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Research Article

Biomass partitioning and physiological responses of four Moroccan barley varieties subjected to salt stress in a hydroponic system

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Abstract A hydroponics experiment was performed to study the physiological and biochemical changes in Moroccan barley (*Hordeum vulgare* L.) varieties cultivated under salt stress conditions. Four barley varieties were grown under exposure to three salt concentrations, including 0, 200, and 300 mM NaCl. The ANOVA for both salt stress-sensitive and resistant varieties indicated that salt treatment represented the main source of variability in all studied traits. Salt treatment significantly reduced root and shoot dry weight (RDW and SDW), relative water content (RWC), and chlorophyll content (Chl a, Chl b, and Chl T). However, increases in electrolyte leakage (EL) along with proline and total soluble sugar (TSS) contents were recorded. In addition, large variations in all measured traits were found between varieties. The 'Massine' and 'Laanaceur' varieties displayed relatively higher RDW and SDW values. The 'Amira' and 'Adrar' varieties showed lower RWC values and Chl contents than those of the controls indicating their relative sensitivity to salt stress. Principal component analysis revealed that most of the variation was captured by PC1 (72% of the total variance) which grouped samples into three categories according to salt treatment. Correlation analyses highlighted significant associations between most parameters. Positive relationships were found between RDW, SDW, RWC, Chl content, and soluble proteins contents, while all of these parameters were negatively associated with EL intensity, proline content, and TSS content. The results from this study showed that the 'Massine' and 'Laanaceur' varieties were relatively salt-tolerant. These two salt-tolerant varieties present a good genetic background for breeding of barley varieties showing high salt tolerance.

Keywords *Hordeum vulgare*, barley, salt stress, Morocco, hydroponic culture

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Introduction

In the next decade, world agricultural production is expected to grow by 1.4% per year to meet the needs of population growth (Hossain and Mohamed 2019). This development will be mainly linked to an increase in grain yields which is challenging because fertile soil is limited, and the land area represents a critical planetary boundary (da Silva et al. 2023; Duro et al. 2020). Fertile lands are threatened by soil degradation, salinization, urbanization, and global warming, which are in continuous increase (Liu et al. 2019). Actually, salinity is considered one of most factors altering land fertility and affecting crop production (Zhao et al. 2021). Saline soils covered in 2006 more than 7% of the total land area on the planet and 70% of all agricultural soils (Rengasamy 2006). In Morocco, mapping soil salinity studies showed that more than half of land area of the country is affected by salinity (Chaaou et al. 2022; Rafik et al. 2022). In fact, roughly 500,000 hectares were estimated to be impacted by salinity (El Goumi et al. 2014). Thus, beside the global warming and the increase of carbon dioxide concentration in the atmosphere, the salinity is considered one of the major abiotic factors influencing crops growth and development.

Cereals take an important place in Moroccan agriculture, which occupy more than 75% of cultivated agricultural areas (Salama et al. 2016). Barley is the second cereal used by the Moroccan population for human alimentation and livestock feeding (El Goumi et al. 2014). In arid and semi-arid regions, soil salinity is a serious obstacle to barley grain production. High salt levels in soil cause various events that negatively impact plant development, by the inhibition of enzymatic activities and reductions in photosynthetic rates (Zeeshan et al. 2020). In addition, salt imposes osmotic stress by decreasing the soil water potential and accumulated ions such as sodium has been shown to be toxic and disrupt several metabolic processes (Lee et al. 2013). Despite this, plants can tolerate high levels of salt by efficient physiological, morphological, and molecular mechanisms, which attenuate salt-induced stress (Ruiz-Carrasco et al. 2011). Such responses depend mainly on the inherent salt tolerance ability of each variety (Munns and Tester 2008). Morphological traits are adopted in several studies as a crucial parameter describing plant resistance to various stresses. Root and shoot dry weights are highly affected by environmental conditions, they are usually measured to evaluate the ability of plants to keep their biomass under stressful conditions (Hellal et al. 2018; Pour-Aboughadareh et al. 2020). In studies describing plant genotypes tolerance to abiotic stresses, the genotypes able to preserve high values of root and shoot dry weights are considered more tolerant (Nguyen et al. 2016; Silvente et al. 2012). On the other hand, a significant decrease in biomass is often recorded in sensitive genotypes, which reflects a shortage of plant resources and leads to stop cell proliferation (Nguyen et al. 2016). Regarding physiological parameters, it is reported that salt stress affects photosynthesis efficiency by thylakoids alteration, chlorophyll degradation, and CO_2 assimilation (Sallam et al. 2019). Moreover, salt stress affects osmotic cell state by modifying water content and osmolytes content (Sallam et al. 2019), and change oxidative status by increasing reactive oxygen species content in the cells (Abdelaal et al. 2020; Shahbaz and Ashraf 2013).

