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ORIGINAL PAPER

Beneficial Effects of Silicon (Si) on Sea Barley (*Hordeum marinum* Huds.) under Salt Stress

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Abstract

Silicon (Si) plays an important role in providing beneficial effects on plant growth and yield, especially under stressful environments such as salinity.

The objective of this work is to study the effects of a fertilizer based on silicon (Na_2SiO_3 synthesized from Tunisian silica sand) on sea barley (*Hordeum marinum* Huds.) under salt stress. Due to its forage potentialities, this species presents a very interesting capacity for the rehabilitation of non-productive marginal areas.

Forty-two-day-old *H. marinum* plants were exposed to three concentrations of Na_2SiO_3 (0, 1, or 2 mM) in the absence or presence of salt (0 or 150 mM NaCl). The examination of the growth parameters, water status, lipid peroxidation, photosynthetic gas exchange, photosynthetic pigment contents, and chlorophyll fluorescence proved that silicon is a great interest support for the remediation of the deleterious effects of salt stress. Therefore, our fertilizer can be considered as an effective solution to cope with salt stress and promote the development of marginal lands. Taking into consideration its high efficiency and its low production cost, this product can compete with other fertilizers.

Keywords Silicon · Salinity · *Hordeum marinum* · Growth · Water status · Photosynthetic activity

1 Introduction

Environmental stresses are the main factors affecting crop yields. About 3.6 billion of the world's 5.2 billion hectares of dry land, used for agriculture, have already suffered soil degradation, erosion, and salinization [1]. This situation is very worrying in the arid and semi-arid regions where climate change is mainly marked by a noticeable increase in the average temperature and a pronounced decline in rainfall.

Salinity is one of the most major environmental factors limiting crop plant productivity, especially in arid and semi-arid regions [2]. According to Abdelly et al. (2011) [3], about 1.5 billion hectares of soils suffer excessive salt levels throughout the world. Tunisia is one of the most salinity-endangered countries whose salt-affected soils cover about 1.5 million hectares or about 10% of the country's surface area and 18% of its arable land [3]. To remedy the depressive effects of this constraint, different approaches (physical, chemical, and biological) have been studied. In this study, we focused on the efficiency and the performance of a sodium silicate treatment (Na_2SiO_3).

Silicon (Si) is the second most abundant element in the Earth's crust after oxygen [4]. Generally, Si is not viewed as an essential element for plant growth. However, its application on plants gives them a better tolerance to various environmental constraints such as salinity, drought, extreme temperatures and nutritional disturbances [5, 6]. Although Si has widely been employed to increase plant tolerance under salt stress. However, the mechanisms of this rise remain poorly understood. In fact, Si can enhance plant growth and water retention by inhibiting water loss, which minimizes salt-induced osmotic stress [7].

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Furthermore, several authors reported that the addition of Si reduced the uptake and translocation of Na^+ minimizing its cellular accumulation in shoot tissues [6, 8, 9]. As mentioned by Coskun et al. (2019) [6], a decrease in Na^+ accumulation, which could be reflected through the oxidative stress alleviation, would considerably reduce the strains imposed on shoot tissues. Moreover, it was revealed that K^+ accumulation (K^+ uptake) can be enhanced by exposing plants to Si treatment [10]. These findings were confirmed by a recent study conducted by Hussain et al. (2018) [11], who noticed that Si application minimizes the harmful consequences of salinity by improving K^+ absorption and reducing Na^+ concentration in shoot tissues. Coskun et al. (2019) [6] report that the addition of Si improved Casparian Band (CB) "development" and apoplastic Si deposition efficiently blocking "bypass route", and thus root-to-shoot Na^+ translocation.

The use of Si as a beneficial nutrient enhances photosynthetic parameters such as stomatal conductance (g_s), net CO_2 assimilation rate (A), intercellular CO_2 concentration (Ci) and transpiration rate (E) [12]. In fact, Khan et al. (2017) [13] found that Si supply improved chlorophyll content, photosynthetic activity (according to g_s, A, Ci, and E parameters), and photochemical efficiency of photosystem II of maize cultivars.

The main objective of our research work is to enhance plant productivity and their tolerance to environmental stresses through the enrichment of culture media with Si. In this study, the effects of a silicon fertilizer, synthesized from sand, were evaluated on sea barley plants (*Hordeum marinum Huds*). Indeed, because of their richness in silica, sands are very interesting relevant supports for the production of Si fertilizers. The present study was undertaken to examine individual and combined effects of sodium chloride (NaCl) and sodium silicate (Na_2SiO_3) on growth, mineral nutrition and photosynthetic behaviour in *H. marinum*. In Tunisia, this annual species, with forage potentialities, is often observed in saline depressions in close association with strict halophytes where it contributes significantly to the biomass production in these ecosystems [14].

2 Materials and Methods

2.1 Sodium Silicate Synthesis

In the present study, sodium silicate synthesis protocol was developed in "Useful Materials Valorization Laboratory, National Center for Research in Materials Sciences (CNRSM, Tunisia)".

Sodium silicate (Na_2O SiO_2) was prepared by reacting silica sand (Borj Hfaiedh deposit sand, North-East of Tunisia, 36°30′27.0" N, 10°33'00.0" E, $SiO_2 > 99\%$) with sodium carbonate Na_2CO_3 (99.5%) (SiO_2:Na_2O = 1:1 M ratio) at high temperatures. Sodium silicate solutions were prepared at different concentrations by the dissolution of the solid compound in an appropriate deionized water volume. For each sodium silicate solution, the checking of experimental concentrations was carried out by analysing SiO_2 and Na^+ contents using gravimetric and flame emission spectroscopy methods, respectively. For each analysis, the difference between theoretical and experimental concentration did not exceed 2% (Fig. 1).

2.2 Plant Material and Growth Conditions

Seeds of *Hordeum marinum* Huds., collected from Soliman Sebkha (North-East of Tunisia, 36°42′6.955" N, 10°27′ 23.287″ E), were kindly provided by Dr. Abderrazak SMAOUI (LPE - CBBC, Tunisia). Seeds were germinated in Petri dishes on sterile Whatman paper moistened with distilled water (in an incubator at 22 °C). Fourteen-day-old seedlings were transferred onto floating support and grown under hydroponic conditions in a diluted Hewitt (1966) [15] nutrient solution. After a pre-treatment phase of 28d (at the age of 42 days), Si was added to the half-strength nutrient solution (T/2), at 0, 1 or 2 mM, in the form of sodium silicate. For each Na_2SiO_3 concentration, two salt treatments were applied (0 or 150 mM NaCl). Each group of 12 plantlets was transferred to a container with 3 L of an aerated nutrient solution which was weekly renewed throughout the culture period. The experiment was conducted in a greenhouse under sunlight conditions at 23/25 °C in the Centre of Biotechnology of Borj-Cedria (North-East of Tunisia, 36°42′32.9"N, 10°25′40.9″E).

2.3 Harvest and Growth Measurements

At the end of the experiment (after 28d of treatment), plants were harvested and separated into shoots and roots. Roots were carefully washed with HCl cold solution (0.01 M) in order to remove extracellular nutrients, then washed with distilled water, and finally dried with filter paper. Fresh shoots and roots were immediately weighted (FW) after the harvest, then oven-dried at 80 °C for 48 h for dry weight (DW) determination.

2.4 Measurement of Gas Exchange Parameters

Net CO_2 assimilation (A), stomatal conductance (g_s), transpiration rate (E), and intercellular CO_2 concentration (Ci) and Intrinsic Water Use Efficiency (IWUE = A/g_s) were determined using a portable Licor gas analyser (LC pro$^+$, ADC BioScientific Ltd. Hoddesdon, United Kingdom). All measurements were performed between 09:30 am and 10:30 am in fully expanded leaves (the same leaf stage from the bottom). Values of the above-mentioned parameters were taken after the stabilization of the photosynthetic levels.

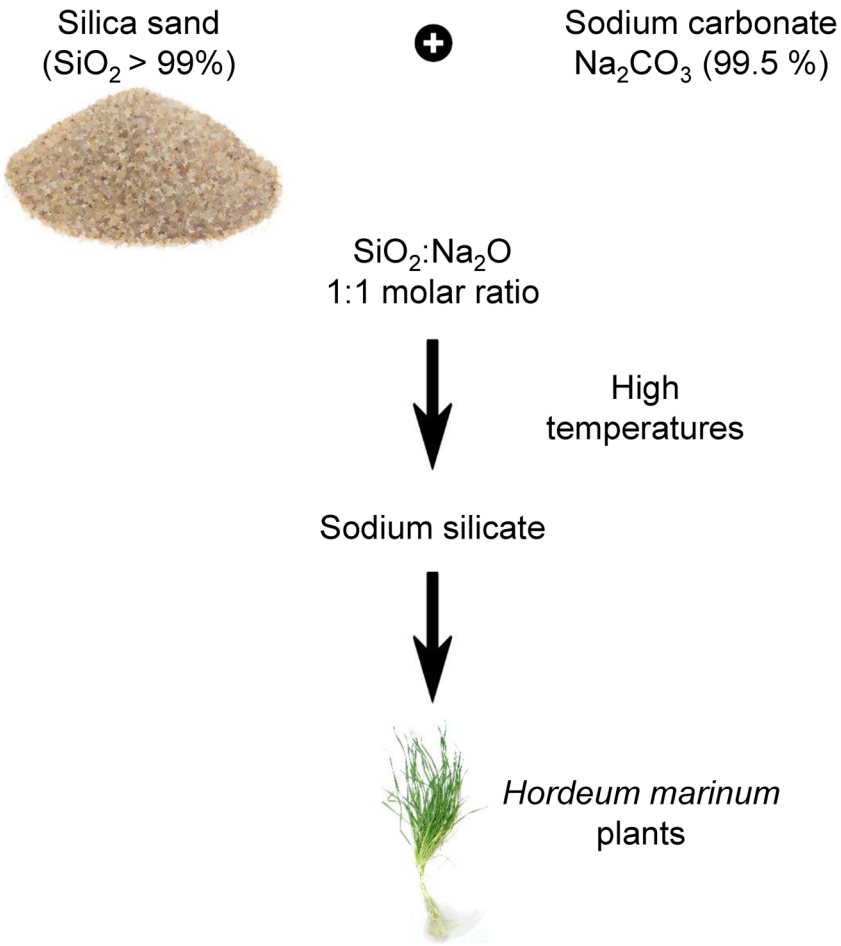

Fig. 1 Experimental protocol adopted in "Useful Materials Valorization Laboratory, National Center for Research in Materials Sciences" (CNRSM, Tunisia), for the production of sodium silicate from Tunisian silica sand. The protocol of sodium silicate synthesis (from silica sand) was developed in "Useful Materials Valorization Laboratory, National Center for Research in Materials Sciences" (CNRSM, Tunisia)

