

Evaluating salt tolerance of chickpea genotypes based on morpho-physiological and biochemical parameters

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Abstract

Screening for salinity stress is complicated due to variations in response and sensitivity at different developmental stages of the chickpea crop life cycle. Evaluation of the performance of chickpea in response to NaCl-induced salinity stress at the initial vegetative phase is a quick and cost-effective method for assessing tolerance and survival compared to traditional field approaches. An experiment was carried out under hydroponic conditions to evaluate the performance of two chickpea genotypes ('Elmo' and 'Orion'), under different salinity stress levels (25, 50 and 75 mM NaCl). Increased levels of NaCl in the growing medium caused a significant decrease in leaf relative water content, where the percentage of reduction at the highest salt level was approximately 16.9% compared to the control. 'Orion' was able to produce and accumulate a higher amount of proline (3.45 $\mu\text{mol g dwt.}^{-1}$), compared to the 'Elmo' (2.95 $\mu\text{mol g dwt.}^{-1}$), which enabled plants to absorb a greater quantity of water and maintain a higher relative water content in the 'Orion' (88%) compared to 'Elmo' (84.1%), and accordingly the percentage of solutes leakage and MDA content were significantly higher in 'Elmo' (72.2% and 49.7 $\mu\text{mol g dwt.}^{-1}$, respectively) compared to 'Orion' (60.3% and 29.5 $\mu\text{mol g dwt.}^{-1}$, respectively). The results indicate the importance of the osmotic adjustment mechanism in maintaining protoplast hydration and membrane stability under salinity stress. Based on the investigated parameters, genotypic differences were found in the response to salt treatments. 'Orion' genotype was found to be more salt-tolerant compared to 'Elmo' one.

Keywords: *Cicer arietinum* L.; growth traits; hydroponics; NaCl; proline; salinity

Introduction

The world population has reached 7.93 billion in March 2022 according to the most recent United Nations estimates (World Risk Report, 2024), and it is expected to reach to 9.3 billion at the end of 2050, thereby it would be necessary to boost the output of food from both strategic food cereals and legumes in the next few years without expanding agricultural land and using less agricultural inputs per cultivated area, without causing deterioration in the farming systems. A major challenge towards world agriculture involves the production of 70% more food for an additional 1.37 billion people by 2050 worldwide. The global land area

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amounts to 13.2 billion ha, of which 4.8 billion ha are agricultural, while 0.9 billion ha are covered with saline (0.34×10^9 ha) or sodic (0.56×10^9 ha) soils (FAOSTAT, 2023). Salinity is a major environmental limiting factor for plant growth, development and economic yield, particularly in arid and semi-arid regions (Varshney *et al.*, 2013; Qadir *et al.*, 2014), causing substantial seed yield losses (Zulfiqar and Ashraf, 2021; Ashraf and Munns, 2022). The extent of saline agricultural land continues to increase mainly due to poor management practices and the utilization of poor-quality water (Rengasamy, 2016). The agricultural sector needs to reduce its reliance on limited freshwater resources by using low-quality water instead. This shift is driven by the increasing demand for domestic and industrial water use and the reduction of groundwater levels. These issues are further exacerbated by alarming climate change and global warming, which raise atmospheric temperatures and increase water loss by evaporation. Consequently, soluble salts become more concentrated in the soil solution, making soils unsuitable for cultivating salinity-sensitive crops such as chickpea (Rani *et al.*, 2020). Therefore, using saline water in the future for agricultural production is unavoidable (Munns and Tester, 2008).