In this context, a study of physiological, morphological, and biochemical traits under salinity would improve our understanding of salt tolerance in barley. To date, only a few researches have investigated the effects of salt stress on Moroccan barley (El Goumi et al. 2014). To our knowledge, there is no report in the literature about salt effects on physiological traits in Moroccan barley varieties under the hydroponic system. Hence, the objective of this study was to evaluate the responses of four Moroccan varieties under different levels of salt stress in the hydroponic system. In particular, the aims of this research were (i) to assess the physiological, morphological, and biochemical parameters of the Moroccan varieties during the vegetative stage; and (ii) to dissect the relationship between these traits.

Materials and Methods

Experimental details and plant materials

The experiment was carried out in the greenhouse of the Natural Resources and Environment Laboratory at the Polydisciplinary Faculty of Taza, Morocco. Four leading Moroccan barley varieties (‘Massine’; ‘Laanaceur’, ‘Amira’ and ‘Adrar’) were chosen for this experiment. Seeds were provided by the Moroccan National Institute for Agricultural Research (INRA) (Table 1). The seeds were disinfected with 10% solution of sodium hypochlorite for 15 minutes and then washed three times with distilled water. After that, the seeds were put on wet filter paper in Petri dishes in the dark at 25°C for 5 days. Seedlings of barley were transferred in plastic containers (10 L) with three replicates per treatment, and supplied with continuously aerated nutrient Hoagland solution. Salt stress treatment was applied by adjustment of the suitable concentration of NaCl in the nutrient solution at 0 mM for control and at 200 and 300 mM for the two levels of salt stress. The temperature and photoperiod are both strictly regulated during the duration of the experiment. Plants were cultivated under natural light supplemented with an artificial light (HPS lamps, 400 W) in a day/night regime of 16 h at 24°C/8 h at

Table 1 Characteristics of the barley collection genotypes used in this study

Variety	Year of release	Program	Spring/winter type	Row type
‘Adrar’	1998	INRA Morocco	Spring type	2 rows
‘Amira’	1996	INRA Morocco	Winter type	6 rows
‘Laanaceur’	1991	INRA Morocco	Winter type	6 rows
‘Massine’	1994	INRA Morocco	Winter type	6 rows

23°C. After fifteen days of salt treatment, plants were harvested and fresh shoots and roots samples were collected for analysis.

Analytical measurements

Morphological, physiological, and biochemical parameters such as root and shoot dry weight, RWC (relative water content), electrolytes leakage (EL), photosynthetic pigments content, and osmolytes contents were recorded in shoots at the vegetative stage. When harvested, roots and shoots were separated and placed in a dry oven at 65°C for root and shoot dry weights determination. RWC was obtained by Lara et al. (2003) method. The assessment of electrolytes leakage in shoots was done by using methods of Bajji et al. (2001). The different photosynthetic pigments, i.e., Chl a (chlorophyll a), Chl b (chlorophyll b), and Chl T (Total chlorophyll) were analyzed in shoots following the method described by Burnison (1980) using DMSO. Osmolytes accumulations (proline, soluble proteins, and total soluble sugars contents) were assessed in shoots. Proline content (ProC) was estimated by the method of Bates et al. (1973) with the use of 3% sulphosalicylic acid. Total soluble sugars (TSS) were determined using anthrone reagent by the method of Yemm and Willis (1954). Total soluble proteins content was determined by Lowry's method (Lowry et al. 1951) and using Bovine Serum Albumin.

Statistical analysis

Analysis of data was done by combined analyses of variance (ANOVA) across the salt treatment levels and the different varieties. The least significant difference (LSD) values were calculated at the 5% probability level. Based on the mean values, a correlation matrix between the studied parameters and principal component analyses (PCA) was performed by using the STATGRAPHICS Centurion XVII package (Stat point Technologies). All statistical analyses were done with the XLSTAT software (2016.02.28451 version).