Photosynthetically Active Radiation (PAR) during measurement under sunlight conditions was about 800 µmol m^{-2} s^{-1}. During gas exchange measurements, the leaf chamber temperature and the ambient CO_2 concentration were 23 °C ± 2 °C and 350 µmol mol^{-1}, respectively.

2.5 Extraction and Determination of Chlorophyll and Carotenoid Concentrations

For pigment analysis, 100 mg of fresh leaf samples were crushed in 5 ml of 80% acetone. After incubation in the dark at 4 °C for 72 h, a visible UV spectrophotometer was used (Dual Beam 8 Auto Cell UVS-2700) to determine absorbance extract at 470, 646, and 663 nm for chlorophyll *a* (Chl. *a*), chlorophyll *b* (Chl. *b*) and total carotenoids. Pigment concentrations were calculated according to Lichtenthaler (1987) [16] equations:

Chl. *a* (µg/ml) = 12.21 (A_{663}) - 2.81 (A_{646}).Chl. *b* (µg/ml) = 20.13 (A_{646}) - 5.03 (A_{663}).Carotenoids (µg/ml) = (1000A_{470}–3.27[Chl. *a*] - 104[Chl. *b*])/227.

Where A663, A646, and A470 represent extract absorbance at 663, 646, and 470 nm, respectively.

2.6 Measurement of Chlorophyll Fluorescence

Chlorophyll fluorescence was measured by pulse-modulated fluorometer (OS1p – Opti-Sciences Inc., USA) on leaves of *H. marinum*. Fluorescence parameters were determined in dark-adapted (30 min) leaves of control and treated plants. Subsequently, these leaves were exposed to modulated light of low intensity for F0 (minimal fluorescence) measurements. The values of maximal fluorescence (Fm) and the maximum photochemical efficiency of PSII (Fv/fm = (Fm–F0)/fm) were also determined after an exposure to a saturation pulse. Then, leaves were subjected to an actinic light that initiated electron transport between photosystems (PSII and PSI) to record the steady state of PSII operating efficiency (ϕPSII or Y(II) = (Fm′–Fs)/fm′), the non-photochemical quenching (NPQ), the regulated non-photochemical quenching (Y(NPQ)) and the non-regulated non-

photochemical quenching (Y(NO)). The maximum efficiency of PSII open centres in the light-adapted state (Fv′/fm′ = (Fm′–F0′)/fm′) was calculated according to Genty et al. (1989) [17].

2.7 Lipid Peroxidation

Membrane lipid peroxidation was assessed by measuring leaf malonyldialdehyde (MDA) concentration. Fresh shoot samples (500 mg) were homogenized in 0.1% (*w*/*v*) trichloroacetic acid (TCA) solution. The homogenate was centrifuged at 15000 *g* for 15 min at 4 °C. An aliquot of the supernatant (1 mL) was added to 0.5% thiobarbituric acid (TBA) prepared in 20% TCA. The mixture was heated at 95 °C for 30 min in a shaking water bath and then cooled in an ice bath. The samples were centrifuged at 10000 *g* for 10 min and the absorbance of the supernatant was measured at 535, and 600 nm [18]. The concentration of MDA was calculated according to the following equation:

MDA (nmol. g^{-1} FW) = $((DO_{532}\text{-}DO_{600}) *1000*DF) / 155*M*10^{-3}$.

DF denotes the dilution factor, 155 is the extinction coefficient, and M corresponds to the mass of the used fresh material.

2.8 Nutrient Extraction and Analysis

For nutrient extraction, dried samples dried tissues were incubated in 1 N H_2SO_4 (20 mL) at 80 °C for 1 h [19, 20]. K^+ and Na^+ concentrations were determined by flame photometer (BWB) and those of Ca^{2+}, Zn^{2+} and Fe^{2+} were measured by an atomic absorption spectrophotometry (SpectrAA 220; Varian, Australia) in the same extract. The data obtained using the Varian SpectrAA 220 was manipulated utilizing SpectrAA Worksheet Software (Agilent Technologies; www.agilent.com).

2.9 Statistical Analysis

Data were subjected to a one-way ANOVA test using XLSTAT software v. 2014 (Addinsoft, Paris, France) and means were compared according to Duncan's multiple range test at 5% level of significance. A Principal Component Analysis (PCA) was carried out using XLSTAT software (v. 2014), considering variables centred on their means and normalized with a standard deviation of 1.

3 Results

3.1 Plant Biomass

Salt stress impaired significantly growth of *H. marinum* plants (Figs. 2 and 3). In fact, both shoot and root dry weights were negatively affected when subjected to 150 mM NaCl. At control conditions (0 mM NaCl and 0 mM Na_2SiO_3), *H. marinum* showed a whole plant dry weight of 1 g distributed as follows: 16% in roots and 84% in shoots. Increasing salt concentration

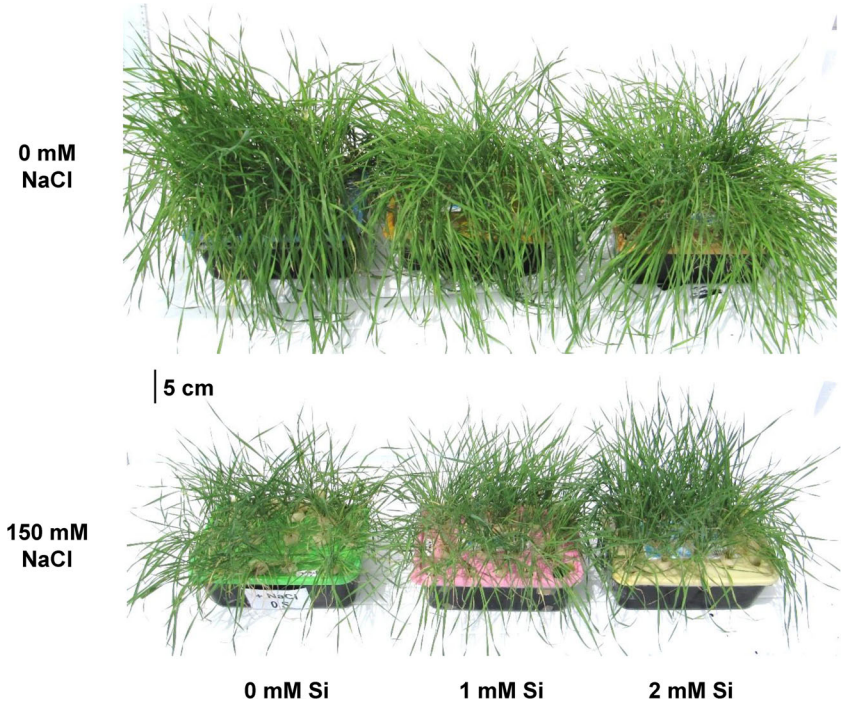

Fig. 2 Morphological aspect of *H. marinum* plants, at the age of 70 days. Plants were exposed to 3 concentrations of Na_2SiO_3 (0, 1 or 2 mM) in the absence or presence of NaCl (150 mM) during the last 28 days of culture