During the initial phases of salinity stress, water absorption capacity of root systems decreases and water loss from leaves is accelerated due to osmotic stress of high salt accumulation in soil/hydroponic solutions and plants, therefore salinity stress is also considered as hyperosmotic stress and the most detrimental abiotic stresses for crop growth, development and production capacity (Ceritoğlu *et al.*, 2020). Most salinity studies have used NaCl as the main source of salt, and stress symptoms have been related, in particular, to sodium toxicity alone (Annunziata *et al.*, 2017). Undoubtedly, NaCl concentrations higher than 30 - 40 mM can limit plant growth and development of many susceptible to moderately sensitive crops by affecting both water and nutrients uptake during the initial phase (Shin *et al.*, 2020). In general, planting legumes in saline soil is important for the conservation of the sustainability of production. However, legumes, including chickpea (*Cicer arietinum* L.), show a remarkable seed yield reduction in saline conditions (Samineni *et al.*, 2011). Unfortunately, chickpea, which is one of the most produced agricultural products overall the world, is classified as very susceptible to salt stress, especially during the early vegetative and reproductive (flowering and seed filling) stages (Hadi and Karimi, 2012). With salinity imposition, as plant water content decreases, the cells shrink, and the cell wall relaxes, resulting in loss of turgor, causing a reduction in leaf water potential (Ψ) and expansion (Farooq *et al.*, 2009). When compared to the corresponding controls, the findings of Kaur *et al.* (2021) demonstrated that salinity decreased the length of the root and shoot as well as the fresh and dry weight of the root and shoot of the 10 genotypes under investigation. Because salinized plants first experience osmotic stress, which restricts water uptake, cell expansion, and ultimately ion toxicity, generating nutritional imbalance, the decline in root-shoot length may be the result of stopped cell growth and reduced nutrient availability (Kumar *et al.*, 2019). Reduced leaf area and number could be the cause of the drop in shoot fresh and dry weight (Buttar *et al.*, 2020; Kumar *et al.*, 2020). Reduced water intake caused by salinity and an increase in solute concentration in the root zone results in decreased water potential (Ψ) and osmotic potential (Ψ_s). Compared to roots, shoots have higher osmotic and water potentials (Kaur *et al.*, 2021). Reduced Ψ in roots and shoots may result from increased toxic ion accumulation, such as Na^+ and Cl^- , interfering with other physiological and biochemical properties (Soni *et al.*, 2021). Conversely, an increase in osmotic potential values may indicate a genotype's capacity to tolerate salinity-induced physiological drought conditions while maintaining pressure potential. During long-term exposure, this is often accompanied by ion-specific effects, due to the accumulation of harmful ions such as Na^+ and Cl^- in the cytoplasm of the plant cells, causing cell division inhibition, which manifest in the form of chlorosis and necrosis (Ceritoğlu *et al.*, 2020). If the salinity-induced osmotic stress is imposed early in the developmental stages, the inhibition of cell expansion results in a reduced leaf area, and stunted growth of both shoots and roots (Farooq *et al.*, 2012), disturbance of cytoplasmic membranes (Flowers *et al.*, 2010), a partial or complete stomatal closure (Samineni *et al.*, 2011) and an increase of proline accumulation (Shahid *et al.*, 2018). However, different genotypes of the same crop species may differently respond to salinity stress at different developmental stages and the stress tolerance associated traits may also vary (Toker *et al.*, 2021). Therefore, the identification and introduction of salt-

tolerant chickpea genotypes/lines would be of great help for the development of salt-tolerant cultivars with high-yielding capacity via breeding programs to effectively ensure sustainable crop production in moderate salt-affected soils, so it is necessary to identify critical limits of salinity and some morphological, physiological and biochemical parameters of chickpea genotypes that could be used as a basis for the successful growing of this crop in relatively salt-affected lands. So, the main objectives of this trial, which has been conducted under hydroponic conditions were to understand the effects of NaCl-induced salinity stress on the performance of two chickpea genotypes ('Elmo' and 'Orion') based on some morphological, physiological and biochemical traits and the differential responses of these genotypes during the early-35 days vegetative growth stage.

Materials and Methods

Biological material and procedures

The assessment of the impact of NaCl-induced salinity stress was established under hydroponic conditions in a controlled environment chamber at the Department of Applied Plant Biology, University of Debrecen. The experimental plants were chickpea (*Cicer arietinum* L.) genotypes, 'Elmo' and 'Orion'. The air temperature was maintained at 24/18 °C (± 2 °C) day/night temperature; 10/14 h light/dark photoperiod; 45% relative humidity, and 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ light intensity. Seed surfaces of the two investigated chickpea genotypes were surface sterilized with 6% [v/v] H_2O_2 for 20 minutes before being properly washed and rinsed with deionized water, then stimulated geotropically at 24 °C between moist filter papers. Soaked and sprouted seeds (small seedlings: five-day age) were transplanted into plastic pots (1.7 L: 4 plants per pot) in a hydroponic environment, filled with dicot nutrient solution that consisted of the following substances (0.7 mM K_2SO_4 , 0.5 mM MgSO_4 , 0.1 mM KH_2PO_4 , 0.1 mM KCl, 0.5 μM MnSO_4 , 0.5 μM ZnSO_4 , 10 μM H_3BO_3 , and 0.2 μM CuSO_4 along with 2.0 mM Ca $(\text{NO}_3)_2$. Additionally, iron was given in the form of 10^{-4} M Fe-EDTA (Marschner *et al.*, 1990). The treatments were applied on the day of placing on the nutrient solution: 25, 50 and 75 mM NaCl. The nutrient solution of each pot was replaced with a fresh alternative every 3 days. Samples were collected from 35-day-old seedlings after salinity stress treatment, for estimation of the investigated morphological, physiological and biochemical parameters.

Measurement of dry weight and length of the shoot and root

The three seedlings' shoot and root dry weight were measured and stated in grams after they were dried in an oven (Memmert GmbH, Germany) at 70 °C until a constant weight was attained. The shoot and root length were measured using a measuring scale (cm).