Results

Data variability

Analysis of variance (Table 2) showed a significant ($p \leq 0.05$) impact of three levels of salt stress on all parameters studied in leaves of resistant and sensitive Moroccan barley varieties. Regarding the resistant varieties, our results

Table 2 Mean squares of the combined analyses of variance for various physiological and biochemical parameters of four Moroccan barley varieties grown under exposure to three salt concentrations (0, 200, and 300 mM NaCl) to the vegetative stage

	DF	RDW	SDW	RWC	EL	Chl a	Chl b	Chl T	ProC	TSS	Proteins
					Salt-resistant						
V	1	0.069 ***	0.835 ***	1.211	3.21 *	0.130 ***	0.044 ***	0.030 *	3889 ***	1.142 **	0.012
TR	2	0.080 ***	3.547 ***	801.136 ***	1675.37 ***	0.655 ***	0.108 ***	0.931 ***	204723 ***	9.458 **	1.563 ***
GS	2	0.000	0.019	3.404	0.91	0.002	0.002	0.005	4	0.064	0.009
V × TR	2	0.002 **	0.048	48.736 **	0.36 *	0.010 *	0.033 ***	0.004	2323 ***	0.788 **	0.541 ***
Residual	10	0.000	0.014	5.086	0.50	0.002	0.001	0.006	10	0.049	0.011
Total (corrected)	17										
					Salt-sensitive						
V	1	0.658 ***	1.720 ***	0.05	118.88 ***	0.063 **	0.003	0.145 ***	722.8 ***	0.155 *	1.019 ***
TR	2	0.587 ***	4.262 ***	1261.95 ***	2482.13 ***	3.803 ***	1.274 ***	6.520 ***	47011 ***	13.222 **	1.730 ***
GS	2	0.001	0.011	4.39	1.55	0.003	0.003	0.003	4.3	0.001	0.059
V × TR	2	0.060 ***	0.428 ***	72.82 ***	13.35 **	0.500 ***	0.230 ***	0.012 **	1422.4 ***	0.069	0.478 ***
Residual	10	0.001	0.014	1.05	1.46	0.004	0.002	0.001	15.4	0.023	0.028
Total (corrected)	17										

*Significant at $p < 0.05$ probability level; **Significant at $p < 0.01$ probability level; ***Significant at $p < 0.001$ probability level. RDW, root dry weight; SDW, shoot dry weight; RWC, leaf relative water content; EL, electrolyte leakage; Chl a, chlorophyll a; Chl b, chlorophyll b; Chl T, total chlorophyll content; ProC, proline content; TSS, total soluble sugar; V, variety; TR, treatment; GS, replicate.

showed that the treatment factor contributed to most of the variation in all studied traits (over 88%), except for RDW and Chl b which were explained by 53% and 58%, respectively. In contrast, the effect of variety was relatively not significant, contributing less than 4% of the total variance in all parameters, except for SDW, RDW, and Chl b, which explicated 46, 19 and 23%, respectively. In the case of sensitive varieties, around 90% of the variation in all traits was attributed to the treatment factor, except for protein and RDW, which being elucidated by 52% and 45%, respectively. The effect of variety was not significant, contributing less than 2% of the total variance in studied parameters, except for SDW, RDW, and protein, which were expounded 40, 27 and 31%, respectively. Furthermore, RDW was attributed in equal proportion to both NaCl treatment and variety effects. The interaction between the two factors was generally not significant.

Growth status, water content, and electrolytes leakage

The results presented in Fig. 1 confirmed that salt stress had a significant impact on barley plants, with notable variations observed among different varieties. Concerning shoot and root dry weight in plants grown at 200 mM of NaCl, SDW declined by around 57% in 'Adrar', 'Laanaceur', and 'Massine', and 33% in 'Amira' when compared to the control (Fig. 1b). Furthermore, root dry weight (RDW) decreased significantly in 'Adrar' and 'Amira' by 45%, while the reduction was about 25% in 'Laanaceur' and 'Massine'. When grown with 300 mM of NaCl, 'Amira' experienced the most significant decrease in both SDW and RDW (75% and 60%, respectively), followed by 'Adrar' with a reduction of 60% in RDW. However, in 'Laanaceur' and 'Massine', RDW reduction was only around 45%. Moreover, there was no significant difference between the barley plants grown in 200 mM and 300 mM of NaCl in the 'Laanaceur' variety (Fig. 1a);

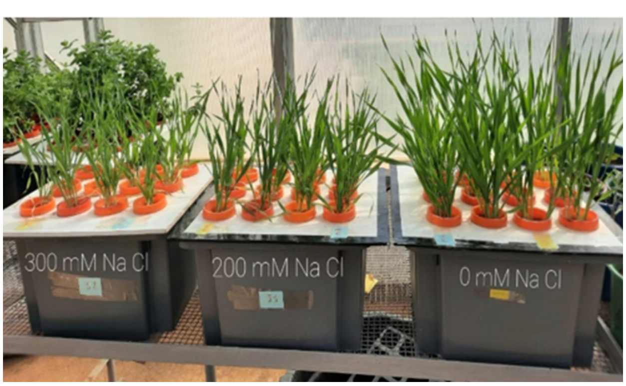

Fig. 1 Growth of seedlings of four Moroccan barley varieties, including Massine, Laanaceur, Adrar, and Amira, at 15 d after treatment with NaCl

For RWC trait, 'Adrar' was the most affected variety (Fig. 1c). When compared to the control, the degree of decrease was approximately 25% and 35% in plants grown with 200 mM and 300 mM of NaCl, respectively. In 'Amira' and 'Laanaceur' varieties, NaCl reduced RWC by 20%. However, there is no significant difference between plants in the two salt treatments. In 'Massine' variety, the percentage of decline was 17% and 14% in the 200 mM and 300 mM NaCl treatments, respectively.