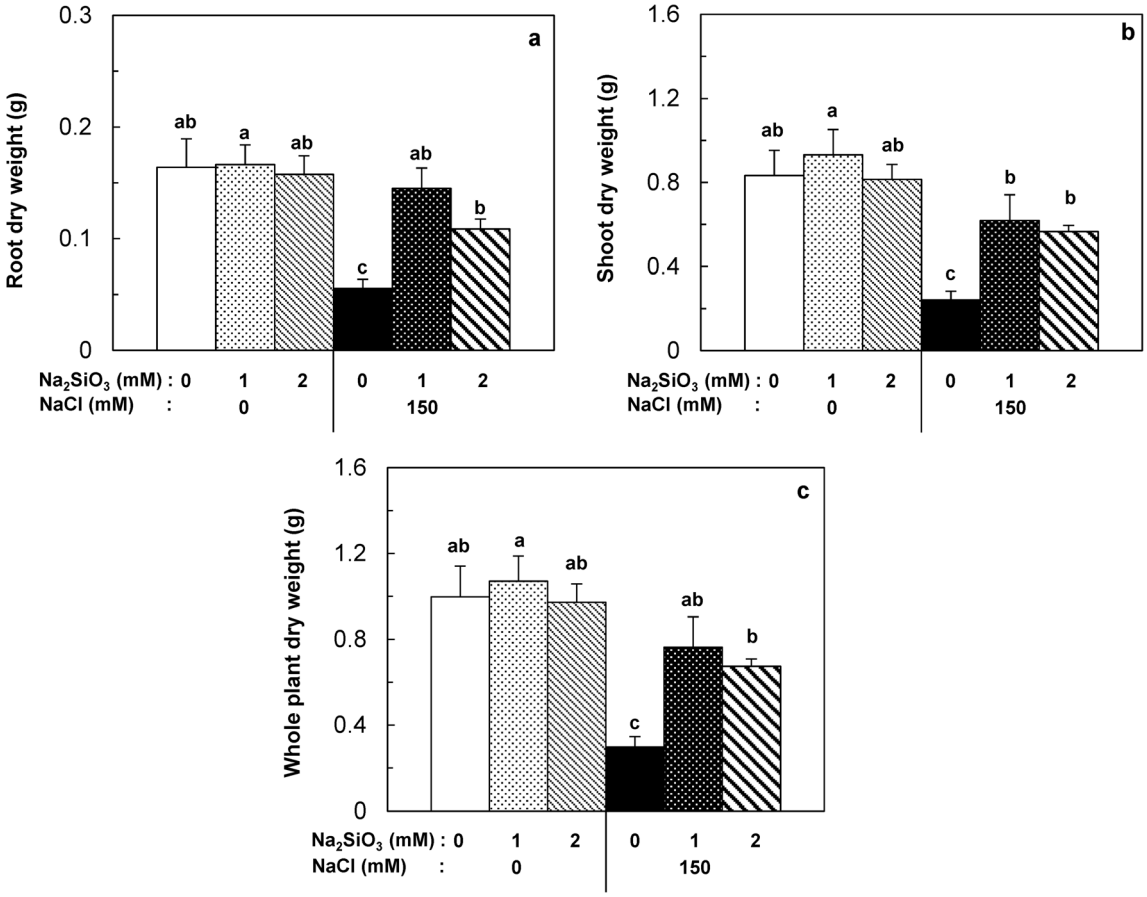

Fig. 3 Root, shoot and whole plant dry weights of *H. marinum* cultivated for 70 days. Plants were exposed to 3 concentrations of Na_2SiO_3 (0, 1 or 2 mM) in the absence or presence of NaCl (150 mM) during the last 28 days of culture. Values are means ± SE of 6 individual plants. Bars marked with the same lower-case letters in each panel are not significantly different at $P \leq 0.05$ (Duncan's test)

in the medium to 150 mM NaCl, impaired significantly root and shoot growth which were significantly decreased by 62.5% and 71.42%, respectively (Fig. 3a, b).

When applied separately, Na_2SiO_3 did not affect the production of dry biomass. The same effect was noticed for the whole plant dry weight as well as for the different plant parts (shoots and roots). However, Na_2SiO_3 application significantly improved plant dry biomass production by almost 200% when combined to NaCl treatment (Fig. 3c). Hence, the beneficial effect of added Na_2SiO_3 was obvious in salt-treated *H. marinum* plants indicating its stimulating effect on plant growth grown under stress conditions (Figs. 2 and 3).

3.2 Root and Shoot Length

At 0 mM Na_2SiO_3, root length values ranged from 18 cm to 20 cm, in plants cultivated in the presence or absence of NaCl, which proved that root length was not affected by salt stress (Fig. 4a).

However, the salinity decreased the shoot length approximately by 34% in comparison to the corresponding controls (without NaCl treatment). Moreover, the addition of Na_2SiO_3 did not affect the length of aerial parts in plants cultivated under 0 or 150 mM NaCl (Fig. 4b).

3.3 Water Content

Na_2SiO_3 application resulted in a significant increase in root water content under control conditions. However, no difference was recorded in root hydration in salt-treated plants (Fig. 4c). Salinity application reduced significantly shoot water content by 36.7%, compared to control plants. By contrast, the adverse effect of NaCl treatment was alleviated by Na_2SiO_3 addition which considerably improved shoot water content (Fig. 4d).

3.4 Photosynthetic Pigments

No difference was recorded in Chl. *a* and carotenoid concentrations in leaves of control and treated plants. Indeed, the presence of NaCl as well, as Na_2SiO_3, did not affect the contents of these pigments in *H. marinum* plants (Fig. 5a-c).

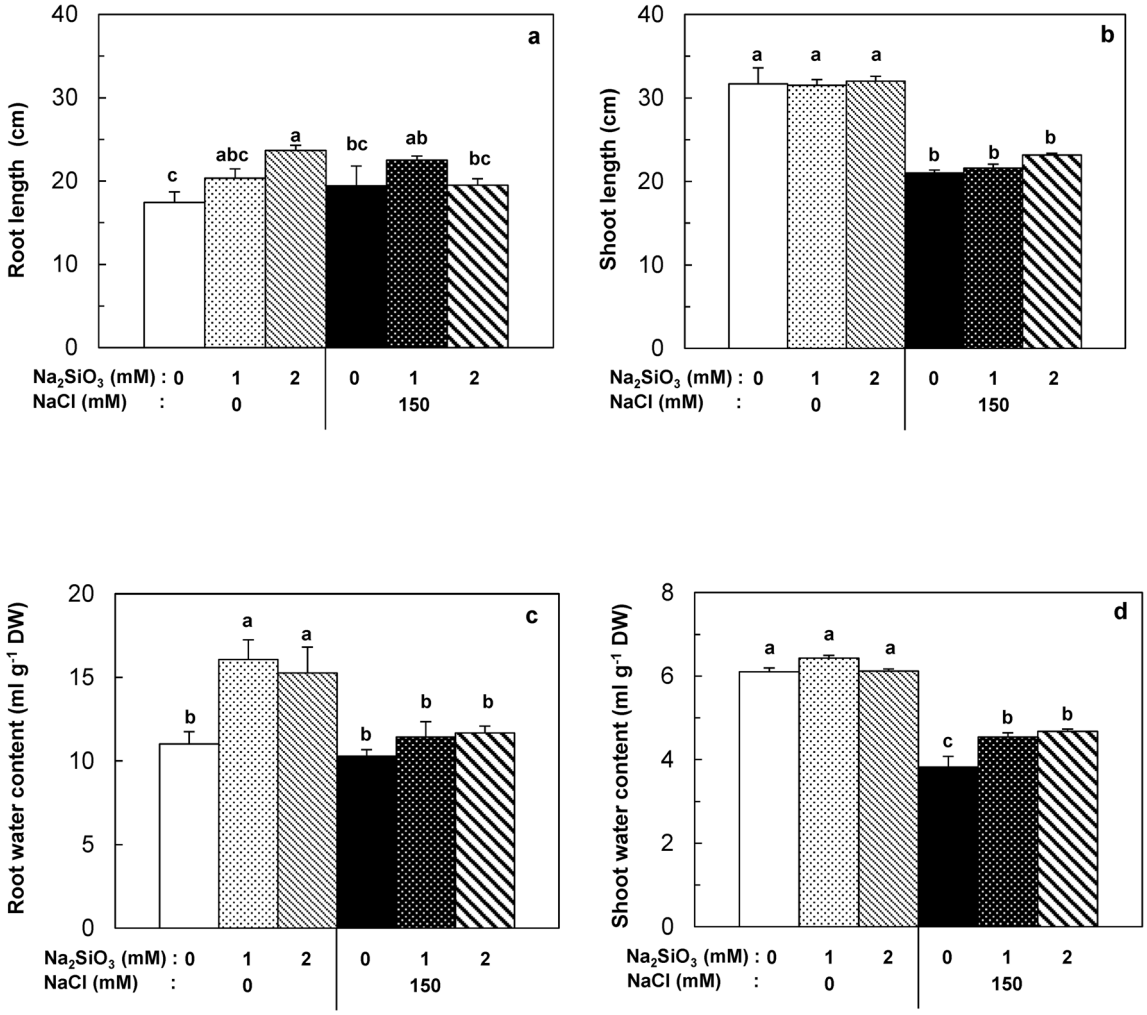

Fig. 4 Root and shoot length, and root and shoot water content of *H. marinum* cultivated for 70 days. Plants were exposed to 3 concentrations of Na_2SiO_3 (0, 1 or 2 mM) in the absence or presence of NaCl (150 mM) during the last 28 days of culture. Values are means ± SE of 6 individual plants. Bars marked with the same lower-case letters in each panel are not significantly different at $P \leq 0.05$ (Duncan's test)

Similarly, salt stress did not affect Chl. *b* contents; whereas the addition of 1 mM Na_2SiO_3 resulted in a significant rise of Chl. *b* in leaves of plants grown under 0 or 150 mM NaCl (Fig. 5b).

3.5 Gas Exchange

A beneficial effect of 1 mM Na_2SiO_3 application was noticed in the improvement of net CO_2 assimilation (*A*) in plants cultivated under salt-free conditions. However, an antagonistic effect of 1 mM Na_2SiO_3 was observed, when applied at 150 mM NaCl (Fig. 6a). In the absence of Na_2SiO_3, stomatal conductance (g_s) decreased by almost 57% under salinity application. By contrast, this parameter increased significantly by 42% at the treatment 2 mM Na_2SiO_3–0 mM NaCl, compared to the control (Fig. 6b).

Increasing salt concentration in the medium, impaired significantly transpiration rate (*E*) which was significantly decreased. Interestingly, a stimulating effect of Na_2SiO_3 was observed, on control and salt-treated plants, indicating a beneficial effect of silicon on transpiration rate (*E*) (Fig. 6c).

