

Sodium exclusion as a key trait for maize adaptation to salinity: Relationship with photosynthetic efficiency and membrane integrity

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Abstract

Maize is widely used for human consumption but its cultivation is hampered by salinity. Photosynthetic activity and hence, growth are adversely affected by salt stress due to salt accumulation in the plant tissues. Thus, it is of paramount significance to identify reliable salt-tolerant cultivars able to minimize the uptake of salt ions and preserve several physiological and metabolic processes under such circumstances. Here, the behaviour of two maize cultivars ('SY Verdemax' and 'SY Sincero', respectively Na⁺ includer and Na⁺ excluder) subjected to long term salinity stress was addressed. Salinity, especially at 150 mM NaCl inhibited several growth-related traits, chlorophyll concentrations, photosynthetic activity and leaf hydration in both cultivars, but 'SY Verdemax' which showed higher Na⁺ contents in leaves was more salt-sensitive. Salinity reduced proline content and led to oxidative damage reflected by disturbed membrane integrity and lower chlorophyll stability index, especially in 'SY Verdemax'. We assume that the better behavior of 'SY Sincero' when salt-challenged would be partly related to its ability to restrict Na⁺ accumulation in leaves (as shown by lower Na⁺ translocation index) and its immobilization in roots, which allows to maintain the photosynthetic machinery functioning and sustain plant growth. Besides, limiting excessive Na⁺ buildup in shoot reduced water loss, preserved chlorophyll synthesis while minimizing oxidative stress damage to cell membranes. Taken together, our results further highlight the significance of sodium exclusion in the response of maize to salt stress, and strongly suggest that 'SY Sincero' would be a suitable candidate for maize cultivation in moderately salt-affected soils.

Keywords: growth traits; maize; membrane integrity; Na⁺ exclusion; photosynthetic efficiency; salinity

Introduction

Salinization is a serious problem affecting approximately 20% of cultivated soils and 33% of irrigated lands worldwide (Goswami *et al.*, 2024). Salinity hampers plant productivity by disturbing major vital physiological and biochemical paths and triggering osmotic stress and ionic imbalance leading to problems of

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nutrient deficiencies (Isayenkov and Maathuis, 2019; Arif *et al.*, 2020; El-Ramady *et al.*, 2024; Hualpa-Ramirez *et al.*, 2024; Zhou *et al.*, 2024). Besides, it restricts CO₂ absorption as well as the efficiency of both photosystems I and II and consequently reduces the photosynthetic rate (Hameed *et al.*, 2021; Moustakas *et al.*, 2022; Farooq *et al.*, 2023). NaCl salinity impacts the photosynthetic process in two distinct ways, (i) it hinders the dynamic stomatal and photosynthetic kinetics via osmotic effects and (ii) reduces photosynthetic capacity via ionic effects (Zhang *et al.*, 2022). Several photosynthetic traits including transpiration, gas exchange parameters, chlorophyll content, and chloroplast ultrastructure were reported to be severely affected by salinity stress notably due to the passive accumulation of high salt amounts in the transpiration stream zone (Parihar *et al.*, 2015; Hamani *et al.*, 2020; Hameed *et al.*, 2021). As biomass production biomass closely depends on photosynthesis and nutrient uptake from the soil, any salt-induced alteration of one or both processes results in a severe reduction of the plant growth (Safdar *et al.*, 2019).

Plants have developed several mechanisms to overcome salt stress mainly *via* (i) the vacuolar accumulation of Na⁺ in leaves (includer species) or their exclusion at the root plasmalemma (excluder species), (ii) the synthesis of osmolytes and (iii) energy redistribution in favor of cell defense systems known as metabolic switch (Khan *et al.*, 2020). The efficiency of the abovementioned adaptive mechanisms depends on salt stress intensity and the plant species, so that crops are classified into sensitive, moderately sensitive, moderately tolerant, and tolerant (El-Ramady *et al.*, 2024).

Maize (*Zea mays* L) is an important staple food and a multi-purpose crop, widely cultivated for human consumption and animal feeding (Erenstein *et al.*, 2022). It is a potent source of energy and proteins (Salika and Riffat, 2021) and was shown to play a crucial role in ensuring food security, especially in Africa (Grote *et al.*, 2021). Maize grain production represents the third of the global grain yield and therefore is termed as the king of grain crops (Dossa and Miassi, 2023, González-Rodríguez and García-Lara, 2024). According to Tilman *et al.* (2011), maize productivity needs to be doubled by 2050 to fulfil the increasing demand of population. Yet, maize cultivation is facing many challenges notably salinity, which is exacerbated by the current climate changes affecting precipitation level and occurrence and causing temperature increase (Tebaldi and Lobell, 2018; Corwin, 2021; Ullah *et al.*, 2021).

Several approaches used to attenuate salinity stress on cereal-based foods intended for human consumption include (i) physical, (ii) chemical and (iii) biological methods. Among the physical methods widely used to remove salts from soils, leaching, which consists on applying important quality of water to surface soil to leach salts (Shaygan *et al.*, 2017). Chemical practices are based on the use of calcium in the form of CaCO₃ (Ullah *et al.*, 2021). However, both methods present some disadvantages like high water consumption and salt precipitation due to of the low solubility of several inorganic amendments (notably CaCO₃). Selecting cultivars with high tolerance to salt stress is a useful biological method that must be integral to any program aiming at reclaiming salt affected soils and improving the productivity of cereal crops grown in such areas (Anshori *et al.*, 2018) as it enables to distinguish cultivars with contrasting behavior. Thus, in the present investigation, two maize cultivars were compared for their tolerance to prolonged salinity based on their morphology, growth activity, water status, mineral nutrition, and photosynthetic activity. More elaborated leaf traits were also included in this comparative study to identify reliable stress tolerance markers that could be used for screening of maize (and generally cereal) long-term salt response.

Materials and Methods

Plant materiel and culture conditions

Z. mays L seeds were obtained from National Institute of Agricultural Research of Tunisia (INRAT). Two cultivars were used in this study: 'SY Verdemax' and 'SY Sincero'. Seeds were sown in plastic pots filled

with 5 kg inert sand and irrigated daily with tap water until germination. 7-day-old seedlings were then irrigated with Long Ashton nutrient solution (Hewitt, 1966) diluted four times. Seedlings were grown for further 30 days with the same complete nutrient solution (pre-treatment phase). Plants were later divided in three lots (treatment phase) as follows: plants irrigated for 60 days with the Hewitt nutrient solution containing 0 mM NaCl (C), 100 mM NaCl (S1), and 150 mM NaCl (S2). Plants were grown in a greenhouse located at the Center of Biotechnology of Borj-Cedria under semi-controlled conditions (North-East of Tunisia, 36°42'32.9" N, 10°25'40.9" E). Salinity concentrations were gradually increased by adding 50 mM to prevent osmotic shock. Figure 1 shows the experimental design used for this study.