Salt treatment increased significantly EL with different levels in the four varieties studied. In 'Adrar' and 'Amira' varieties, NaCl treatment in the both levels increased EL by 50% when compared to the control. In 'Laanaceur' and 'Massine' varieties, EL increased by approximately 45% with 200 mM of NaCl and up to 55% with 300 mM of NaCl (Fig. 1d).

Chlorophyll content

The comparison between barley varieties indicated a decrease in all photosynthetic pigments under salinity stress (Fig. 1 e, f, and g). In fact, we found that chl a, chl b, and chl T concentrations decreased significantly in plants grown under 200 mM NaCl compared to the control, with the most reduction observed in 'Adrar' and 'Amira' (65%). 'Laanaceur' and 'Massine' varieties exhibited a slight reduction (8% and 16%, respectively). At a high level of salinity (300 mM NaCl), all varieties were affected and the chlorophyll values (Chl a, Chl b, and Chl T) decreased significantly. 'Adrar' and 'Amira' showed the highest scores of reductions (66% and 54%, respectively), however, when compared to controls, 'Laanaceur' and 'Massine', loss 36% and 33% respectively.

Osmolytes accumulation

Mean values of proline content, soluble sugars content, and soluble proteins contents for all varieties under salt stress were shown in (Fig. 1h, 1i and 1j). In plants grown with 200 mM of NaCl, no significant difference was noted in 'Adrar' and 'Amira' varieties when compared to the control. However, in 'Laanaceur' and 'Massine', the proline content increased by 75% and 80% respectively. At 300 mM NaCl all varieties showed an increase in proline content. In fact, the highest level of proline content was observed in 'Laanaceur' and 'Massine' with 92% and 94% respectively (Fig. 1h). The same trend was noted for soluble sugars content, with a significant increase in accumulation in all studied varieties (Fig. 1 i). Thus, at the extreme level of salinity (300 mM of NaCl), the soluble sugars content increased considerably in 'Laanaceur' and 'Massine' varieties (68% and 55% respectively). Regarding soluble proteins content, our results showed a very significant reduction in soluble proteins in the leaves of all varieties (Fig. 1j). We found that at 200 mM of NaCl, protein contents in 'Massine' and 'Adrar' decreased by 34% and 26%, respectively. In contrast, a moderate decrease in protein content in 'Laanaceur' and 'Amira', with only 11% and 5%, respectively. At 300 mM NaCl, all studied varieties showed a decrease in proteins content of about 50%.

Correlation analysis

As demonstrated in Table 3, several significant correlations were observed among the parameters studied. Positive and significant correlations were observed between RWC, SDW, RDW, Chl a, Chl b, and Chl T. In contrast, these traits were negatively correlated with EL %. Proline content was found to be significantly and negatively related to SDW and Chl a content. Proteins content was positively associated with RDW, SDW, RWC, and Chl T. Additionally, proteins content displayed a significant and negative correlation with EL %, proline, and TSS contents.

Principal component analysis

Principal component analysis (PCA) was used as a preferment tool to investigate associations between variables using a minimum of uncorrelated principal components. This analysis was performed separately for the treatment and variety factors. The analysis considered the two first top principal components (PC1 and PC2), which showed a cumulative variance of 72% and 11%, respectively. The first component (PC1), separates clearly between unstressed plants (Control), plants submitted to moderate salt stress (200 mM), and those grown under severe salt stress (300 mM). Indeed, it shows that control points are linked with high values of RDW, SDW, RWC, Chl a, Chl b, Chl T, and proteins contents (Fig. 2). On the other hand, severe salt stress treatment points were discriminated with high scores of EL%, and proline and TSS contents. The second component (PC2) separated clearly between sensitive and tolerant varieties. The biplot (Fig. 3) showed that 'Amira' and 'Adrar' are discriminated with high levels of RDW, SDW, RWC, and Chl a, and proteins contents. However, the cluster corresponding to 'Massine' and 'Laanaceur' varieties was located on the negative side, with high values of RWC, Chl a, Chl T, and proline content.

