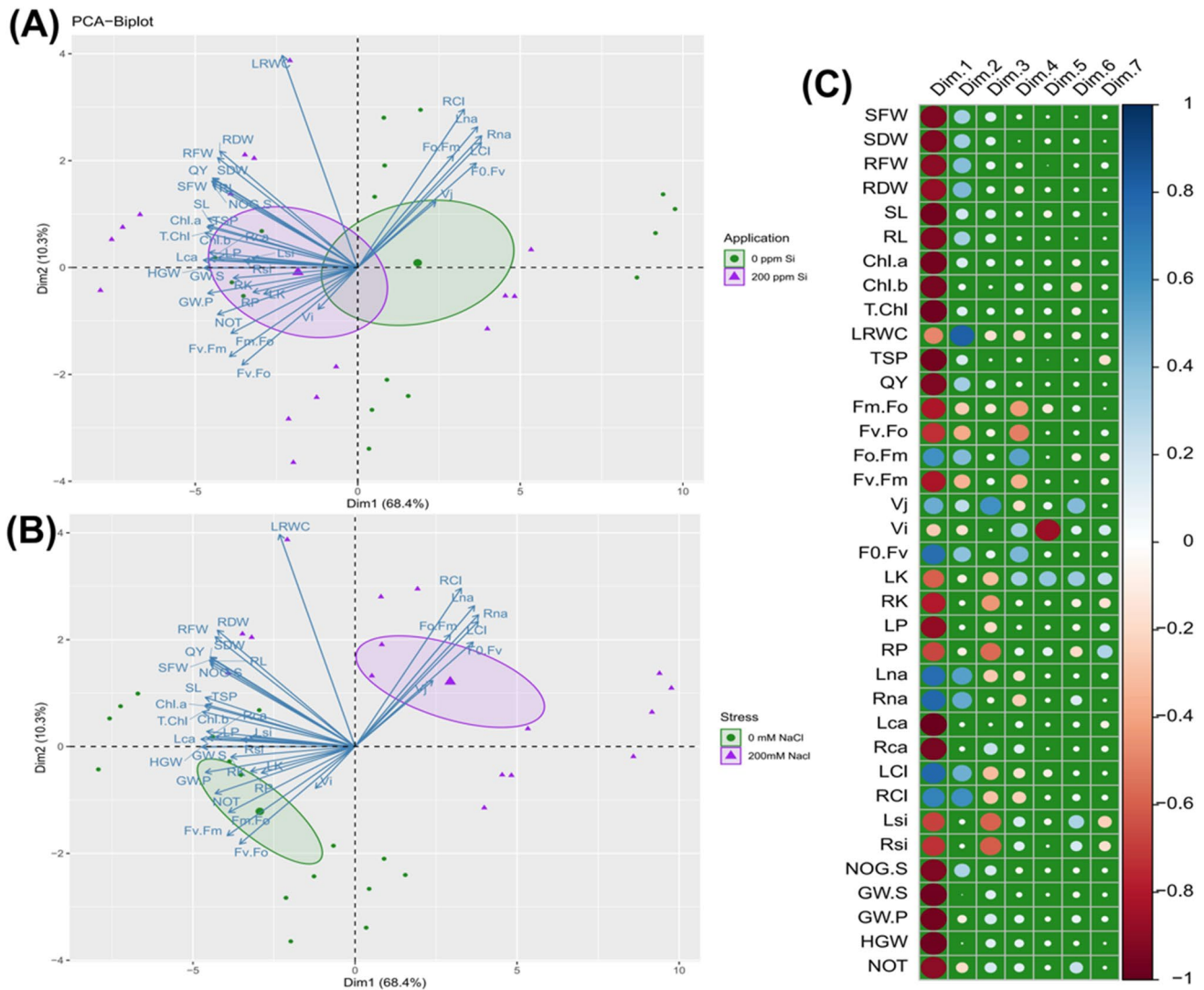


Fig. 7 Principal component analysis of barley genotypes under rooting application of silicon and salt stress. PCA-Biplot representing the **A** relationship of rooting application of silicon, **B** relationship of salt stress, and **C** corplot against different dimensions of PCA on studied parameters respectively. SFW, shoot fresh weight; SDW, shoot dry weight; RFW, root fresh weight; RDW, root dry weights; SL, shoot length; RL, root length; Chl-a, chlorophyll- α ; Chl-b, chlorophyll-b; T-Chl., total chlorophyll; LRWC, leaf relative water contents; TSP, total soluble protein contents; QY, quantum yield; Fm/Fo, rate of electron transport through PSII; Fv/Fo, size and number

of active reaction centers of photosynthetic apparatus; Fo/Fm, quantum yield of baseline; Fv/Fm, maximum quantum yield of PSII; V_j , variable fluorescence at J step; V_i , variable fluorescence at I step; Fo/Fv, efficiency of water splitting complex; Lna, leaf sodium; Rna, root sodium; LCl, leaf chlorine; RCl, root chlorine; LK, leaf potassium; RK, root potassium; Lca, leaf calcium; Rca, root calcium; LP, leaf phosphorous; RP, root phosphorous; Lsi, leaf silicon; Rsi, root silicon; NOG.S, number of grains/spike; GW.P, grain weight/plant; HGW, hundred grain weight; NOT, number of tillers; GW.S, grain weight/spike

photosynthetic machinery (PSII and ETC), and ionic uptake by reducing the accumulation of Na^+ and Cl^- in roots and leaves of barley plants thus enlightening yield under salt stress. The upregulation of TSP synthesis and regulation in PSII activity after application of Si especially under salinity stress also helped barley plants to show better growth and yield. Although the genotype B-10008 was more resistant to salt stress, the sensitivity of B-14011 was more pronounced with Si rooting application under saline stress.

6 Suggestions and Recommendation

In Pakistan, the use of silicon fertilizer is minimal due to lack of knowledge about Si fertilizers and low production of Si-rich fertilizers from the industry. Studies like this can prompt the fertilizer scientists and industrialists to manufacture Si-rich fertilizers to enhance the yield of essential crops to cope with the demands and needs of the increasing population.

Author Contribution Conceptualization, M.S.A. and S.N.; methodology, M.R., M.N.A., and M.S.A.; software, M.A. and K.H.S.; resources, J.A. and M.O.; investigation, M.S.A., S.N., and S.M.; draft preparation, M.S.A.; writing and reviewing, M.S.A. and S.N.; project administration, Z.U.Z., S.M., and S.N.

Data Availability Data will be available on demand.

Declarations

Conflict of Interest The authors declare no competing interests.

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