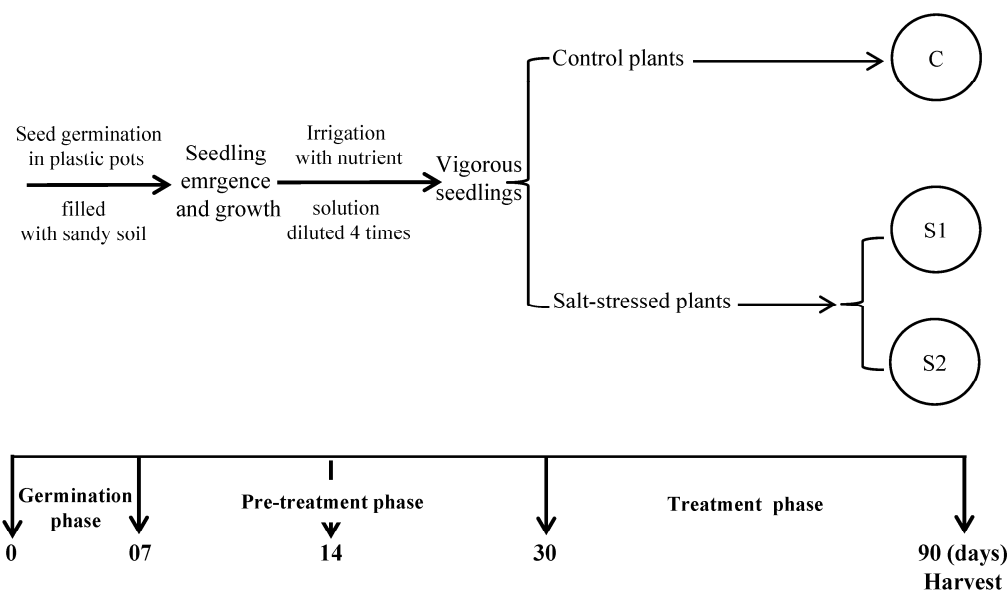


Figure 1. Experimental design used to study the effect of salinity (S1: 100 mM NaCl, S2: 150 mM NaCl) on two *Z. mays* cultivars ('SY Verdemax' and 'SY Sincero')

Plant harvest and growth parameters

At the final harvest, plants were assessed first based on their aspect and the occurrence of salt-induced morphological changes (including salt injury symptoms). Further biometric traits were determined for plants from each treatment including leaf number, total leaf surface area (cm²) and root length (cm). Root volume (cm³) was also determined according to Pang *et al.* (2011). Leaf and root fresh weight (FW) was determined before oven-drying both organs at 60 °C for dry weight (DW) evaluation and mineral analysis.

Plant growth sensitivity to salt stress was further evaluated by calculating stress susceptibility index (SSI) based on shoot, root and whole plant dry weights (Fischer and Maurer, 1978) as:

$$SSI = (1 - Y_s/Y_p) / SI$$

Where SI is salinity stress intensity calculated as $SI = 1 - (MY_s/MY_p)$, MY_s is the mean dry weight of all cultivars under stress conditions, MY_p is the mean dry weight of all cultivars under control conditions, Y_s is the mean cultivar dry weight under salinity stress and Y_p is the mean cultivar dry weight under control conditions. According to Jamshidi and Javanmard (2018), if SSI is less than 1, the genotype is considered more tolerant to salinity stress.

Photosynthetic pigment content and leaf gas exchange measurements

Chlorophyll a (Chla), Chlorophyll b (Chlb), Chlorophyll a+b (Chla+b) and carotenoids (Car) contents (µg. mg⁻¹ FW) were determined according to the methods of Torrecillas *et al.* (1984) and Arnon

(1949). Briefly, 100 mg of fresh leaf material was incubated in 5 mL of pure acetone in the dark at 4 °C for 72-h. Absorbance was read at 665 and 649 nm (for Chla, Chlb and Chla+b determination) and at 470, 663 and 647 nm (for Car determination).

Photosynthesis assimilation rate (A), stomatal conductance (g_s) and transpiration (E) were determined using a LCpro+ meter. Measurements were taken between 10:00 and 14:00 h.

Ion status

Leaf and root samples were oven-dried at 60 °C and ground to a fine powder. 20-30 mg was digested in nitric acid (HNO₃, 0.5N). The extracts were filtered and used for the determination of mineral cations and anions. Na⁺ and K⁺ concentrations were determined by a flame emission using an atomic absorption spectrophotometer (IL 151). Cl⁻ ions were measured using a Haake-Buchler type chloridometer.

Leaf water relations

Leaf water content (LWC) was calculated using leaf FW and DW as follows:

$$\text{LWC (mL g}^{-1}\text{)} = (\text{FW} - \text{DW}) / \text{DW}$$

Leaf water potential (L Ψ w) was measured in fully expanded leaves exposed to direct light radiation using the Scholander pressure-chamber technique 6-8 h after the onset of the light period as described previously by Scholander *et al.* (1965).

Leaf water use efficiency (LWUE) and leaf intrinsic water use efficiency (LIWUE) were calculated as the ratio of photosynthesis assimilation rate to transpiration or to stomatal conductance, respectively (Mujawamariya *et al.*, 2018).

Leaf mass area (LMA) was calculated as the ratio of leaf fresh or dry weight to leaf surface area (Fernández-García *et al.*, 2014).

Membrane integrity

To assess leaf membrane integrity, electrolyte leakage (EL) was assayed using the method described by Dionisio-Sese and Tobita (1998). 100 mg of the freshly harvested leaves were cut into small fragments and placed in Teflon tubes filled with 10 ml of deionized water. Tubes were incubated in a water bath at 32 °C for 2 h. The electrical conductivity (C1) was measured using a Metrohm 712 type conductivity meter. The same tubes were autoclaved at 121 °C for 20 min and then cooled at room temperature, before determining the second electrical conductivity (C2). EL was then calculated as:

$$\text{EL (\%)} = (\text{C1}/\text{C2}) \times 100$$

Proline content

Proline content was assayed according to the protocol of Bates *et al.* (1973) using an extraction medium containing sulfosalicylic acid (3%).

Statistical Analysis

Data were analyzed by one-way ANOVA (SPSS, Statgraphics Centurion 16.103), and the different treatments were compared using Duncan's test at $p \leq 0.05$. Data are means of three different replicates.