Discussion

The Mediterranean basin is considered one of the most susceptible area to climate change (Mansour et al. 2021). The principal limits to grain yield formation in the Mediterranean basin are in continuous increase year-to-year as a consequence of the climate change and abiotic factors (Boussakouran et al. 2021). Salinity is one of the osmotic stressors that have affected plant growth and development, as shown by the reduction in biomass output and shoots expansion (Nefissi Ouertani et al. 2022). In addition, under salt stress, plants demonstrate a wide range of

Table 3 Correlations between analyzed traits of four Moroccan barley varieties grown under exposure to three salt concentrations (0, 200, and 300 mM NaCl) to the vegetative stage

	SDW	RWC	EL	Chl a	Chl b	Chl T	ProC	TSS	Proteins
RDW	0.873 ***	0.617 *	-0.477	0.666 *	0.635 *	0.615 *	-0.532	-0.356	0.725 **
SDW		0.840 ***	-0.747 ***	0.719 **	0.698 *	0.731 **	-0.651 *	-0.640 *	0.866 ***
RWC			-0.892 ***	0.791 ***	0.827 ***	0.876 ***	-0.532	-0.761 ***	0.667 *
EL				-0.679 *	-0.696 *	-0.903 ***	0.497	0.920 ***	-0.663 *
Chl a					0.973 ***	0.889 ***	-0.645 *	-0.540	0.568
Chl b						0.902 ***	-0.517	-0.565	0.548
Chl T							-0.503	-0.788 ***	0.602 *
ProC								0.397	-0.661 *
TSS									-0.620 *

*Significant at $p < 0.05$ probability level; **Significant at $p < 0.01$ probability level; ***Significant at $p < 0.001$ probability level. RDW, root dry weight; SDW, shoot dry weight; RWC, leaf relative water content; EL, electrolyte leakage; Chl a, chlorophyll a; Chl b, chlorophyll b; Chl T, total chlorophyll content; ProC, proline content; TSS, total soluble sugar.