At 150 mM NaCl, *Ci* decreased by 21% in untreated plants with Na_2SiO_3 as compared to control ones (0 mM Na_2SiO_3 and 0 mM NaCl). However, this reduction was entirely restored with the addition of Na_2SiO_3 (Fig. 6d).

Intrinsic Water Use Efficiency (IWUE) was significantly induced under salt conditions. IWUE values were restored to control level with the addition of 1 mM Na_2SiO_3, contrarily to a dose of 2 mM which showed a different effect. In fact, this parameter was stimulated when plants were exposed to 2 mM Na_2SiO_3 at 150 mM NaCl (Fig. 6e).

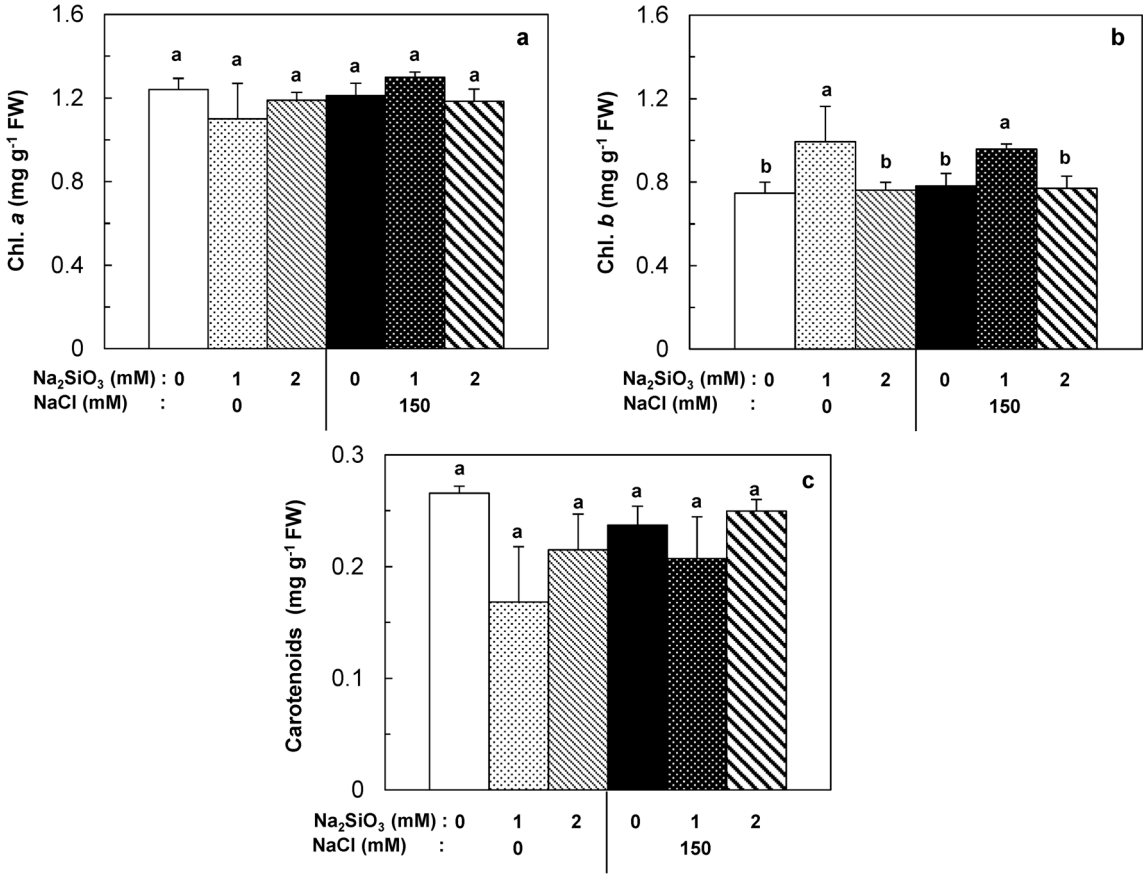

Fig. 5 Photosynthetic pigment concentrations in leaves of *H. marinum* cultivated for 70 days. Plants were exposed to 3 concentrations of Na_2SiO_3 (0, 1 or 2 mM) in the absence or presence of NaCl (150 mM) during the last 28 days of culture. Values are means ± SE of 4 individual plants. Bars marked with the same lower-case letters in each panel are not significantly different at $P \leq 0.05$ (Duncan's test)

3.6 Chlorophyll Fluorescence

No difference was recorded in the following fluorescence parameters: Fv/fm, Fv'/fm′, NPQ, and in *H. marinum* leaves under the different applied conditions (Fig. 7).

Regardless of NaCl concentration and under the action of Na_2SiO_3, Y (II) and Y (NO) did not show noticeable change (Fig. 8). However, under salt-free conditions, Y(NPQ) parameter was increased by 3% at 2 mM Na_2SiO_3 (from 57% to 60%, compared to the control). Under salt conditions, Y (NPQ) was significantly reduced by 2% in the presence of 1 mM Na_2SiO_3 (from 57% to 55%, compared to the control) (Fig. 8).

3.7 Lipid peroxidation

Results of Fig. 9 showed that MDA contents were maintained unchanged in leaves of *H. marinum* plants exposed to different concentrations of Na_2SiO_3 (0, 1, and 2 mM) under salt-free conditions. However, salinity stress resulted in a significant increase of MDA by 57% in plants cultivated at 0 mM Na_2SiO_3. This increase was alleviated by sodium silicate application. Therefore, MDA values decreased in salt-treated plants exposed to Na_2SiO_3 treatment to reach their normal levels (Fig. 9).

3.8 Sodium Content

Salinity application increased root and shoot Na contents by 229% and 126%, respectively, compared to the control. Addition of Na_2SiO_3 did not show any effect in these plant parts under salt-free conditions. However, at 150 mM NaCl sodium contents were significantly reduced in *H. marinum* shoots exposed to Na_2SiO_3 treatment (Fig. 10a, b).

Thus, we may conclude that the beneficial effect of Na_2SiO_3 appeared only on the aerial parts of this species.

3.9 Potassium Content

Without salinity and at 1 mM Na_2SiO_3, a significant increase was observed in root K contents. Moreover, with salinity stress, K contents decreased under Na_2SiO_3 application mainly at 2 mM concentration (Fig. 10c). However, both salt and Si addition did not affect shoot K contents (Fig. 10d).

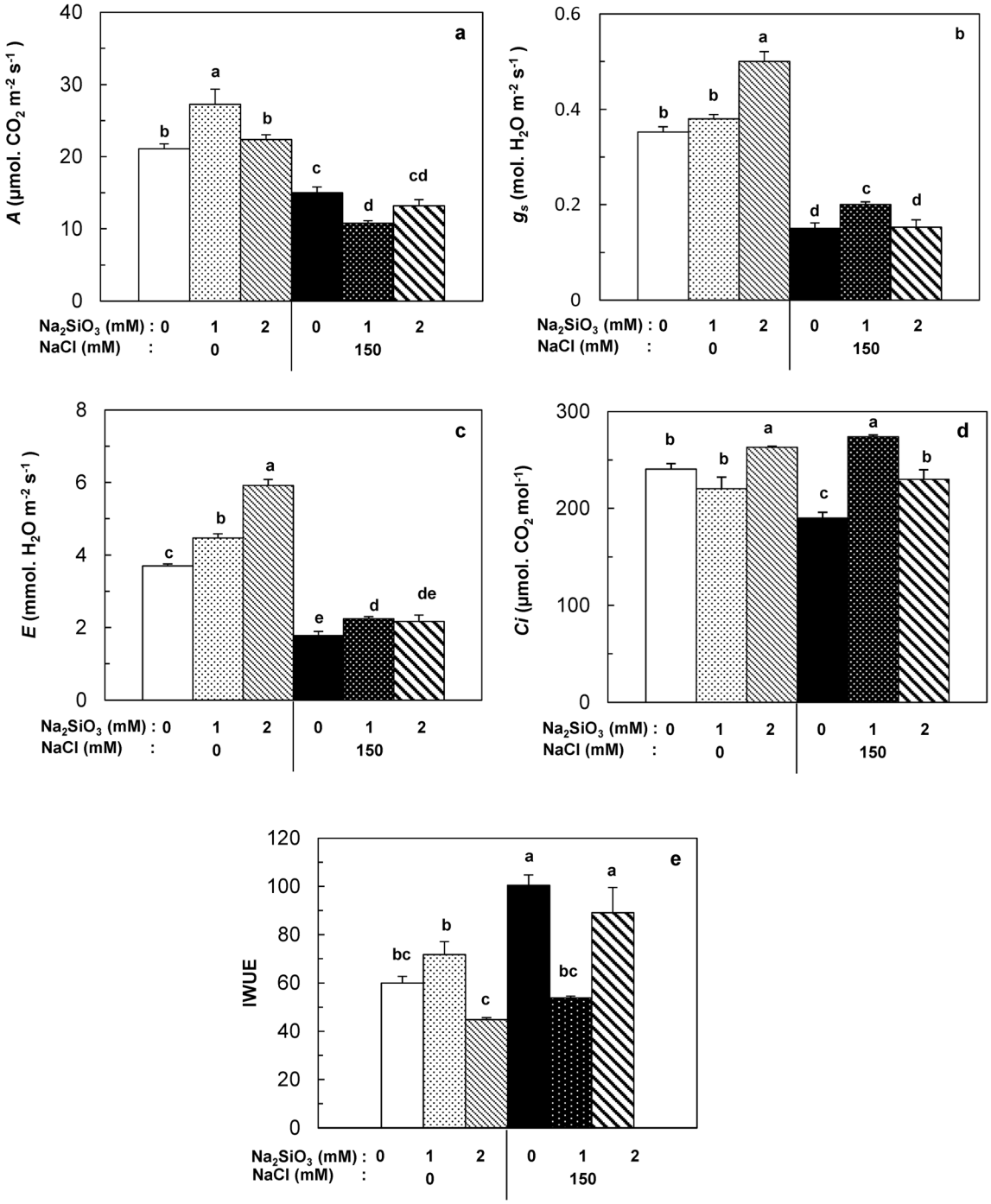

Fig. 6 CO_2 assimilation (*A*), stomatal conductance (g_s), transpiration (*E*), Intercellular CO_2 concentrations (Ci), and iWUE: intrinsic Water Use Efficiency of *H. marinum* cultivated for 70 days. Plants were exposed to 3 concentrations of Na_2SiO_3 (0, 1 or 2 mM) in the absence or presence of NaCl (150 mM) during the last 28 days of culture. Values are means ± SE of 4 individual plants. Bars marked with the same lower-case letters in each panel are not significantly different at $P \leq 0.05$ (Duncan's test)