Determination of leaf relative water content

For each of the three replicate plants, sample of the upper two fully expanded and healthy leaves was collected, and the fresh weight (FW) was noted. The leaves' turgid weight (TW) was measured eight hours after they were submerged in deionized water. After being placed in paper bags, the samples were dried in a hot air oven set at 80 °C for two days. As per Parida and Jha (2013), the relative water content was calculated using the following formula:

$$\text{RWC} = \{(\text{FW}-\text{DW})/(\text{TW}-\text{DW})\} \times 100 \dots (1)$$

Measurement of membrane integrity (solute leakage)

Premachandra *et al.* (1990) estimated the electrolytes that dissolved into distilled water as part of the assay process. Two sets of leaves were placed in 10 milliliters of distilled water. A conductivity meter was used to record the conductivity (C1) of the first set after it had been maintained at 40 °C for 30 minutes. After

recording the conductivity (C2) of the second set, which was maintained at 100 °C for ten minutes, the membrane integrity was determined using the following formula:

$$(C1/C2) \times 100 \dots\dots (II)$$

Proline content determination

Using a technique established by Bates *et al.* (1973), proline was extracted from 0.2 g of leaf tissues homogenized in 4 ml of 3% aqueous sulfosalicylic acid. 2 ml of the supernatant was combined with 2 ml of ninhydrin and 2 ml of glacial acetic acid after centrifugation at 10,000 rpm. This mixture was then heated for an hour at 100 °C. 4 milliliters of toluene were used to extract the reaction mixture, and 590 nm was used to measure the absorbance. The standard curve was used to compute the final proline concentration.

Malondialdehyde content

The approach from Heath and Packer (1968) was used to calculate the membrane lipid peroxidation in terms of malondialdehyde (MDA) generation. Thus, 5 ml of 0.1% Trichloroacetic acid (TCA) was used to grind 0.2 g of fresh leaf tissue, which was then centrifuged at 10,000 rpm. After thoroughly mixing 20% TCA with 0.5% thiobarbituric acid in a 1:4 (v/v) ratio, the supernatant was heated for 30 minutes at 90 °C. The following formula was used to determine the amount of oxidized MDA:

$$MDA = A_{532-600} / 1.55 \times 10^5 \text{ M cm}^{-1} \times b \text{ (III)}$$

Experimental design and statistical analysis

The experiment was done as a factorial arrangement (genotype × salt concentration) in a completely randomized design (CRD), with three independent replications. Recorded data were statistically analyzed using the MSTAT-C program to estimate the least significant difference (LSD) at 1% level of significance and coefficient of variation (CV%) among the salinity levels, genotypes and the mutual interaction between them.

Results

Growth traits

Shoot length and dry weight

Results did not show significant differences in the shoot length and shoot dry weight between the two investigated chickpea genotypes, while the differences were significant ($p \leq 0.01$) among the salt levels and the interaction between the genotypes and the salt levels. It is noted that the shoot length and dry weight were significantly higher in the control treatment (31.7 cm; 0.91 g, respectively), while they were significantly lower at the highest salt level of 75 mM NaCl (14.5 cm; 0.23 g, respectively) (Table 1; Figure 1).

Table 1. Effect of NaCl-induced salinity stress (control, 25,50,75 mM) on shoot length (cm) of two chickpea genotypes ('Elmo', 'Orion') under hydroponic conditions

Salinity level (mM NaCl)	'Elmo'	'Orion'	Mean
Control	33.4a	30.4ab	31.7A
25	23.6cd	25.4bc	24.5B
50	19.8de	22.6cd	21.2B
75	16.6ef	12.3f	14.5C
Mean	23.4A	22.7A	-
Variable	Genotypes	Salinity levels	Interaction
LSD (0.01)	4.20	3.64	5.15
CV (%)	8.96		

*Different small letters indicate significant differences at the 0.01 level ($p \leq 0.01$) for the interactions between salt levels and genotypes, while the capital letters indicate the differences for the general means of salt treatments and genotypes

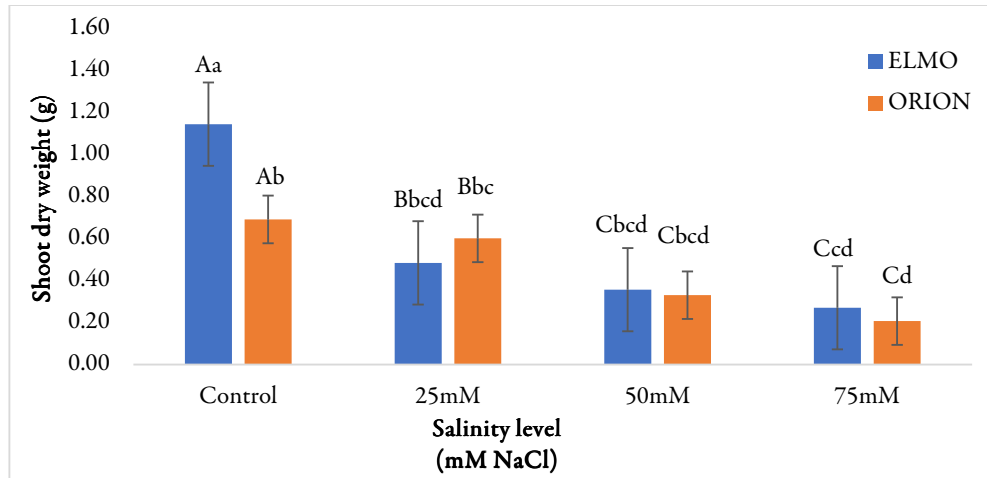


Figure 1. Effect of NaCl-induced salinity stress (control, 25, 50, 75 mM) on shoot dry weight (g) of two chickpea genotypes ('Elmo', 'Orion') under hydroponic conditions (n = 3; mean \pm S.E.)