Results

Effects of salinity stress on Z. mays morphological aspects

Significant phenotypic differences were observed between plants cultivated in free-salt medium and those exposed to 100 or 150 mM NaCl. 'SY Sincero' appeared to be more productive than 'SY Verdemax'

whether plants were grown on salt-free medium or under salinity stress (Figure 2). Salt toxicity-induced symptoms were detected after two months of treatment with 100 and 150 mM NaCl (Figure 2). They initially consisted of leaf dehydration especially at the distal extremity and a reduction in shoot length. At 150 mM NaCl, the effect was more pronounced in both genotypes, with leaf injury symptoms including chlorosis, wilting, decline in leaf size and leaf rolling (Figure 2).

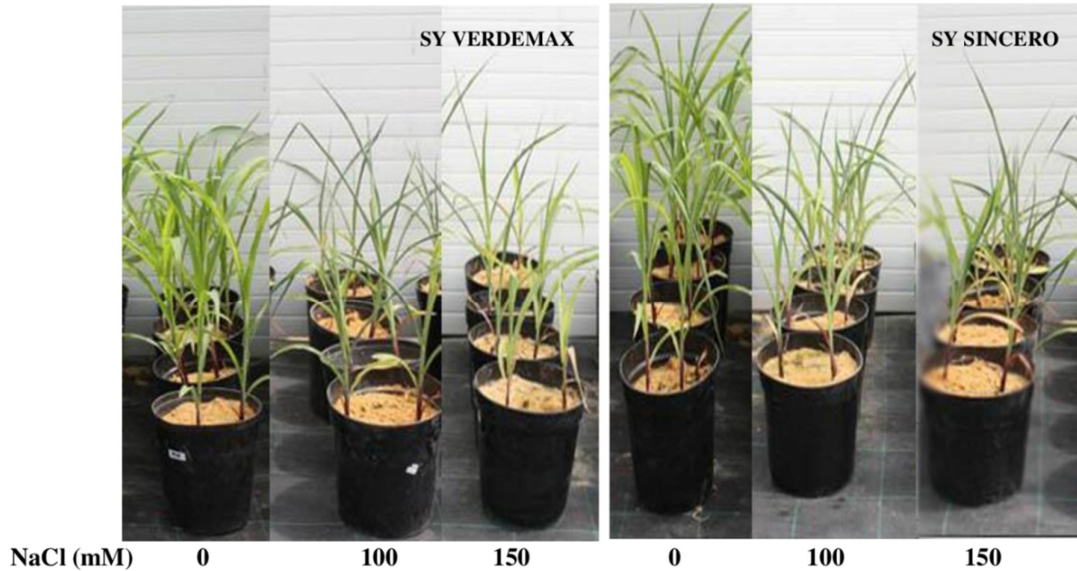
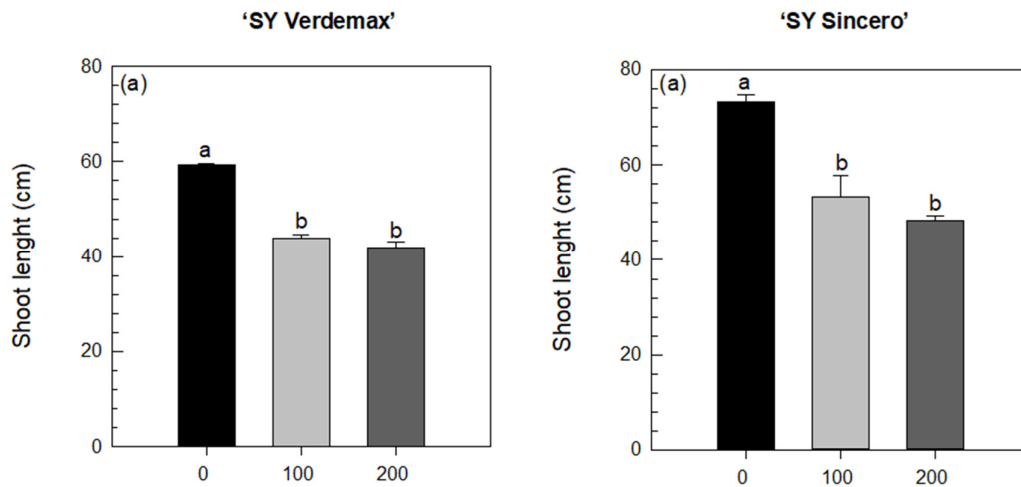


Figure 2. Phenotype of *Z. mays* seedlings ('SY Verdemax' and 'SY Sincero') grown for 60 days in a free-salt medium (0 mM NaCl) or exposed to 100 or 150 mM NaCl

Effect of salinity on leaf and root biometric parameters

'SY Verdemax' plants grown in a salt-free medium had higher shoot length as compared to 'SY Sincero'. Salinity (100 and 150 mM NaCl) reduced significantly shoot length of both cultivars (Figure 3a). Leaf number was not affected by 100 mM NaCl in both cultivars while 150 mM NaCl reduced significantly this parameter (Figure 3b). Leaf area decreased significantly with increasing salinity in both maize varieties (Figure 3c).