3.10 Sodium and Potassium Translocations from Roots to Shoots

Without salt treatment Si addition has no effect on the translocation of Na and K in *H. marinum* plants.Under salt conditions, sodium translocation from the roots to the aerial parts was significantly declined by Si addition. However, at 2 mM Na_2SiO_3, potassium translocation from the roots to the shoots increased by approximately 31% (Fig. 10e, f).

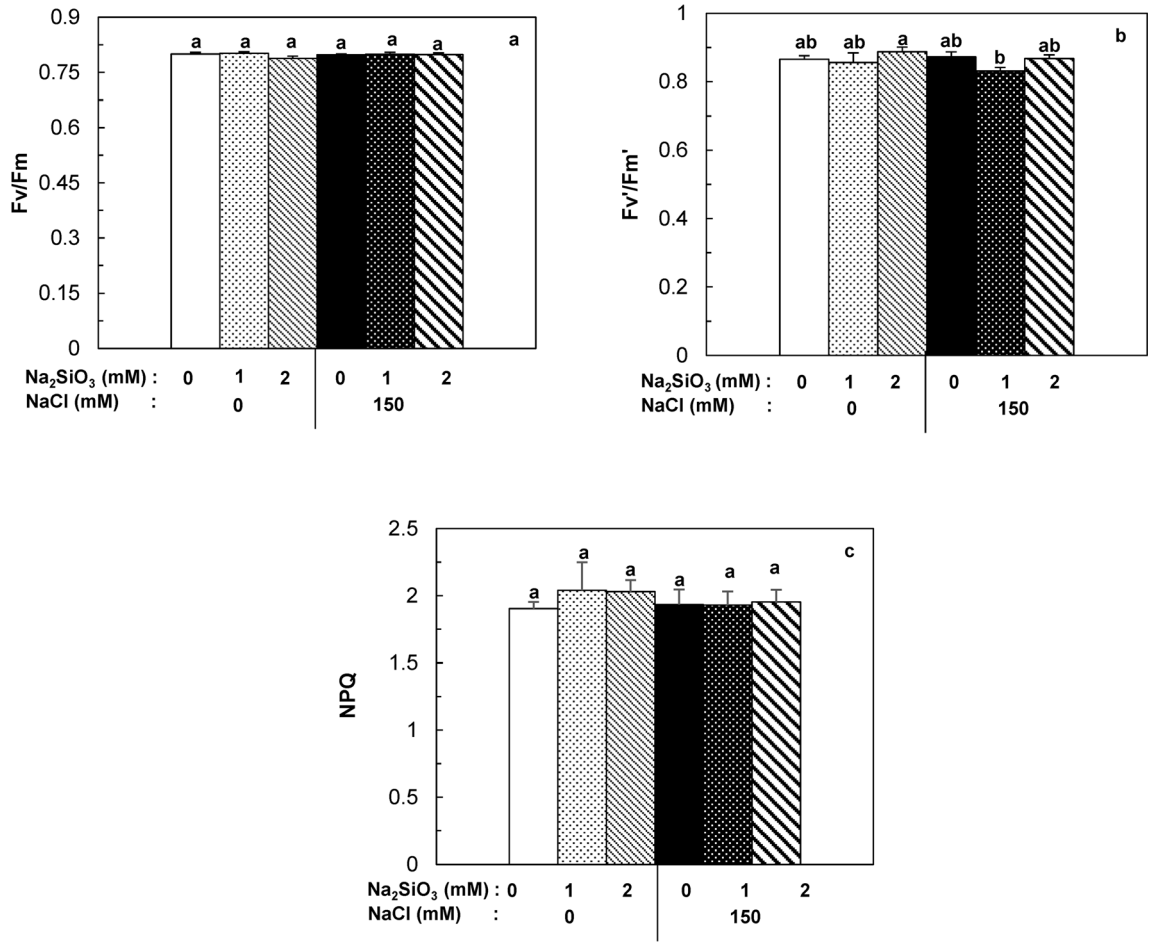

Fig. 7 Chlorophyll fluorescence parameters of *H. marinum* cultivated for 70 days. Plants were exposed to 3 concentrations of Na_2SiO_3 (0, 1 or 2 mM) in the absence or presence of NaCl (150 mM) during the last 28 days of culture. Fv/Fm (maximum photochemical efficiency of PSII) = (Fm–F0)/Fm; Fv (variable fluorescence) = (Fm-F0); Fm: maximal fluorescence; F0: minimal fluorescence; Fv′/Fm′ (maximum efficiency of PSII open centres in the light-adapted state) = (Fm′–F0′)/Fm′); Fm′: maximal fluorescence in the light-adapted state; F0′: minimal fluorescence in the light-adapted state; NPQ: non-photochemical quenching. Values are means ± SE of 4 individual plants. Bars marked with the same lower-case letters in each panel are not significantly different at $P \leq 0.05$ (Duncan's test)

3.11 Nutrient Content

Under salt-free conditions, no effect on calcium contents was observed. However, at 150 mM NaCl and 0 mM Na_2SiO_3, root Ca contents were significantly increased. By adding both concentrations of Si (1 mM and 2 mM), Ca contents were significantly reduced in roots under salt stress. The same effect was also noticed in shoot calcium contents which were markedly decreased under Na_2SiO_3 application at 150 mM NaCl (Table 1).

Root iron (Fe) contents were significantly increased under salt stress in the absence of sodium silicate. By contrast, the application of 1 and 2 mM Na_2SiO_3 resulted in a marked decrease of these contents. An antagonistic effect was observed in shoots of slat-treated plants, which showed a significant increase of their Fe contents with the addition of Na_2SiO_3 (Table 1).

Zinc (Zn) concentrations in roots were clearly higher at 150 mM NaCl when applied separately. However, when combined to Na_2SiO_3 treatment, these concentrations were significantly reduced. Both NaCl and Na_2SiO_3 addition did not affect shoot zinc contents (Table 1).

3.12 Principal Component Analysis (PCA) and Correlation Analysis

In order to improve our investigation, the trait-by-trait analyses were completed by a PCA as well as by correlation analysis, which took into account all analysed traits characterizing plants subject to salinity and Si application (Table 2; Fig. 11).

The results obtained by PCA and correlation analysis revealed a perfect match with our trait-by-trait analyses which showed positive and negative correlations between the studied parameters. At 0 mM Na_2SiO_3, many negative