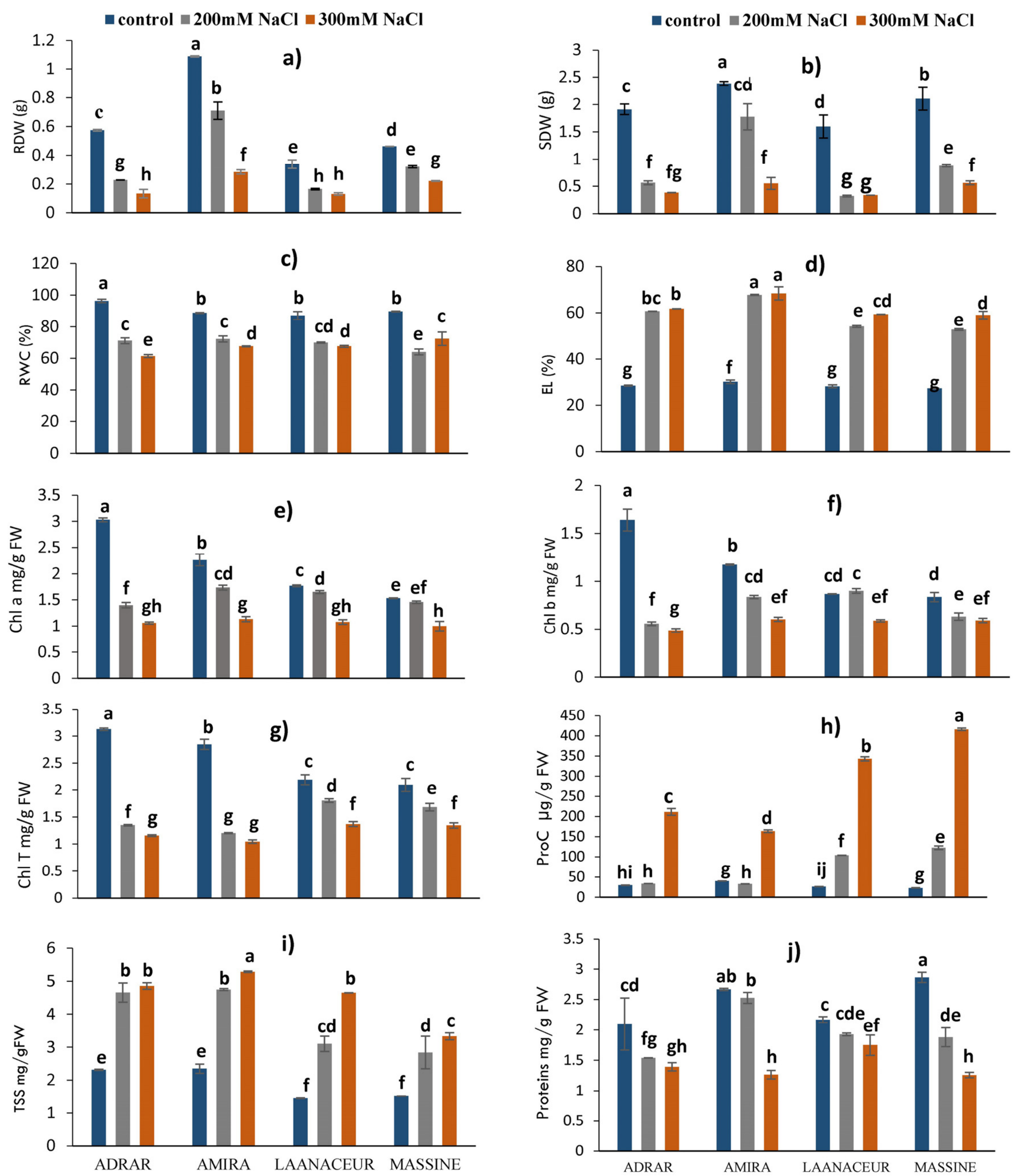

Fig. 2 Effect of salinity stress on different traits of four Moroccan barley varieties grown under exposure to three salt concentrations (0, 200, and 300 mM NaCl) to the vegetative stage. (a) RDW, (b) SDW, (c) leaf RWC, (d) EL, (e) Chl a, (f) Chl b, (g) Chl T, (h) proline content, (i) TSS, and (j) proteins. The bars indicate the mean values of three replicates ± standard error. Values with the same letters are not significantly different based on Duncan's test at $p \leq 0.05$. RDW, root dry weight; SDW, shoot dry weight; RWC, leaf relative water content; EL, electrolyte leakage; Chl a, chlorophyll a; Chl b, chlorophyll b; Chl T, total chlorophyll content; ProC, proline content; TSS, total soluble sugar; FW, fresh weight

physiological, biochemical, and molecular processes (Narimani et al. 2020). Improving salinity tolerance needs a comprehensive grasp of the physiological processes related to plant reaction to salt stress. Various strategies, including the modification of morphological, physiological and biochemical parameters, are used by plants to ameliorate the effects of salt (Walia et al. 2006). In the present study, four Moroccan barley varieties were examined under two levels of salt concentrations to determine their responses. Overall, as indicated in the results section, different morphological, physiological, and biochemical parameters were mainly under treatment effects, while variety effects were lesser. These results were in conformity with similar studies previously published on barley and other crops

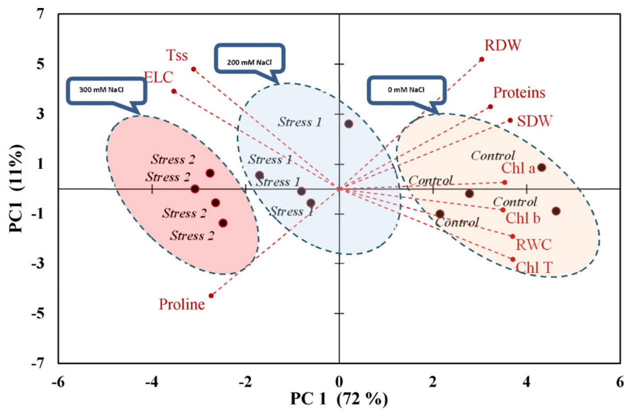

Fig. 3 Principal component analysis projections on axes 1 and 2 accounting for 83% of total variance. Eigenvalues of the correlation matrix are presented as vectors representing parameters that influence each axis the most. The 22 points representing the parameter mean values for each salt treatment (0, 200, and 300 mM NaCl) are plotted on the plane determined by axes 1 and 2. PC, principal component; RDW, root dry weight; SDW, shoot dry weight; RWC, leaf relative water content; EL, electrolyte leakage; Chl a, chlorophyll a; Chl b, chlorophyll b; Chl T, total chlorophyll content; ProC, proline content; TSS, total soluble sugar