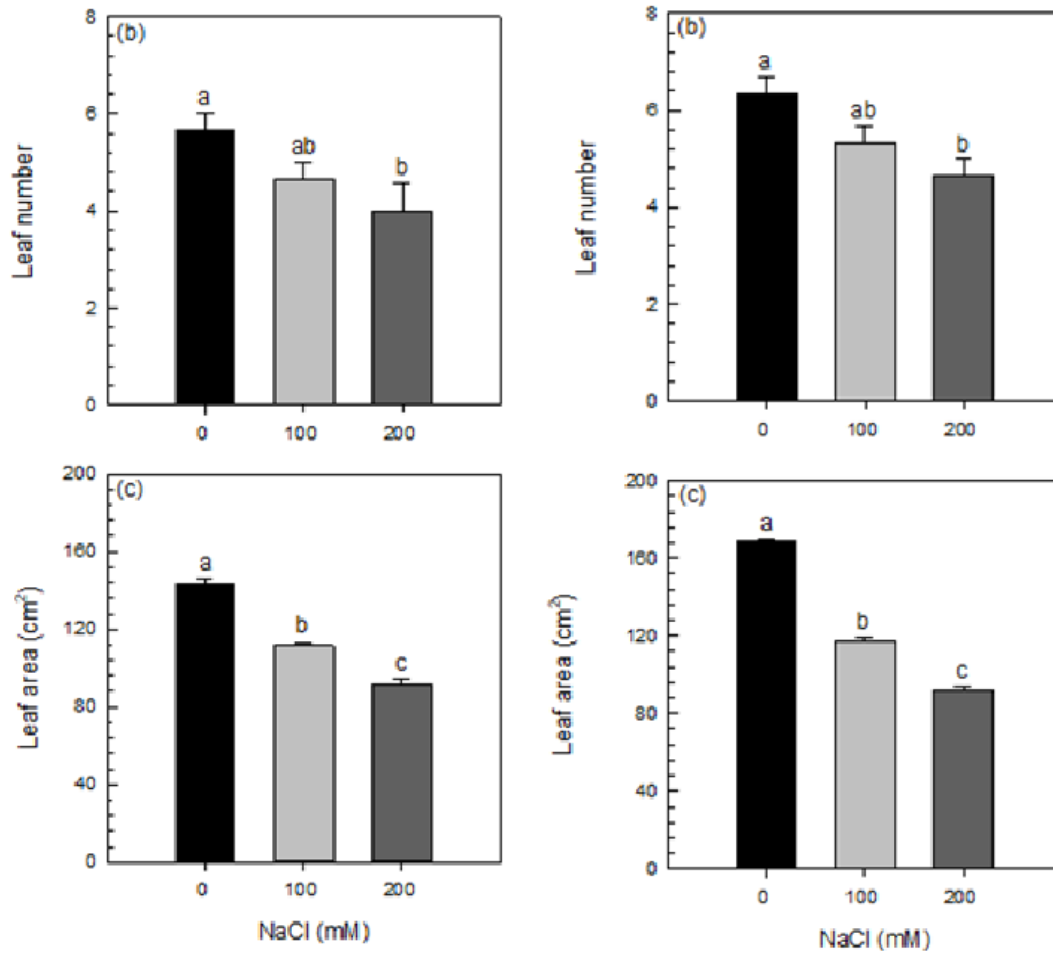


Figure 3. Variation in (a) shoot length, (b) leaf number and (c) leaf surface area of two *Z. mays* genotypes ('SY Verdemax' and 'SY Sincero') subjected to salinity (0, 100 and 150 mM NaCl) for 60 days. Data are means of three different replicates. Different letters denoted significant differences at $p \leq 0.05$

Root length was only reduced by 150 mM NaCl in 'SY Verdemax' (-18%) and remained unaffected by both salinity concentrations in 'SY Sincero' (Figure 4a). Root volume was drastically affected by both salinities in 'SY Verdemax' with reductions reaching 70% at 150 mM NaCl, while in 'SY Sincero' this parameter was only decreased by high salinity (Figure 4b).

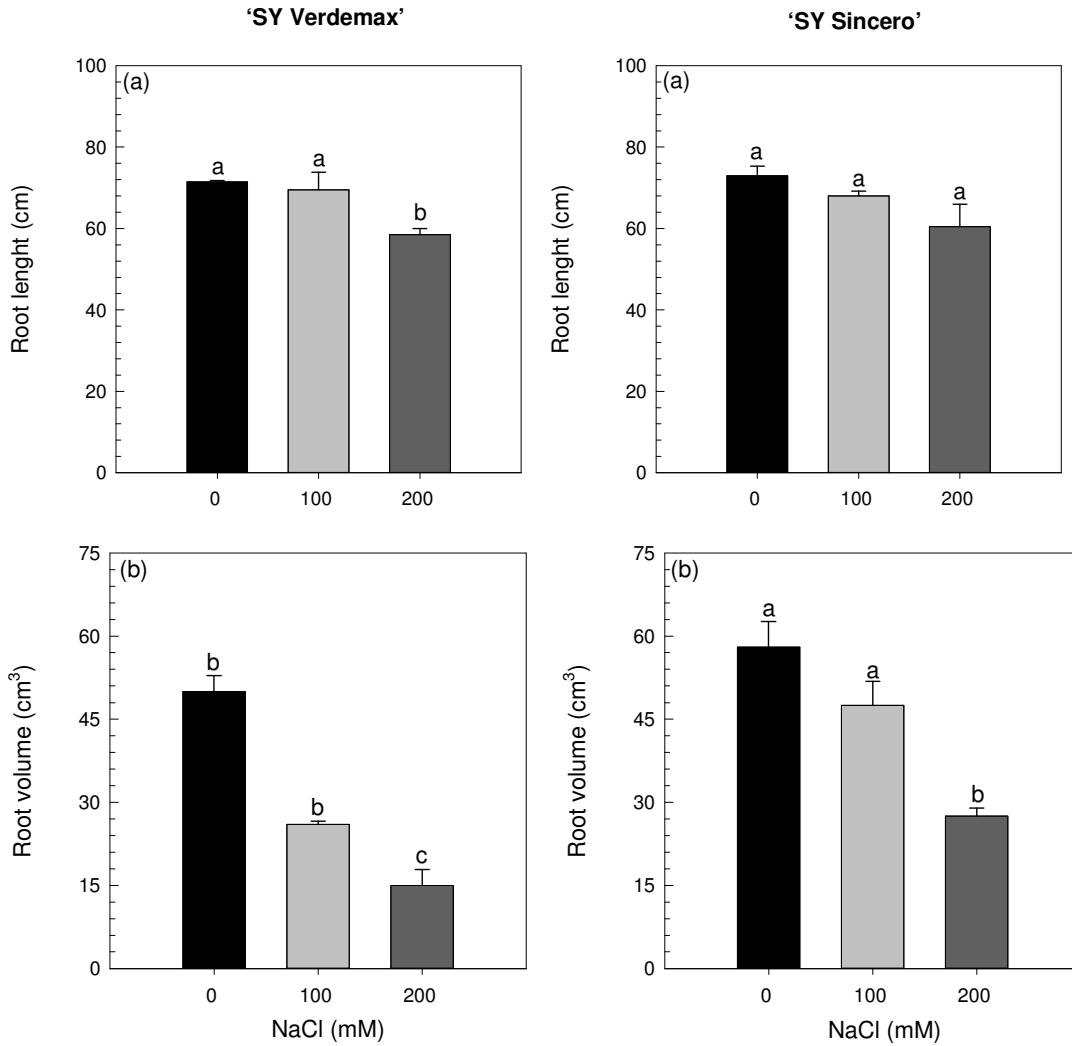


Figure 4. Variation in (a) root length, and (b) root volume of two *Z. mays* genotypes ('SY Verdemax' and 'SY Sincero') subjected to salinity (0, 100 and 150 mM NaCl) for 60 days
Data are means of three different replicates. Different letters denoted significant differences at $p \leq 0.05$

Effect of salinity on plant growth

The plant phenotype depicted a negative impact of mild and high salinity on plant growth of both studied genotypes (Figure 2). These morphological observations were associated with a significant decrease in shoot fresh weight with the highest reduction registered in 'SY Verdemax' exposed to 150 mM NaCl (-52 %; Figure 5a). Root fresh weight was not affected by 100 mM NaCl in 'SY Verdemax' while it was significantly restricted in 'SY Sincero' (Figure 5b). Nevertheless, 150 mM NaCl reduced this parameter in both varieties with the highest reduction registered in 'SY Verdemax' (-40%, Figure 5b).