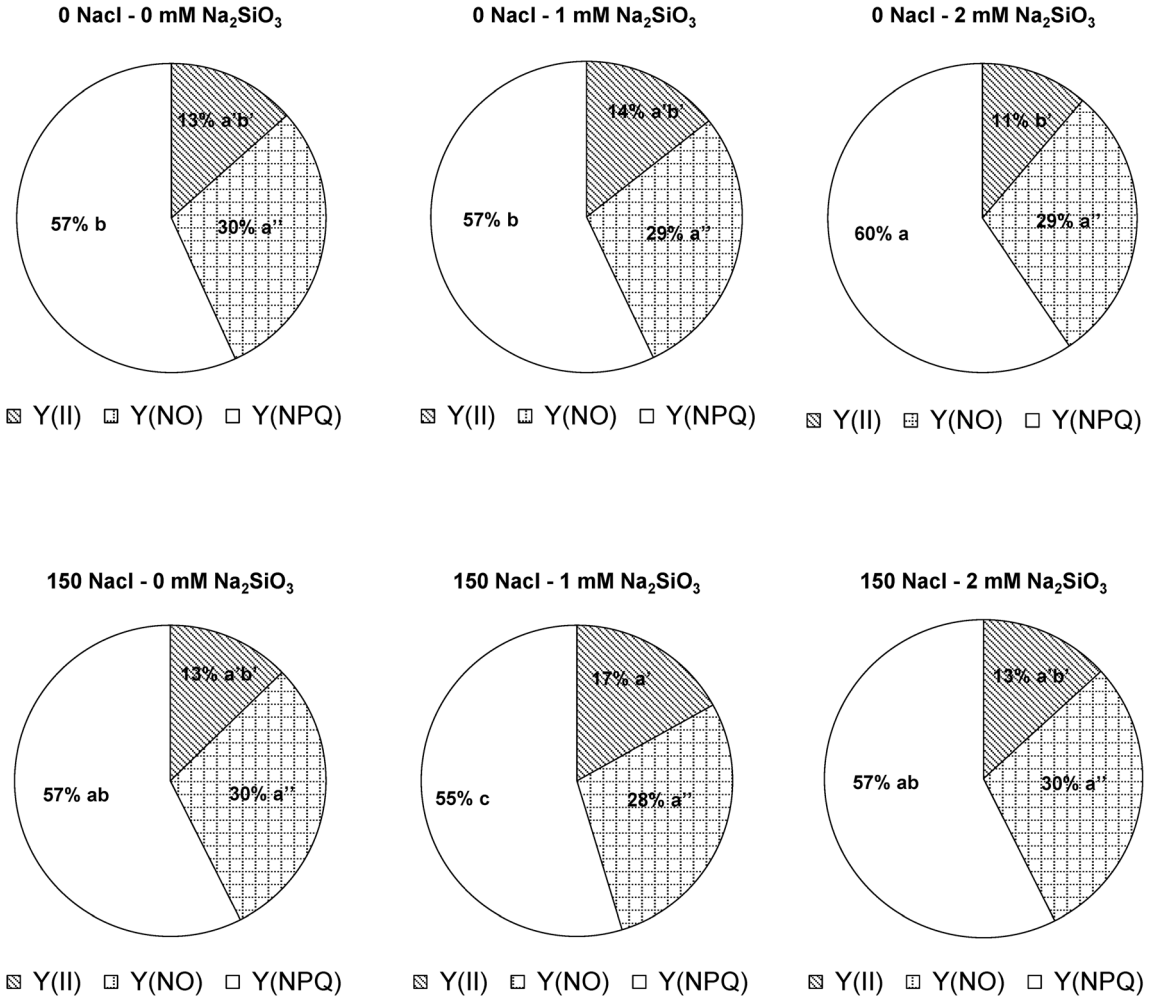

Fig. 8 Photosystem II (PSII) energy distribution diagram to photochemical process (Y(II)), regulated non-photochemical quenching (Y(NPQ)), and non-regulated non-photochemical quenching (Y(NO)) in *H. marinum* plants cultivated for 70 days. Plants were exposed to 3 concentrations of Na_2SiO_3 (0, 1 or 2 mM) in the absence or presence of NaCl (150 mM) during the last 28 days of culture. Values are means ± SE of 4 individual plants. Bars marked with the same lower-case letters in each panel are not significantly different at $P \leq 0.05$ (Duncan's test)

correlations on root dry weight (Pearson correlation coefficient R = −0.72), shoot dry weight (R = −0.70), whole plant dry weight (R = −0.69), shoot length (R = −0.52), shoot water content (R = −0.71), *E* (R = −0.66), *Ci* (R = −0.82), shoot K content/root K content (R = −0.57) and Fe content (R = −0.82), were observed. These correlations proved that the absence of Na_2SiO_3 under salt stress promotes the decrease of all these parameters. This treatment also increased the MDA levels (R = 0.69), *A* (R = 0.65), shoot Na content (R = 0.61), root K content (R = 0.69), shoot Na content/root Na content (R = 0.75), root Ca content (R = 0.64), shoot Ca content (R = 0.55), root Fe content (R = 0.81), root Zn content (R = 0.58), and shoot Zn content (R = 0.43). Positive correlations were also found at 1 mM Na_2SiO_3 for root dry weight (R = 0.64), Chl. *b* (R = 0.64), g_s (R = 0.75), *Ci* (R = 0.85), Y(II) (R = 0.73) and shoot Fe content (R = 0.60). However, negative correlations on *A* (R = −0.73), IWUE (R = −0.82), Fv'/fm′ (R = −0.72), Y(NPQ) (R = −0.90) and root Fe content (R = −0.62), were noticed. At 2 mM Na_2SiO_3, positive correlations were observed on shoot length (R = 0.71) and shoot K content/root K content (R = 0.72), while negative correlations were observed for root K content (R = −0.56) and shoot Zn content (R = −0.64) (Table 2).

Finally, the results obtained by PCA and correlation analysis showed a perfect match with our trait-by-trait analyses. These analyses confirmed the previously observed positive effect of silicon application.

4 Discussion

In the present work, obtained results showed that moderate salinity stress may reduce *H. marinum* growth. In fact, addition of 150 mM NaCl decreased significantly the fresh and dry

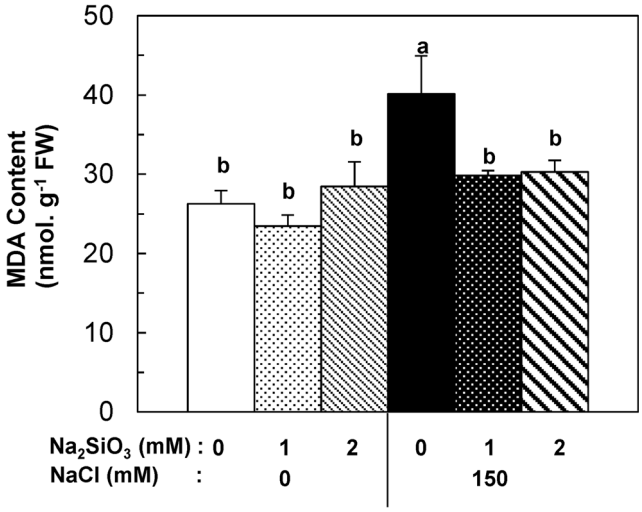

Fig. 9 MDA shoot concentrations of *H. marinum* cultivated for 70 days. Plants were exposed to 3 concentrations of Na_2SiO_3 (0, 1 or 2 mM) in the absence or presence of NaCl (150 mM) during the last 28 days of culture. Values are means ± SE of 4 individual plants. Bars marked with the same lower-case letters in each panel are not significantly different at $P \leq 0.05$ (Duncan's test)

biomassesof *H. marinum* in all organs of the plant (roots, shoots, and whole plant) (Fig. 3).

Similar findings are reported by several others [2, 21], who indicated that salinity often led to a decrease in plant production. Similar results were also observed in *Arabidopsis thaliana* [22], *Hordeum vulgare* [23] and *H. marinum* [24]. In agreement with these reports, Ben-Abdallah et al. (2019) [25] found that salt significantly decreased growth parameters of *Solanum villosum* seedlings. The observed deleterious effects of salt stress on plant growth can be mainly attributed to an osmotic effect, disturbance of mineral nutrition, and ion toxicity [26].

On the other hand, Si application was found to mitigate salinity effects and to improve significantly the production of biomass of *H. marinum* (Fig. 3). These results confirm previous observations reporting the beneficial effect of Si intake, under salt stress, on the growth of many species such as sorghum [27], rice [28–30], wheat [31], cucumber [32], tomato [33], etc. Growth stimulation observed in these plants could be explained by a protective effect of Si against salt stress [6]. However, the beneficial role of Si remains less marked in the absence of salt stress, which is in agreement with several research studies suggesting that this effect is strongly related to salinity stress impact [34].

Under saline conditions, *H. marinum* exhibited reduced water content in the aerial parts, contrarily, to that of roots which was remained unchanged (Fig. 4). These findings were concomitant with those obtained by Hafsi et al. (2007) [14], who showed that salt stress decreased water content at the level of the aerial parts in *H. marinum*. A positive effect of Si was observed in shoot hydration of salt-stressed plants (Fig. 4). In fact, according to several authors, silicon deposition in cuticles has been shown to prevent water loss via evapotranspiration, thereby protecting plants [6, 34, 35].

Moreover, Si did not affect Chl. *a* and carotenoid contents, whereas Chl. *b* contents were significantly enhanced at 1 mM Si with or without NaCl (Fig. 5). Indeed, several studies proved that Si can improve chlorophyll concentrations under saline stress [31]. For instance, Sattar et al. (2017) [36] revealed that the salt stress reduced Chl. *a*, Chl. *b* and total chlorophyll contents. However, this negative impact observed under salinity conditions was alleviated by Si application leading to the enhancement of photosynthetic pigment production in wheat plants. Within this framework, Delavar et al. [37] demonstrated that exogenous Si supply increased chlorophyll contents under salt stress.

Under free-salt conditions, Si supply was found to enhance *A* at 1 mM Si. However, Si effect was more obvious under salinity resulting in the restoration of gas exchange measurements (g_s, *Ci,* and *E* which was improved at both doses of Si (1 mM and 2 mM)) (Fig. 6). It is well known that salinity stress, minimized *A*, g_s, *E* and *Ci*. According to Ouerghi et al. (2000) [38], reduced *Ci* under salt stress is linked to the decrease of g_s resulting in the impairment of photosynthetic capacity.

Several studies were in accordance with indicate that Si application, under salt stress, enhanced *A*, g_s [39] and Ci [40]. Our results are also in agreement with those of Yin et al. (2013) [41] who showed an improvement in g_s and *E* in association with Si supply in Sorghum (*Sorghum bicolor*) stressed plants.

Concerning the fluorescence parameters, no change was observed in Fv/Fm and Fv'/Fm′ in *H. marinum* PSII grown under salt stress in combination with Si (Fig. 7). This confirms different previous observations reported by Al-Aghabary et al. (2005) [42], and Mateos-Naranjo et al. (2013) [40]. According to Maxwell and Johnson (2000) [43], the maintenance of a constant Fv/Fm ratio in plants subjected to salinity and /or Si sustained photoinhibition capacity. In addition, the preservation of the Y(II) can also be strongly linked to maintenance of qP and NPQ, which indicates that plants dissipate the same fraction in the form of thermal energy considered as a protective mechanism of the reaction of photosynthesis centres. These findings were proved by NPQ analysis which were unaffected under salinity conditions in the absence or the presence of Si.