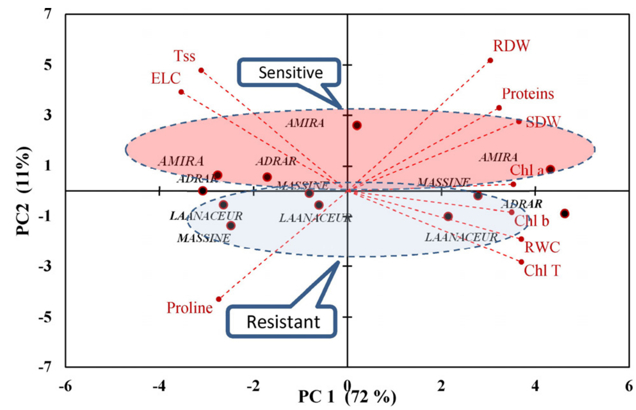

Fig. 4 Principal component analysis projections on PC1 and PC2. The eigenvalues are presented as segments representing traits that most affect each principal component. The 22 points are the mean accession values of each studied parameter of the four barley varieties grown under NaCl treatment (0, 200, and 300 mM NaCl). PC, principal component; RDW, root dry weight; SDW, shoot dry weight; RWC, leaf relative water content; EL, electrolyte leakage; Chl a, chlorophyll a; Chl b, chlorophyll b; Chl T, total chlorophyll content; ProC, proline content; TSS, total soluble sugar

(Allel et al. 2018; Dell'aversana et al. 2021; Jamshidi and Javanmard 2018; Oubaidou et al. 2021).

The salt treatment had different impacts on the plant parts, it is necessary to examine the effects of the treatments independently in shoots and roots (Zeeshan et al. 2020). The results revealed that salt stress reduced significantly root and shoot dry weights of all barley varieties. Our findings were in accordance with results documented in other studies (Ahmed et al. 2013; Allel et al. 2018; Anwar et al. 2011; Tirry et al. 2023). This decrease in weight may be due to a restricted supply of metabolites to early developing tissues. In fact, the metabolic output is greatly disrupted under high salt stress, either as a result of reduced water intake or the toxic action of NaCl (Eshel and Waisel 1972).

The results demonstrated that the tolerant variety 'Massine' had a high value of relative water content under salt stress when compared to the sensitive one 'Amira'. This is similar to the findings of (Ahmed et al. 2013; Binott et al. 2017; Dell'aversana et al. 2021; Mahlooji et al. 2018). This means that the 'Amira' variety is less able to keep cell turgor in the leaves under salt stress. However, 'Massine' and 'Laanaceur' are less influenced, meaning the high capability of these varieties to keep cells turgor in their leaves under salt stress conditions (Ferioun et al. 2023). It was reported that considerable relative water content under salt stress indicates a high level of salinity tolerance (Alsamadany et al. 2022). Mahlooji et al (Mahlooji et al. 2018) found that relative water content decreased because of a drop in water availability, and stomatal conductance.

Electrolytes leakage increased in 'Amira' and 'Adrar' varieties as salinity level increased, while it was unaffected in 'Massine' and 'Laanaceur' at 200 mM NaCl but increased significantly at 300 mM NaCl. In agreement with our findings (Bajji et al. 2001; Elsawy et al. 2018) indicated that Electrolytes leakage progressively increased under salt conditions, and the genotypic variations may provide partial reasons for the varied resistance to salinity. In this context, Nguyen et al. (1997) documented that an increase in the amount of electrolyte leakage from damaged leaf tissues is an indication of membrane damage and degradation. Moreover, Wheat et al. (Wheat et al. 2014) reported that solute leakage might be enhanced if the membrane permeability or stability is decreased.

Salinity may have also a negative impact on the processes of photosynthesis, the most basic and complicated physiological activity in cereal crops (Shahbaz and Ashraf 2013). Our result showed that salt stress decreased photosynthetic pigments (chlorophyll a, b, and total chlorophyll) in all barley varieties under 300 mM NaCl (Table 3). Exceptionally at 200 mM NaCl, higher decreases of chlorophyll a, b, and total chlorophyll contents were recorded in 'Amira' and 'Adrar'. Narimani et al. (2020) indicated that salinity stress reduces chlorophyll activity by chlorophyll content increasing and causing the degradation of the chloroplast structure. Furthermore, Salinity may restrict photosynthetic activity via a limitation of CO_2 supply resulting from the partial closure of stomata (stomatal function) or by modifying the biochemical CO_2 fixation mechanism (not stomatal function) or through both processes simultaneously (Senguttuvel et al. 2014). Chlorophyll content may be one of the potential physiological signals of salt tolerance in diverse species such as wheat (Arfan et al. 2007) and barley (Hasanuzzaman et al. 2018).