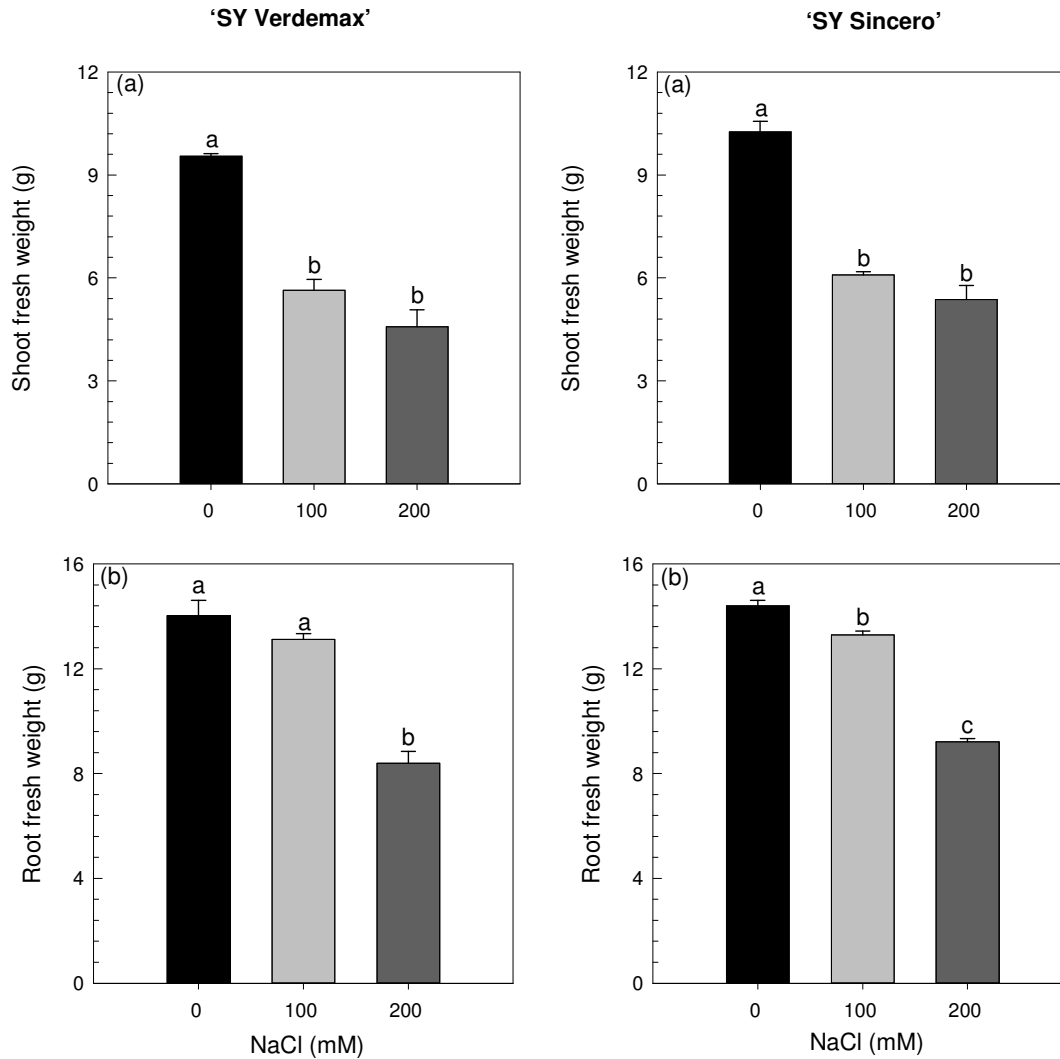


Figure 5. Variation in (a) shoot fresh weight and (b) root fresh weight of two *Z. mays* genotypes ('SY Verdemax' and 'SY Sincero') subjected to three salinity concentrations (0, 100 and 150 mM NaCl) for 60 days
Data are means of three different replicates. Different letters denoted significant differences at $p \leq 0.05$

Growth sensitivity to salt stress

In order to further discriminate between tolerant and sensitive maize cultivars based on plant growth, we calculated the stress sensitivity index (SSI) for shoots, roots and the whole plant, respectively in plants exposed either to 100 or 150 mM NaCl (Figure 6a, b and c). Our results indicate that SSI of "SY Sincero" when challenged with both salinity concentrations was lower than 1, reflecting a relative salt-tolerance (Figure 6a, b and c). By contrast, the highest SSI values were recorded in "SY Verdemax", further suggesting its sensitivity to applied salinities (Figure 6a, b and c).