*Different capital letters among salinity levels indicate significant differences ($p \leq 0.01$). Different small letters at each salinity level between genotypes indicate significant differences ($p \leq 0.01$)

Root length and dry weight

Results did not exhibit significant differences in root length and root dry weight between the two chickpea genotypes, while differences were significant ($p \leq 0.01$) between the salt levels and the interaction between the genotypes and the salt levels. The root length and dry weight were significantly higher in the control (46.7 cm and 0.36 g, respectively), while they were significantly lower in the two higher salt levels (75 and 50 mM NaCl), without significant differences between them (20.6 and 28.1cm; 0.048 and 0.07 g, respectively). It has been observed that the average root length and dry weight were significantly higher in the two chickpea genotypes ('Orion' and 'Elmo') in the control without significant differences between them (47.8 and 45.6cm; 0.31, 0.41 g, respectively). Root length was significantly lower in the 'Elmo' and 'Orion' genotypes at the two salt levels of 75 and 50 mM NaCl, without significant differences among them (16.3, 25.0, 25.0 and 31.3 cm respectively), while root dry weight was significantly the least for the rest interactions with no significant differences among them (Table 2; Figure 2).

Table 2. Effect of NaCl-induced salinity stress (control, 25, 50, 75 mM) on root length (cm) of two chickpea genotypes ('Elmo', 'Orion') under hydroponic conditions

Salinity level (mM NaCl)	'Elmo'	'Orion'	Mean
Control	45.6a	47.8a	46.7A
25	36.6ab	41.6ab	39.1A
50	25.0cd	31.3bc	28.1B
75	16.3d	25.0cd	20.6B
Mean	30.9A	36.4A	-
Variable	Genotypes	Salinity levels	Interaction
LSD (0.01)	9.85	8.20	11.6
CV (%)			13.8

*Different small letters indicate significant differences at the 0.01 level ($p \leq 0.01$) for the interactions between salt levels and genotypes, while the capital letters indicate the differences for the general means of salt treatments and genotypes

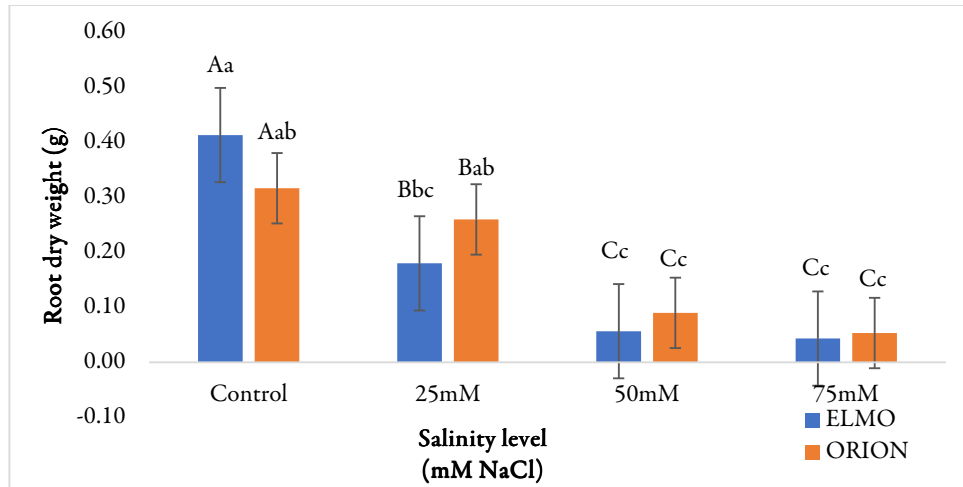


Figure 2. Effect of NaCl-induced salinity stress (control, 25, 50, 75 mM) on root dry weight (g) of two chickpea genotypes (‘Elmo’, ‘Orion’) under hydroponic conditions (n = 3; mean ±S.E.)
 *Different capital letters among salinity levels indicate significant differences (p ≤ 0.01). Different small letters at each salinity level between genotypes indicate significant differences (p ≤ 0.01)

Physiological and biochemical traits

Leaf relative water content

Results showed that there were significant differences (p ≤ 0.01) in the relative water content between the two investigated chickpea genotypes, salt levels, and the interaction between them. The relative water content was significantly higher in the ‘Orion’ genotype (88%) compared to ‘Elmo’ (84%). It was significantly higher at the control and the 25 mM NaCl, without significant differences between them (93 and 90% respectively), while it was significantly lower at the highest salt level (75 mM) (78%) compared with the control. It was significantly higher in the ‘Orion’ and ‘Elmo’ genotypes in the control treatment (95, 91% respectively), while it was significantly lower in ‘Elmo’ at 75 mM NaCl (73%) (Figure 3).