Many stresses, such as high salinity, drought, cold, oxidative stress, and biotic stress, have been shown to cause proline synthesis (Arias-Baldrich et al. 2015). In the present study, our results showed a marked increase in proline levels under salt treatments. 'Massine' and 'Laanceur' barley varieties had a highly significant rise of proline contents in their leaf tissues at 200 and 300 mM NaCl in comparison to 'Amira' and 'Adrar' varieties. This is consistent with previously published works (Gomes Silveira et al. 2003; Khattabi et al. 2022; Noreen et al. 2021; Patterson et al. 2009; Zahra et al. 2022). Numerous efforts have been undertaken for several decades to enhance the accumulation of proline content in plants by transferring genes associated with Proline metabolism and evaluating salt tolerance in transgenic plants (Karthikeyan 2011). Therefore, it has been shown that adaptive responses to abiotic stress include an increase in the concentration of compatible solutes (Harsh et al. 2016). Proline is a very well osmoprotectant in plants, it is a protein stabilizer, hydroxyl radical scavenger, source of carbon and nitrogen, and cell membrane stabilizer (Kishor and Sreenivasulu 2014). Thus, proline accumulation appears to be cured by desiccation, whether this happens in the normal course of growth or is produced by exogenous stress. The control of proline accumulation in both circumstances relies on the activity of P5CS, a rate-limiting enzyme in its production. As a result, the accumulation of proline was validated as a suitable biomarker of salt tolerance in the majority of plant species including cereal crops (Ashraf et al. 2018).

Salinity-induced osmotic and oxidative stress may be mitigated by the creation and accumulation of compatible solutes. In fact, stressed crops benefit significantly from osmoprotectants and the buildup of these compounds in the plants (Ranganayakulu et al. 2013). Our data show that the salt treatment successfully increased the amounts of total soluble sugars in 'Massine' and 'Laanaceur' varieties at 200 and 300 mM NaCl, with significant increases of soluble carbohydrates contents in 'Amira' and 'Adrar' at 300 mM only. This is compatible with previous observations that salt-tolerant barley variety accumulate total soluble sugars in their leaves (Chiahi and Brinis 2020; Nemati et al. 2011). Thus, accumulation of soluble sugars is required to maintain sub-cellular structures (membrane and proteins), decrease the osmotic imbalance induced by saline stress and increase carbon metabolism. In addition, soluble carbohydrates appear to have two distinct roles in regard to Reactive oxygen species, which can be produced during metabolic processes using soluble carbohydrates. On the other hand, soluble carbohydrates may support metabolic processes that generate NADPH, such as the oxidative pentose-phosphate (OPP) pathway, which can assist to scavenge Reactive oxygen species (Couée et al. 2006).

The accumulation of protein compounds is a key part of how a plant responds to salt stress. Increased production of proteins and other nitrogen compounds may trigger the biosynthesis of osmotically active organic molecules, such as soluble proteins with osmo-protective properties (Galston et al. 1997). In general, plants that are subjected to the effects of NaCl stress have relatively lower amounts of protein, which often leads to a loss of cellular turgor (Mukami et al. 2020). In our case, barley plants treated with salinity treatments showed a decrease in soluble proteins content in leaves. A similar observation was recently found by Mukami et al. (2020) who worked on responses to salinity stress in a set of Kenyan finger millet variety. Furthermore, new investigations support the idea that ribosomal proteins are destroyed for N recycling and mobilization via autophagy, implying that ribosomes are key temporary N sources. Vegetative storage proteins (VSPs) are proteins that are solely responsible for N storage in vegetative tissues. VSPs have been identified mostly in legumes, although they exist in all plant species and accumulate under stress situations when plant development stops. VSPs have high sequence homology with pathogenesis-related proteins like abscisic acid and jasmonic acid-responsive proteins, indicating that VSPs play an additional function in plant adaptation to abiotic or biotic stresses (Tegeder 2018). It is hypothesized that the decrease in protein levels in the leaves of barley plants under unfavorable conditions is due to the plant degrading its protein stores for recycling and mobilization of N. Waiting for the optimal conditions, plants move either amino acids or proteins from the leaves to the stems and roots.

Conclusion

The responses of four Moroccan barley varieties grown under salt stress conditions were investigated using hydroponic method. Results of this research revealed that, due to the highest root and shoot dry weight in salinity conditions, 'Massine' and 'Laanaceur' varieties are the most tolerant to salinity stress, when compared to 'Amira' and 'Adrar'. This property in 'Massine' and 'Laanaceur' is due to the accumulation of compatible osmoregulation in the cytoplasm. All morphological, physiological, and biochemical traits measured in the present study could be important factors and valuable tools for screening a large number of samples in a short period of time, as well as providing plant breeders with helpful information about stress tolerance mechanisms for selecting and developing barley salt-tolerant varieties.

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Conflicts of Interest

The authors declare no conflict of interest

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