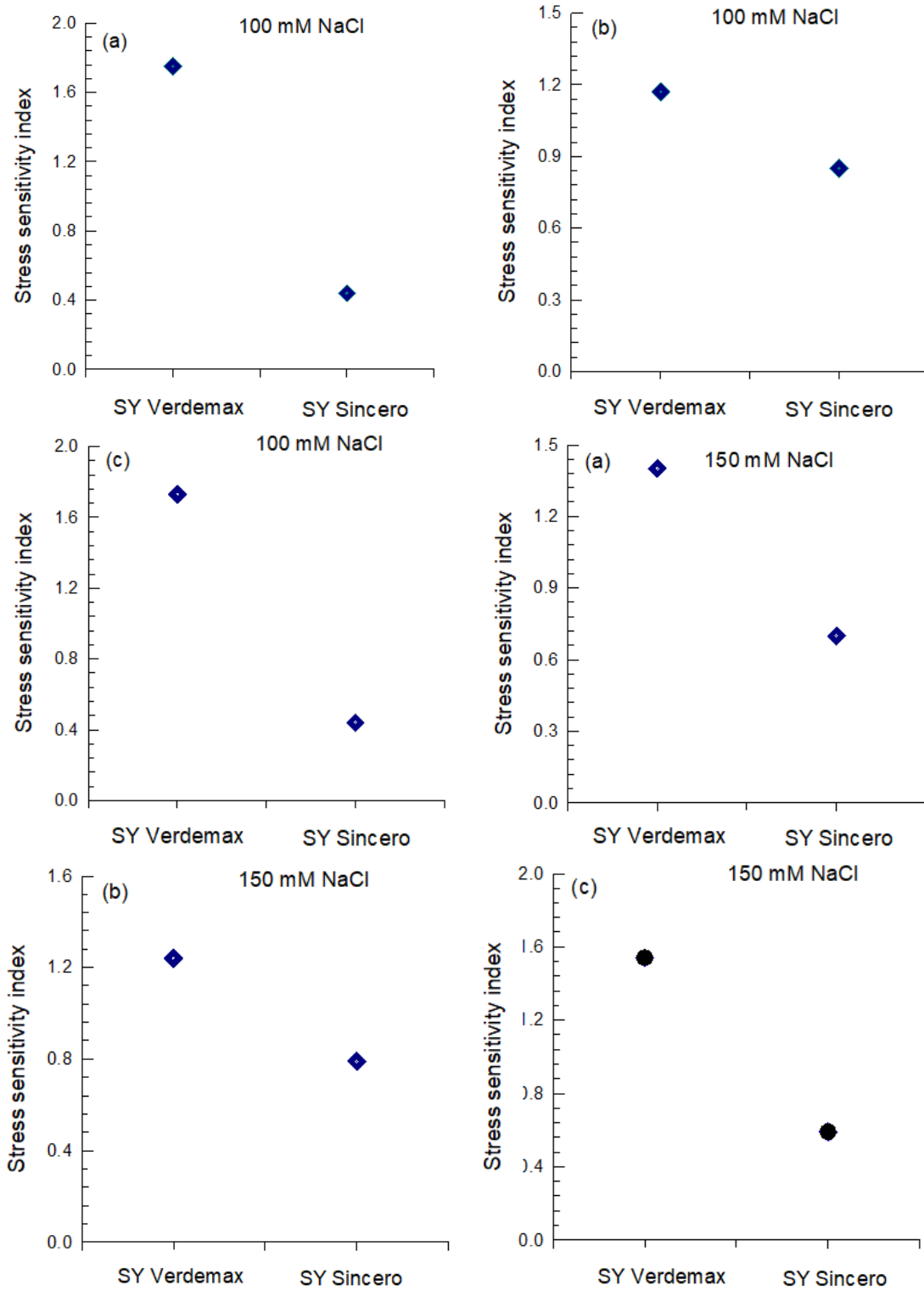


Figure 6. Variation in sensitivity index (SSI) in (a) leaves, (b) roots and (c) whole plant of two *Z. mays* genotypes ('SY Verdemax' and 'SY Sincero') subjected to three salinity concentrations (0, 100 and 150 mM NaCl) for 60 days
 Data are means of three different replicates. Different letters denoted significant differences at $p \leq 0.05$

Effect of salinity on chlorophyll concentrations

Chlorophyll a was similarly reduced by 100 and 150 mM NaCl in 'SY Sincero' whereas it gradually decreased with increasing NaCl concentration in 'SY Verdemax' (-31.57 % and 44.36 % at 100 and 150 mM NaCl, respectively, Table 1). Chlorophyll b was not affected by moderate salinity (100 mM NaCl) in 'SY Verdemax', but decreased significantly at 150 mM NaCl (-48.13%). By contrast, both NaCl concentrations did not affect chlorophyllb concentration in 'SY Sincero' (Table 1). A similar trend was observed for total chlorophyll concentration with a marked decrease in 'SY Verdemax' at 150 mM NaCl (-44.25%).

Table 1. Variation in chlorophyll a (Chla, $\mu\text{g mg}^{-1}$ FW), chlorophyll b (Chlb, $\mu\text{g g}^{-1}$ FW), total chlorophyll (Chla+b, $\mu\text{g g}^{-1}$ FW) and carotenoid content ($\mu\text{g g}^{-1}$ FW) of two *Z. mays* genotypes ('SY Verdemax' and 'SY Sincero') exposed to NaCl salinity (0, 100 and 150 mM) for 60 days

Genotype	Salinity	Pigment content ($\mu\text{g g}^{-1}$ DW)			
		Chla	Chlb	Chla+b	Carotenoids
'SY Verdemax'	0 mM NaCl	13.30a	21.40a	34.80a	46.40a
	100 mM NaCl	9.10b	21.90a	30.10a	16.10b
	150 mM NaCl	7.40c	11.10b	19.40b	10.60b
'SY Sincero'	0 mM NaCl	12.80a	24.20a	36.12a	28.60a
	100 mM NaCl	9.30b	22.90a	31.20a	25.00a
	150 mM NaCl	9.30b	24.00a	30.40a	22.10a

Data are means of three different replicates. Different letters denote significant differences at $p \leq 0.05$

For further understanding the effect of salinity on chlorophyll synthesis, we evaluated the percentage of total chlorophyll degradation (% of the control) in both cultivars by subtracting total chlorophyll concentration of stressed plants from the value 1 and dividing the obtained result by total chlorophyll of control plants. We found that in 'SY Verdemax', chlorophyll degradation increased from 13.50% at 100 mM NaCl to 44.25% at 150 mM NaCl while in 'SY Sincero', values were maintained in the range between 13.62 and 15.83% at both salinities concentration, respectively.

Besides, chlorophyll stability index (CSI) was calculated based on chlorophyll content under normal and salinity stress conditions. We found that CSI was decreased from 100 % in control plants to 86.49% and 55.74% in 'SY Verdemax' exposed to 100 and 150 mM NaCl, respectively. In 'SY Sincero', CSI was equal to 86.37% and 84.16% when plants were challenged with both salinity concentrations, respectively.

Carotenoid concentration was severely reduced by 100 and 150 mM NaCl in 'SY Verdemax' (-65 and 77%, respectively) and remained unaffected by both salinity concentrations in 'SY Sincero' (Table 1).

Effect of salinity on photosynthetic gas exchanges

Leaf gas exchange parameters decreased significantly in salt-treated plants (Figure 7). Photosynthesis assimilation rate (A) decreased gradually with increasing salinity in both genotypes (Figure 7a). The effect was more obvious in 'SY Verdemax' exposed to 150 mM NaCl (-57.35%). Stomatal conductance (gs) was reduced by both salinity concentrations in 'SY Verdemax' reaching 30% at 150 mM NaCl while it remained unaffected in 'SY Sincero' subjected either to 100 or 150 mM NaCl (Figure 7b). Mild and high salinity reduced similarly the transpiration rate (E) in both cultivars (Figure 7c). Yet, 'SY Verdemax' showed the highest reductions upon high salinity exposure (-31.5 %).