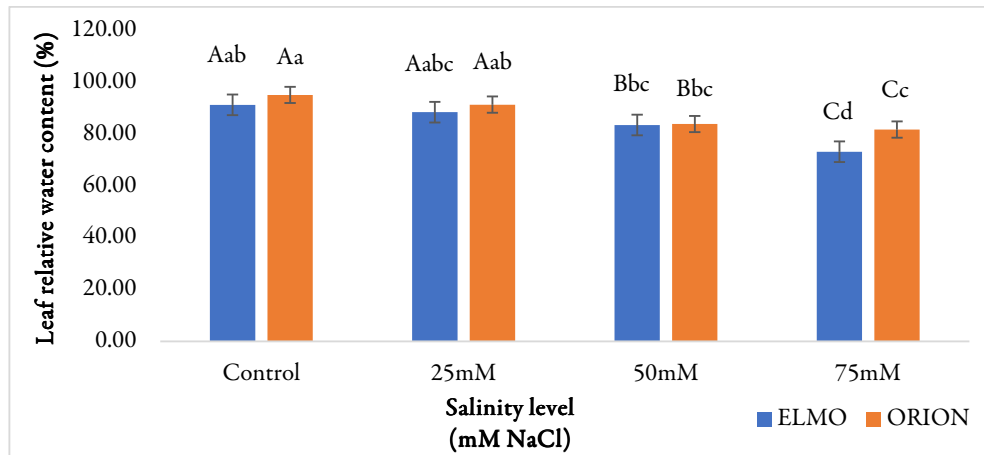


Figure 3. Effect of NaCl-induced salinity stress (control, 25, 50, 75 mM) on leaf relative water content (%) of two chickpea genotypes (‘Elmo’, ‘Orion’) under hydroponic conditions (n = 3; mean ±S.E.)
 *Different capital letters among salinity levels indicate significant differences (p ≤ 0.01). Different small letters at each salinity level between genotypes indicate significant differences (p ≤ 0.01)

Changes in the values of proline content of shoots

It has been shown that the proline content was significantly higher in the 'Orion' genotype ($3.45 \mu\text{mol g dwt.}^{-1}$) compared to the 'Elmo' ($2.95 \mu\text{mol g dwt.}^{-1}$) (Figure 4).

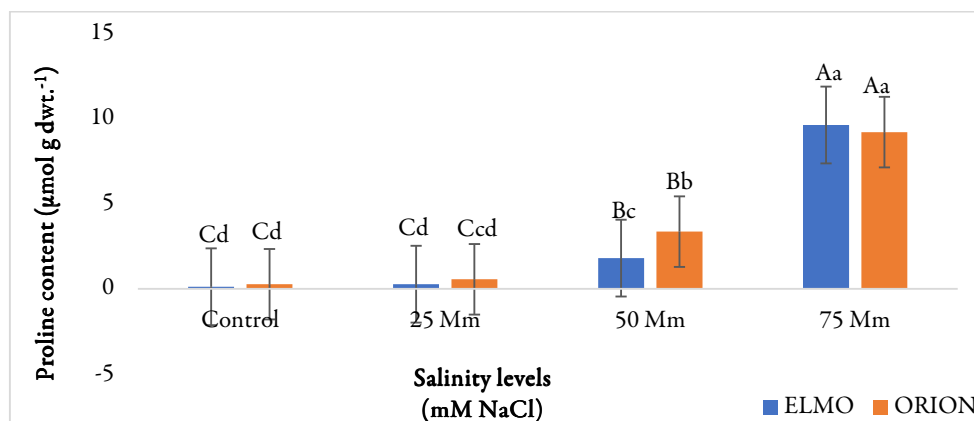


Figure 4. Effect of NaCl-induced salinity stress (control, 25, 50, 75 mM) on proline content ($\mu\text{mol g dwt.}^{-1}$) of two chickpea genotypes ('Elmo', 'Orion') under hydroponic conditions ($n = 3$; mean \pm S.E.)
*Different capital letters among salinity levels indicate significant differences ($p \leq 0.01$). Different small letters at each salinity level between genotypes indicate significant differences ($p \leq 0.01$)

The average proline content was significantly higher at the 75 mM NaCl salt level ($9.41 \mu\text{mol g dwt.}^{-1}$), while it was significantly lower at the control and the 25 mM NaCl level, without significant differences between them ($0.20, 0.42 \mu\text{mol g dwt.}^{-1}$ respectively). Results revealed that the proline content was significantly higher among the two genotypes ('Elmo' and 'Orion') at the higher salt level (75 mM NaCl), without significant differences between them (9.62 and $9.20 \mu\text{mol g dwt.}^{-1}$ respectively), followed with significant differences by the genotype 'Orion' at the salt level 50 mM NaCl ($3.36 \mu\text{mol g dwt.}^{-1}$), and the 'Elmo' genotype at the 50 mM NaCl salt level ($1.80 \mu\text{mol g dwt.}^{-1}$), while it was significantly lower for the rest of the interactions without significant differences among them.