The performed analyses demonstrate that Y (NPQ) changed only at 2 mM Si condition under salt-free conditions. These results are in agreement with those obtained by Moinuddin et al. (2017) [44], whose study showed no variation in Y(NPQ) in four halophytic species at 200 mM NaCl, and with the results found by Perez et al. (2014) [45] who examined the effect of Si on wheat. Similarly, no difference was noticed in Y(NO) parameter under salinity conditions and/or in the presence of Si in *H. marinum* plants. These results showed that salinity did

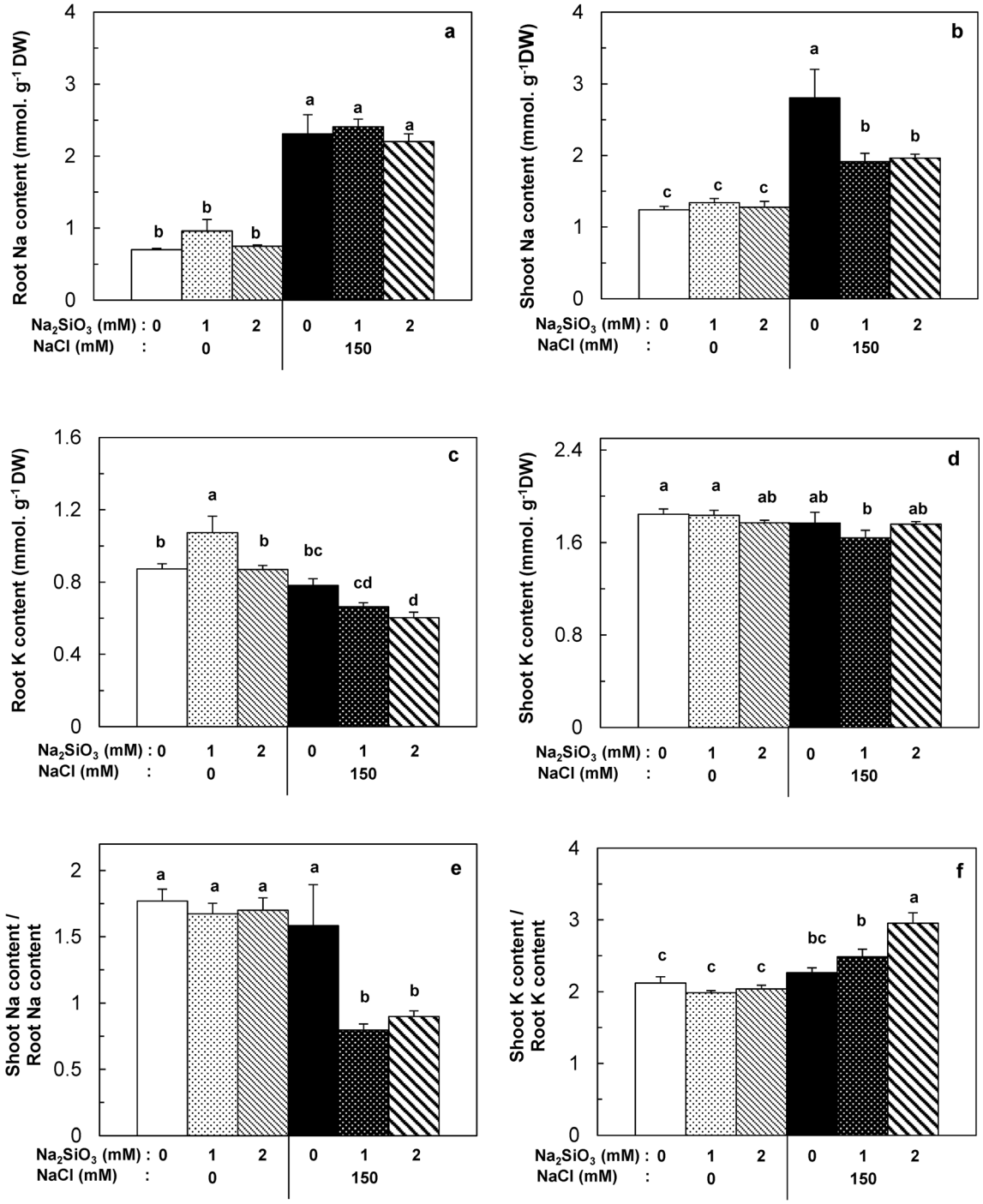

Fig. 10 Sodium and potassium content in roots and shoots, and translocation of sodium and potassium from the roots to the shoots of *H. marinum* cultivated for 70 days. Plants were exposed to 3 concentrations of Na_2SiO_3 (0, 1 or 2 mM) in the absence or presence of NaCl (150 mM) during the last 28 days of culture. Values are means ± SE of 6 individual plants. Bars marked with the same lower-case letters in each panel are not significantly different at $P \leq 0.05$ (Duncan's test)

not affect PSII structure as well as the number of its reaction centres contributing to electron transport, regardless of the medium Si concentration.

It was also noticed that the lipid peroxidation was significantly mitigated in salt-stressed plants exposed to Si application. In these plants, MDA concentrations were restored to control levels indicating that the adverse effect of salinity were alleviated by Si supply (Fig. 9). Si seems to play a crucial role in lipid peroxidation restoration through a decrease in production of lipid-derived radicals that are responsible for oxidative stress. Liang (1999) [46] reported that Si decreased the concentration of MDA in barley, while Zhang et al. (2017) [47]

Table 1 Ca, Fe and Zn concentrations (expressed in μg g^{-1} DW) in roots and shoots of *H. marinum* cultivated for 70 days. Plants were exposed to 3 concentrations of Na_2SiO_3 (0, 1 and 2 mM) in the absence or presence of NaCl (150 mM) during the last 28 days of culture. Values are means ± SE of 6 individual plants. Values marked with the same lower-case letters in each "element" and "organ" are not significantly different at $P \leq 0.05$ (Duncan's test)

Roots

Treatment	Ca content	Fe content	Zn content
0 mM NaCl 0 mM Si	76,419 ± 12,523 bc	3618 ± 482 c	120 ± 1.39 a
0 mM NaCl 1 mM Si	54,493 ± 5687 c	2899 ± 196 c	107 ± 1.27 b
0 mM NaCl 2 mM Si	87,874 ± 8009 ab	3608 ± 331 c	102 ± 0.94 b
150 mM NaCl 0 mM Si	110,159 ± 15,582 a	8196 ± 816 a	209 ± 0.41 b
150 mM NaCl 1 mM Si	76,030 ± 7850 bc	3951 ± 233 bc	87.7 ± 1.74 b
150 mM NaCl 2 mM Si	63,927 ± 6132 c	5172 ± 594 b	106 ± 1.66 b

Shoots

Treatment	Ca content	Fe content	Zn content
0 mM NaCl 0 mM Si	7320 ± 501 a	200 ± 35 c	65 ± 1.59 bc
0 mM NaCl 1 mM Si	8064 ± 688 a	280 ± 33 c	104 ± 1.2 a
0 mM NaCl 2 mM Si	6486 ± 143 ab	264 ± 39 c	68.8 ± 1.86 bc
150 mM NaCl 0 mM Si	7187 ± 958 a	216 ± 32 c	80.2 ± 2.24 b
150 mM NaCl 1 mM Si	5238 ± 299 b	1006 ± 82 a	75.7 ± 1.38bc
150 mM NaCl 2 mM Si	5033 ± 538 b	770 ± 65 b	56.9 ± 1.96 c

showed that Si treatment reduced MDA contents in *Glycyrrhiza uralensis* subjected to salt stress. This reduction led to alleviation of oxidative damage caused by lipid peroxidation of membranes.

A significant increase of sodium contents was also noticed with the addition of NaCl both at root and shoot parts (Fig. 10). Similar results were exhibited by Khan et al. (2017) [13] in two maize cultivars. This increase in sodium levels recorded in the aerial parts of *H. marinum* was alleviated by the addition of Si. These results are consistent with those found by Liang (1999) [46] and Liu et al. (2019) [48] who showed that adding Si in the nutrient solution decreased Na levels in rice, wheat and barley. Similarly, we revealed that the addition of Si dramatically decreased the translocation of sodium from the roots to the aerial parts and increased that of potassium (Fig. 10).

Our results support "the apoplastic obstruction hypothesis" sustained by Coskun et al. 2019 [6]. According to these authors, in the presence of silicon, plants improve Casparian Band (CB) "development", as well as apoplastic silicon deposition (as SiO_2), effectively blocking "bypass routes", and thus root-to-shoot translocation of sodium.

Salt stress induces an increased accumulation of reactive oxygen species (ROS) which can disrupt the normal metabolism of plants, application of Si has an enhancing effect in the regulation of antioxidant responses [49, 50]. Si causes reduction of ROS in rice [49] and Cowpea [50].

Si can actively involve in physiological and biochemical metabolism by regulating gene expression related to the biosynthesis of phytohormones (such as abscisic acid (ABA) and jasmonic acid (JA)) [49]. Khan et al. 2020 [51] showed that Si decreases the level of endogenous ABA under salt stress on the date palm (*Phoenix dactylifera* L.). Also, the addition of Si induces a reduction in CAT and POD enzymatic activities in the date palm under saline stress [51]. In fact, Si can actively involve metabolism by regulating gene expression related to antioxidant defence enzymes (such as superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD), proton pumps, and osmolytes, which improves plant tolerance to salinity [7].