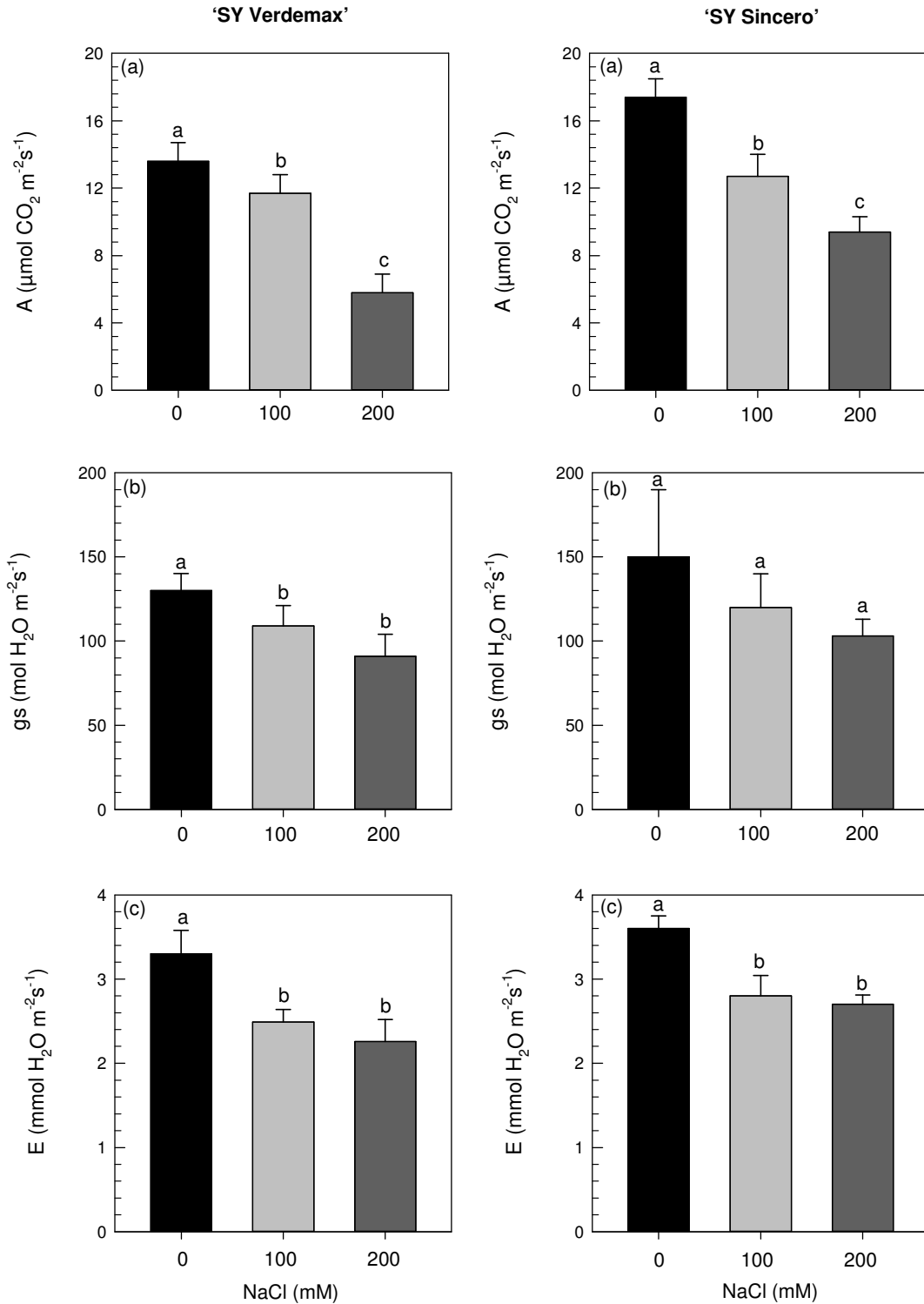


Figure 7. Variation in (a) net photosynthesis assimilation rate (A), (b) stomatal conductance and (c) transpiration rate (E) of two *Z. mays* genotypes ('SY Verdemax' and 'SY Sincero') subjected to three salinity concentrations (0, 100 and 150 mM NaCl) for 60 days. Data are means of three different replicates. Different letters denote significant differences at $p \leq 0.05$

To further evaluate the effect of salinity on the photosynthetic activity, photosynthesis assimilation stress tolerance index (ASTI), transpiration rate stress tolerance index (TrSTI) and stomatal conductance stress tolerance index (ScSTI) were calculated based on the value of each photosynthetic parameter under salt-free and salinity stress conditions. In 'SY Verdemax', ASTI decreased from 100% in control plants to 86.03% and 42.65% in plants subjected to 100 or 150 mM NaCl, respectively. By contrast in 'SY Sincero', this parameter was less affected (decreases were about 72.99 and 54.02% at both salinity concentrations, respectively). TrSTI also decreased to 75.45% and 68.48% at 100 and 150 mM NaCl, respectively in the sensitive cultivar whereas for 'SY Sincero', values varied between 77.77% and 75% at both salinity concentrations, respectively. ScSTI was reduced to 83.85% and 70% upon exposure of 'SY Verdemax' to 100 and 150 mM NaCl, respectively, while in 'SY Sincero', ScSTI declined to 80% and 68.48% in plants subjected to the two abovementioned salinities, respectively.

Effect of salinity on ion contents

For both genotypes, leaf and root Na⁺ concentrations increased with increasing NaCl concentration in the irrigation solution (Table 2). At 150 mM NaCl, Na⁺ was accumulated in leaves rather than in roots (Table 2). Besides, 'SY Verdemax' (salt-sensitive) accumulated more Na⁺ in leaves than 'SY Sincero' (salt-tolerant). Leaf Na⁺ concentration in 'SY Verdemax' was 6- and 9-fold higher at 100 and 150 mM NaCl, respectively as compared to control plants. In contrast, 'SY Sincero' accumulated more Na⁺ in roots than 'SY Verdemax', with root Na⁺ concentrations increasing by 10- and 11-fold at both salinity levels, respectively as compared to plants grown in NaCl-free conditions (Table 2). Cl⁻ concentration was not affected by 100 mM NaCl in leaves of both cultivars but, increased significantly upon exposure to 150 mM NaCl (Table 2). By contrast, significant differences between control and salt-treated plants were recorded in roots of plants subjected to 150 mM NaCl in 'SY Verdemax' while no effect was detected in 'SY Sincero' (Table 2).