Membrane integrity (solute leakage)

'Orion' genotype exhibited significantly higher membrane stability compared with the other genotype, where the solute leakage was significantly ($p \leq 0.01$) higher in 'Elmo' genotype (72.2%) compared to 'Orion' (60.3%). In agreement with this result, membrane integrity decrease has been mentioned in susceptible genotypes of chickpea under stress (Bhushan *et al.*, 2011).

Increased salinity stress caused a significant and steady increase in solute leakage, where it was significantly higher at the higher salt level (75 mM NaCl) (89.0%), compared with the control (44.6%). Solute leakage was significantly higher for the two investigated chickpea genotypes 'Elmo' and 'Orion' at the higher salt level (75 mM NaCl) and for the genotype 'Elmo' at the salt level of 50 mM NaCl, without significant differences among them (92.9, 85.1 and 82.9%, respectively), while it was significantly the lowest in the 'Orion' genotype at the control (35.9%) (Table 3).

Table 3. Effect of NaCl-induced salinity stress (control, 25, 50, 75 mM) on membrane integrity (solute leakage) (%) of two chickpea genotypes ('Elmo', 'Orion') under hydroponic conditions

Salinity level (mM NaCl)	'Elmo'	'Orion'	Average
Control	53.3b	35.9c	44.6D
25	59.9b	54.3b	57.1C
50	82.9a	66.0b	74.5B
75	92.9a	85.1a	89.0A
Average	72.2A	60.3B	-
Variable	Genotypes	Salinity levels	Interaction
LSD (0.01)	6.50	10.2	14.4
CV (%)	8.74		

*Different small letters indicate significant differences at the 0.01 level ($p \leq 0.01$) for the interactions between salt levels and genotypes, while the capital letters indicate the differences for the general means of salt treatments and genotypes

Malondialdehyde (MDA) content

The MDA content of the two genotypes under investigation increased gradually over time in the current study as salinity levels rose. However, the 'Elmo' genotype's MDA content ($49.7 \mu\text{mol g dwt.}^{-1}$) was significantly higher than 'Orion's' ($29.5 \mu\text{mol g dwt.}^{-1}$) (Table 4).

Table 4. Effect of NaCl-induced salinity stress (control, 25, 50, 75 mM) on MDA content ($\mu\text{mol g dwt.}^{-1}$) of two chickpea genotypes ('Elmo', 'Orion') under hydroponic conditions

Salinity level (mM NaCl)	'Elmo'	'Orion'	Average
Control	13.9d	13.9d	13.9C
25	18.9d	19.9d	19.4C
50	61.6b	34.5c	48.1B
75	104.4a	49.5b	67.0A
Average	49.7A	29.5B	-
Variable	Genotypes	Salinity levels	Interaction
LSD (0.01)	16.3	10.1	14.3
CV (%)	4.65		

*Different small letters indicate significant differences at the 0.01 level ($p \leq 0.01$) for the interactions between salt levels and genotypes, while the capital letters indicate the differences for the general means of salt treatments and genotypes

Discussion

The selection of plant varieties that can withstand salinity and the identification of attributes related to this tolerance depend heavily on understanding the physiological and biochemical responses of chickpea genotypes and their efficacy in mitigating salinity. It was noticed by Kafi *et al.* (2011) that under increased salt stress, the tolerant chickpea genotypes grew more quickly. Growth features, therefore, would be highly helpful in programs aimed at improving salinity tolerance, particularly shoot and root dry weight, which have consistently demonstrated a reduction in growth when compared to the controls. The results of this investigation are consistent with those of Demir *et al.* (2003), who found that salinity had a greater negative impact on shoot length and dry weight than root length and dry weight. According to Mudgal *et al.* (2009), there was a noticeable decrease in the dry weight of the roots and shoots in chickpeas as the saline concentration increased. Additionally, the outcome is consistent with research by Millan *et al.* (2006), which found that the root and shoot dry weight of chickpeas dropped as saline concentration increased. According to Flowers *et al.* (2010), a decrease in cell division and cell expansion under salt stress may be the cause of the reduction in shoot and root length and dry weight. It can be suppressed by reducing the number of branches and leaf area via