In the present experiment, the addition of Si was also found to reduce calcium content under salinity stress (Table 1). In a recent study, Jang et al. (2018) [52] showed that Ca uptake in rice plants decreased with increasing Si concentrations.

In our study, the presence of Si led to an increase of shoot Fe accumulation in salt-stressed plants (Table 1). It

Table 2 Pearson's correlation matrix analysing growth parameters, water content, photosynthetic pigment concentrations, fluorescence parameters, MDA contents, Na, K, and nutrient concentrations of *H. marinum* exposed to 3 concentrations of Na_2SiO_3 (0, 1 or 2 mM) in the presence of NaCl (150 mM) during the last 28 days of culture. *A*: Net CO_2 assimilation; g_s: stomatal conductance; *E*: transpiration rate; *Ci*: intercellular CO_2 concentration; IWUE: Intrinsic Water Use Efficiency; Fv/Fm: maximum photochemical efficiency of PSII; Fv′/Fm′: maximum efficiency of PSII open centres in the light-adapted state; Y(II): steady state of PSII operating efficiency; NPQ: non-photochemical quenching; Y(NPQ): regulated non-photochemical quenching; Y(NO): non-regulated non-photochemical quenching. Variables were centred around their means and normalized with a standard deviation of 1. Values in bold (*) represent significant correlations at 0.05 level

Variables	0 mM Si	1 mM Si	2 mM Si
Root Dry Weight	**−0.72***	**0.64***	0.08
Shoot Dry Weight	**−0.70***	0.46	0.24
Whole Plant Dry Weight	**−0.69***	0.42	0.27
Root length	−0.21	0.40	−0.19
Shoot length	**−0.52***	−0.19	**0.71***
Root Water Content	−0.39	0.14	0.25
Shoot Water Content	**−0.71***	0.26	0.45
MDA Content	**0.69***	−0.37	−0.32
Chl. *a*	−0.15	0.48	−0.33
Chl. *b*	−0.29	**0.64***	−0.35
Carotenoids	0.09	−0.37	0.28
A	**0.65***	**−0.73***	0.07
g_s	−0.35	**0.75***	−0.37
E	**−0.66***	0.38	0.26
Ci	**−0.82***	**0.85***	−0.03
IWUE	0.54	**−0.82***	0.26
Fv/Fm	−0.09	0.11	−0.01
Fv'/Fm′	0.43	**−0.72***	0.29
NPQ	−0.03	−0.04	0.07
Y(II)	−0.43	**0.73***	−0.30
Y(NO)	0.21	−0.28	0.06
Y(NPQ)	0.46	**−0.90***	0.44
Root Na Content	0.01	0.18	−0.18
Shoot Na Content	**0.61***	−0.33	−0.28
Root K Content	**0.69***	−0.13	**−0.56***
Shoot K Content	0.20	−0.35	0.16
Shoot Na Content / Root Na Content	**0.75***	−0.43	−0.24
Shoot K Content / Root K Content	**−0.57***	−0.15	**0.72***
Root Ca Content	**0.64***	−0.19	−0.44
Shoot Ca Content	**0.55***	−0.23	−0.32
Root Fe Content	**0.81***	**−0.62***	−0.11
Shoot Fe Content	**−0.82***	**0.60***	0.05
Root Zn Content	**0.58***	−0.37	−0.21
Shoot Zn Content	**0.43***	0.22	**−0.64***

is well established that Fe is a micronutrient essential for the functioning of plant cells and it plays a cofactor role in metabolic processes [53, 54]. As revealed in previous studies, Si application alleviates Fe deficiency in plants and in cucumber by increasing shoot and root biomass and chlorophyll contents [55].

In addition, Si supply was found to improve the ability of roots to inactivate excess Zn in the tissues. Thus, it inhibited translocation of Zn from root to shoot and increased the total root concentration of Zn in rice [56]. The same effect was probably noticed in *H. marinum* roots which showed decreased Zn concentrations due to Si application.

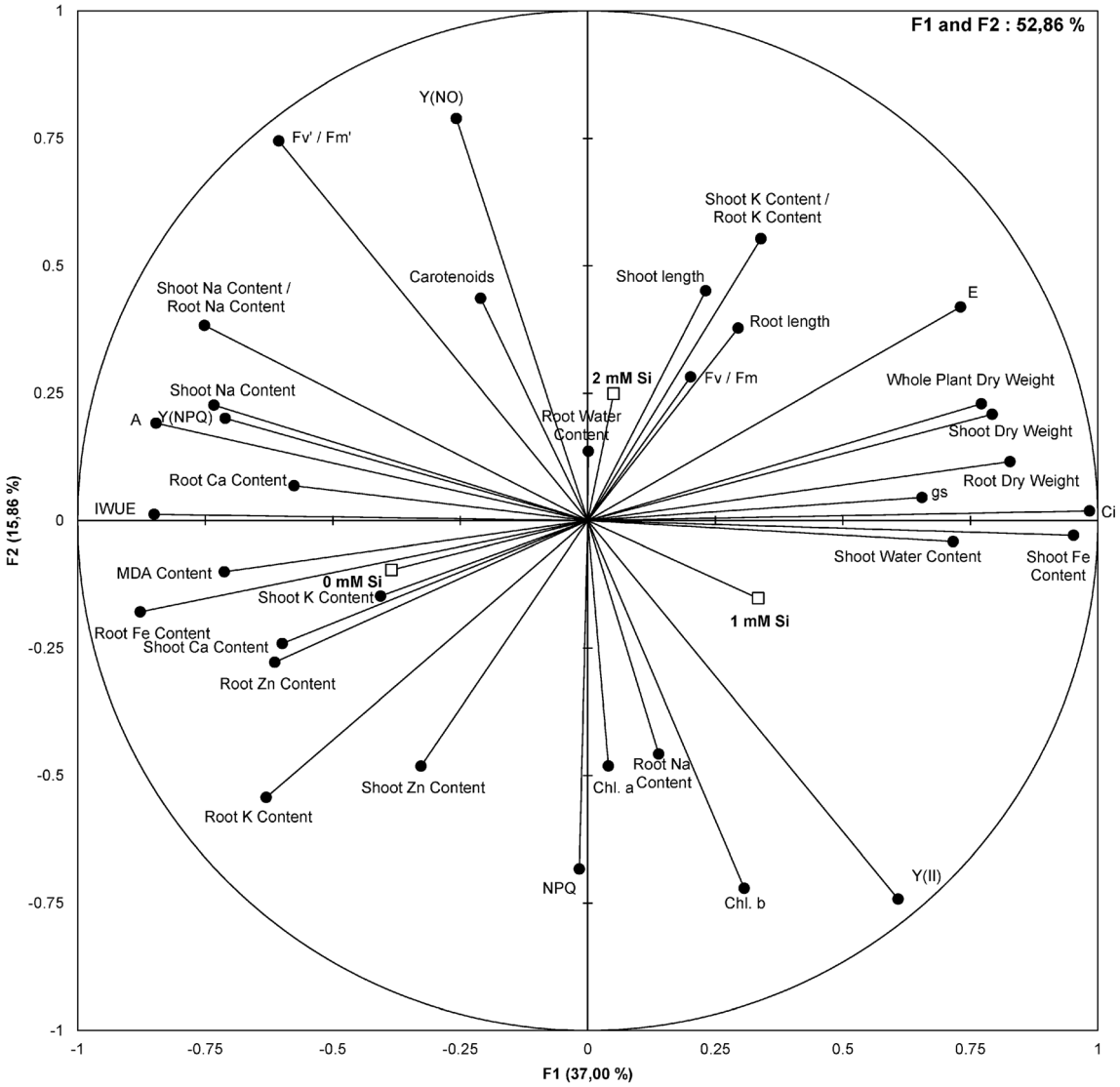

Fig. 11 Principal Component Analysis (PCA). All studied parameters and the different treatments are projected onto the F1-F2 principal factorial plane that explains 52.86% of the variation. *A*: Net CO_2 assimilation; g_s: stomatal conductance; *E*: transpiration rate; *Ci*: intercellular CO_2 concentration; IWUE: Intrinsic Water Use Efficiency; Fv/Fm: maximum photochemical efficiency of PSII; Fv′/Fm′: maximum efficiency of PSII open centres in the light-adapted state; Y(II): steady state of PSII operating efficiency; NPQ: non-photochemical quenching; Y(NPQ): regulated non-photochemical quenching; Y(NO): non-regulated non-photochemical quenching

The beneficial effect of Si application on *H. marinum* plants was confirmed by results obtained by Principal Component Analysis (PCA) and correlation analysis (Table 2; Fig. 11) which showed the positive effect of Si (1 mM) under salinity stress on root dry weight, Chl. *b*, *E*, *Ci*, Y(II) and shoot Fe content (R = 0.64, 0.64, 0.75, 0.85, 0.73 and 0.60, respectively) (Table 2). Hence, Si supply seems to be of a treatment of a high efficiency allowing a successful and quick growth re-establishment in stressed plants through many physiological and metabolic pathways.

Overall, the study of all these parameters reveals that our fertilizer based on Si is a very interesting support for the mitigation of the deleterious effects of salt stress.

5 Conclusion

We conclude that salinity stress negatively affected *H. marinum* growth, water status, mineral nutrition, photosynthesis, chlorophyll pigment levels, fluorescence and MDA concentrations. However, under silicon application, these studied parameters were partially or completely restored in salt-stressed *H. marinum* plants. Silicon can be considered as a promising alternative for the adjustment of salt stress and the development of marginal lands. Hence, this support can be used as a fertilizer of great importance due to its availability in large quantities and can compete with other fertilizers owing to its high efficiency and low price.

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