stopping the water passage from the xylem to the surrounding elongating cells, leading to a remarkable decrease in the water potential (ψ), which leads to a drop in the leaf cells turgor potential (P), thereby inhibiting shoot cell expansion (Cossgrove, 1989). The decrease in root and shoot development could be brought on by an imbalance in the seedlings' nitrogen intake as well as the harmful toxic effects of the Na^+ and Cl^- ions (Manivannan *et al.*, 2007; Shamsi *et al.*, 2010). Salinity slows down or stops the mobilization of reserve nutrients, halts cell division, and damages or enlarges the hypocotyls of chickpea seedlings. These results coincide with the findings of Kaur *et al.* (2021); Ceritoğlu *et al.* (2020) and Farooq *et al.* (2009; 2012), whom correlated the reduction in leaf water potential with the inhibition of cell expansion and division, which end up with a remarkable decrease in both root and shoot growth. The decrease in the turgor potential, due to increasing salinity intensity will also lead to a proportional decline in the stomatal conductance (g), which negatively affects the gas exchange process, thus reducing the rate of CO_2 -diffusion (Samineni *et al.*, 2011), which negatively affects the intercellular CO_2 level in the CO_2 -fixation sites within chloroplasts, leading to a decline in the assimilation rate, and the production and accumulation of dry matter, causing a reduction in the growth rates and shoot and root dry weight (Murumkar and Chavan, 1993; Kaur *et al.*, 2021).

The variation in the relative leaf water content between the two studied genotypes is attributed to the difference in the proline content of the leaves, where the proline content was significantly higher for the 'Orion' genotype ($3.45 \mu\text{mol g dwt.}^{-1}$) compared to the 'Elmo' chickpea genotype. ($2.95 \mu\text{mol g dwt.}^{-1}$) (Fig 4). In general, increasing proline leads to a decrease in the leaf cell water potential, which increases the difference in the water potential gradient between the growth solution and the plant roots, thereby enhancing the water absorption and maintaining the turgor potential. The variation in the leaf relative water content between salt levels is due to the availability of more amount of free water molecules in the growth medium of the control treatment compared with other salt levels. Maintaining cell metabolism and function, and maintaining water status, which is determined by RWC% in this study, are the two basic physiological processes that lead to tolerance and/or adaptation to abiotic stress (Bhushan *et al.*, 2007). While plant damage was negligible at control and lower levels of salt stress, which explains why the leaf relative water content was high when compared to other salinity levels, salt stress causes an osmotic imbalance and damages cell membranes, which may be the reason for a decrease in RWC percentage under those levels. Reduced water intake caused by salinity results in decreased water potential (ψ_w) and osmotic potential (ψ_s) (Kaur *et al.*, 2021). Reduced water potential in roots and shoots which may result from compatible solutes and increased toxic ion (Na^+ and Cl^-) accumulation, interfering with replacement and destruction of proteins involved in the structure of cytoplasmic membranes, and the oxidation of phosphorylated lipids due to the active free oxygen radicals (ROS), thus forming a porous cytoplasmic membrane (Ashraf and Munns, 2022). To minimize the effects of oxidative salt stress, plant cells have evolved a complex antioxidant system, which is composed of low-molecular mass antioxidants (such as ascorbic acid) as well as ROS-scavenging enzymes (SOD, CAT, POD ...etc.) (Khan *et al.*, 2022; Sultan *et al.*, 2021). Protein breakdown is the cause of the elevated proline level observed with an increase in salt stress (Evan Ibrahim, 2012). Proline would interact with proteins in leaf cells or tissues once carbohydrates were available. Proline would be generated through oxidation in conjunction with regular protein synthesis if some of the stored proline remained after translocation and respiration processes depleted the carbs in the leaves (Kafi *et al.*, 2011). Salinity stress causes hyperosmotic stress and, in severe cases, causes oxidative stress in plants as well, which is responsible for the generation of reactive oxygen species (ROS) that are deleterious to plants (Ahmad *et al.*, 2012; Shad *et al.*, 2013) by damaging biomolecules, i.e., lipids, proteins, and nucleic acids (Tuteja *et al.*, 2009). Salt stress (NaCl), especially at high levels, caused a significant increase in proline concentration in the two studied genotypes. In general, the accumulation of proline in the NaCl -stressed plants is explained by the stimulation of its biosynthesis and the termination of its catabolism because of a decrease in the activity of proline-oxidizing enzymes (Amini and Ehsanpour, 2005). Increasing the rate of proline synthesis largely determines the efficiency of the genotype in restoring growth, as proline constitutes an important source of energy and carbon, which plant cells can use to recover when the stressor limiting factors disappear (AL-Ouda, 1999). Proline plays an important role in alleviating the harmful effects of salinity stress,

as well as protecting chloroplasts, mitochondria, nucleic acids and cell membranes from damage caused by oxidative stress. Proline is a powerful antioxidant (Gill and Tuteja, 2010) because it can interact with other chemical compounds such as plant hormones, thus contributing to improving stress tolerance in plants (Per *et al.*, 2017). Proline serves as an osmolyte and scavenges singlet oxygen and free radicals like hydroxyl ions. It is also considered a redox potential regulator and protects macromolecules such as proteins and DNA, and reduces enzyme denaturation caused by salts and heat, etc. (Kumar *et al.*, 2010). According to Bidabadi *et al.* (2012), proline is a unique osmolyte found in plants that increases quickly in low water environments and helps the plants maintain cell turgor. This osmolyte is a compatible solute that acts as a protective reaction for osmotic adjustment (OA) under abiotic stress conditions. Proline levels in resistant genotypes like 'Orion' increased in response to salt stress, which was in line with other studies' findings (Najaphy *et al.*, 2010; Turan *et al.*, 2009). Additionally, Beyaz and Kir (2019) showed that proline accumulation increased after 14 days of salt stress in a medium with 100 mM NaCl.

Apart from measuring MDA content, electrolyte leakage measurement is another often employed criterion to evaluate the degree of membrane stability and oxidative stress connected to solute leakage from the cells (Bandeoğlu *et al.*, 2004). The variation in the percentage of solutes leakage via the cytoplasmic membranes between the studied genotypes, and the salt levels, is mainly attributed to the variation in the relative water content, where it was significantly higher in the 'Orion' genotype compared to 'Elmo' (Table 3), and it was significantly higher in the control and the salt level 25 mM, while it was significantly lower at the highest salt level (75 mM), indicating that maintaining of relatively high cell water content is of great relevance to sustain the integrity and stability of the cytoplasmic membranes under stressful conditions. The variation could also be attributed to the difference in the rate of proline accumulation, where it has been found to be significantly higher in the 'Orion' genotype compared to 'Elmo' and at the 75 mM salt level compared to control (Table 3), indicating the importance of osmotic adjustment mechanism to maintain the integrity and stability of the cytoplasmic membranes, especially under high intensity of salt stress (above 50 mM NaCl), where the toxic effect of the specific harmful ions (Na^+ and Cl^-) leads to the replacement and destruction of proteins involved in the structure of cytoplasmic membranes, and the oxidation of phosphorylated lipids due to the active free oxygen radicals (ROS), thus forming a porous cytoplasmic membranes (Arefian *et al.*, 2014).

An increase in MDA concentration may make it more difficult to scavenge the buildup of oxygen radical species, which could account for the increased membrane damage in leaf tissue (Bandeoğlu *et al.*, 2004). Later, increased electrolyte leakage (decreases in membrane integrity) during salt stress lends credence to this potential process. According to Negrão *et al.* (2016), the breakdown of phosphorylated fatty molecules in cytoplasmic membranes is the cause of MDA accumulation under conditions of increased salt stress. It has been found that the MDA content of the 'Elmo' genotype was significantly higher than that of the 'Orion' genotypes and that the 'Elmo' genotype also exhibited a significantly higher percentage of solute leakage (Table 4). In comparison to the control, there was a notable and consistent rise in the percentage of solute leakage due to the high concentration of soluble salts in the growth medium (Table 4). This demonstrates the significance of measuring MDA levels to determine the integrity of cytoplasmic membranes and, consequently, the effectiveness of genotypes in maintaining plant cell survival and growth following the removal of stress-limiting factors. Since phosphorylated fatty compounds are most impacted by oxidative stress, MDA is often a useful indicator for determining the degree of salt stress tolerance in plants (Smolik *et al.*, 2013; Ahmad *et al.*, 2018). These results align with the research conducted by Ahmad *et al.* (2010), Razmi *et al.* (2017) in the case of soybeans, and Ahmad *et al.* (2018) in the case of faba beans.

Conclusions

Maintaining high values of relative water content in the leaves is one of the most important physiological characteristics determining the cell expansion of both shoots and roots and cytoplasmic membranes integrity under salinity stress conditions. Accumulation of MDA is considered a bio-indicator of membrane damage, while the accumulation of proline was highly associated with membrane stability and maintaining plant water status, and thus the efficiency of the genotypes in preserving the survival and recovery growth of plant cells after alleviating the stressful factor. Results confirm the presence of genetic variability among chickpea genotypes in response to salinity stress under hydroponic conditions, where the 'Orion' genotype was found to be more salt-tolerant compared to the 'Elmo' one. The investigated morph-physiological and biochemical traits can be confidently used as selection criteria for salinity stress tolerance in the breeding program.

Authors' Contributions

Conceptualization: S.V.; Methodology: S.V. and M.S.; Software: A.S.A. and M.S.; Validation: S.V., O.B. and T.B.Z.; Formal analysis: A.S.A.; Investigation: M.S. and T.B.Z.; Resources: S.V.; Data curation: S.V.; Writing – original draft: M.S., T.B.Z., A.S.A., O.B. and S.V.; Writing – review and editing: O.B. and S.V.; Visualization: O.B.; Supervision: S.V.; Project administration: S.V.; Funding acquisition: S.V.

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Conflict of Interests

The authors declare no conflict of interest.

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