Table 2. Variation in Na⁺ and Cl⁻ concentrations (meq g⁻¹ DW) and Na⁺/K⁺ selectivity ratio in leaves and roots of two *Z. mays* genotypes ('SY Verdemax' and 'SY Sincero') exposed to NaCl salinity (0, 100 and 150 mM) for 60 days

Genotype	Salinity	Na ⁺ content		Cl ⁻ content		Na ⁺ /K ⁺ ratio	
		Leaves	Roots	Leaves	Roots	Leaves	Roots
'SY Verdemax'	0 mM NaCl	1.20c	1.20c	1.36b	1.56b	0.80c	1.84c
	100 mM NaCl	7.20b	7.60b	1.82b	1.66b	5.14b	16.52b
	150 mM NaCl	11.00a	8.40a	3.01a	2.33a	8.46a	23.33a
'SY Sincero'	0 mM NaCl	1.70c	0.60b	1.16b	2.16a	0.80c	1.20b
	100 mM NaCl	6.60b	6.00a	1.69b	2.56a	3.66b	15.00a
	150 mM NaCl	8.10a	7.00a	2.81a	2.65a	4.76a	17.50a

Data are means of three different replicates. Different letters denote significant differences at $p \leq 0.05$

To further discriminate between the include and excluder cultivars, Na⁺ translocation index (Na⁺TI) to shoots was calculated as the ratio between Na⁺ content in shoots and Na⁺ content in the whole plant. In 'SY Verdemax', Na⁺TI was equal to 48 under control conditions and to 46.02 and 56.7 upon exposure to 100 and 150 mM NaCl, respectively. In 'SY Sincero', Na⁺TI was equivalent to 72 in control leaves and decreased to 50 and 51 when plants are challenged with both salinity concentrations, respectively, reflecting that 'SY Sincero' accumulated lesser Na⁺ than 'SY Verdemax'.

Na⁺/K⁺ ratio was highly increased in leaves and roots of 'SY Verdemax' and 'SY Sincero' exposed to 100 and 150 mM NaCl (Table 2) reflecting a negative impact of Na⁺ on K⁺ uptake. Interestingly, the effect was more obvious in 'SY Verdemax'.

Effect of salinity on water relations

Leaf water content (LWC) was not affected by mild salinity but decreased significantly at 150 mM NaCl in both cultivars, reaching -46.87 % in the salt-sensitive one (Table 3). As salinity increased, leaf water potential decreased significantly in both cultivars, especially at high salinity (-0.8 and -0.4 MPa in ‘SY Verdemax’ and ‘SY Sincero’, respectively) (Table 3). This effect was more pronounced in ‘SY Verdemax’ (salt-sensitive).

Table 3. Variation in leaf water content (LWC, ml g⁻¹ DW), leaf water potential (LΨ_w, -MPa), leaf water use efficiency (LWUE, μmol CO₂ mmol⁻¹ H₂O), leaf intrinsic water-use efficiency (LIWUE, μmol CO₂ mol⁻¹ H₂O) and leaf specific mass (LSM, mg FW or DW cm⁻²) of two *Z. mays* genotypes (‘SY Verdemax’ and ‘SY Sincero’) exposed to NaCl salinity (0, 100 and 150 mM) for 60 days

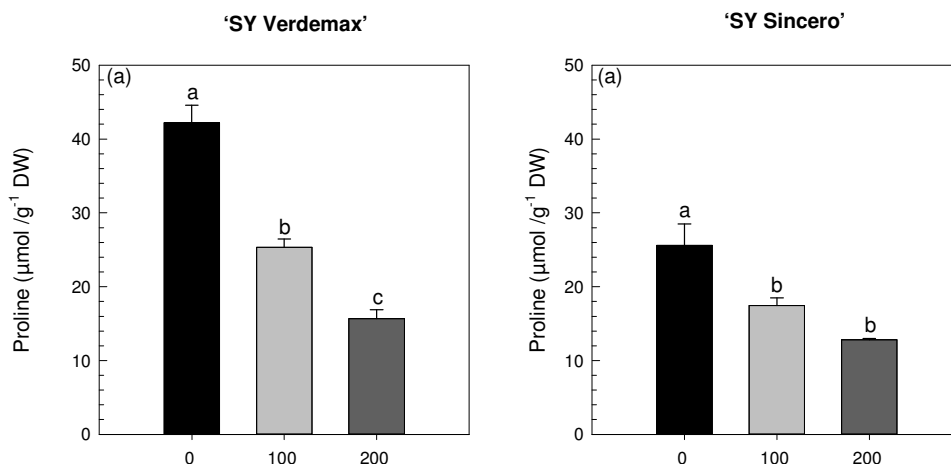
Genotype	Salinity	LWC	LΨ _w	LWUE	LIWUE	LSM (on FW basis)	LSM (on DW basis)
‘SY Verdemax’	0 mM NaCl	3.20 a	0.30 b	4.12 a	0.10 a	66.80 a	8.40 b
	100 mM NaCl	2.40 a	0.60 a	4.70 a	0.11 a	50.58 b	8.07 b
	150 mM NaCl	1.70 b	0.80 a	2.57 b	0.06 b	50.05 b	9.87 a
‘SY Sincero’	0 mM NaCl	3.40 a	0.20 b	4.83 a	0.12 a	60.53 a	9.44 c
	100 mM NaCl	3.20 a	0.30 a	4.53 a	0.11 a	51.96 a	12.81 b
	150 mM NaCl	2.20 b	0.40 a	3.48 b	0.09 b	58.17 a	15.16 a

Data are means of three different replicates. Different letters denote significant differences at $p \leq 0.05$

Other leaf parameters were used to evaluate the effect of salt stress on water relations including leaf water-use efficiency (LWUE), leaf intrinsic water-use efficiency (LIWUE) and leaf specific mass (LSM) (Table 3). LWUE and LIWUE decreased only at 150 mM NaCl with the highest reductions recorded in ‘SY Verdemax’ (-37.73% and -39.08% for LWUE and LIWUE, respectively). When expressed on fresh weight basis, LSM decreased significantly in ‘SY Verdemax’ exposed to 100 or 150 mM NaCl while remaining constant in ‘SY Sincero’ (Table 3). When was expressed on dry weight basis, LSM increased slightly in ‘SY Verdemax’ exposed to 150 mM NaCl while it was significantly enhanced by both salinities in ‘SY Sincero’ (Table 3).

Effect of salinity on leaf proline content and electrolyte leakage

Proline content was higher in plants cultivated in salt-free medium but reduced significantly by salinity in both cultivars (Figure 8a). Interestingly, mild and high salinity reduced similarly proline content in ‘SY Sincero’ while in ‘SY Verdemax’ (salt-sensitive) proline content decreased with increasing salinity being more affected at 150 mM NaCl (-62.8%, Figure 8a).



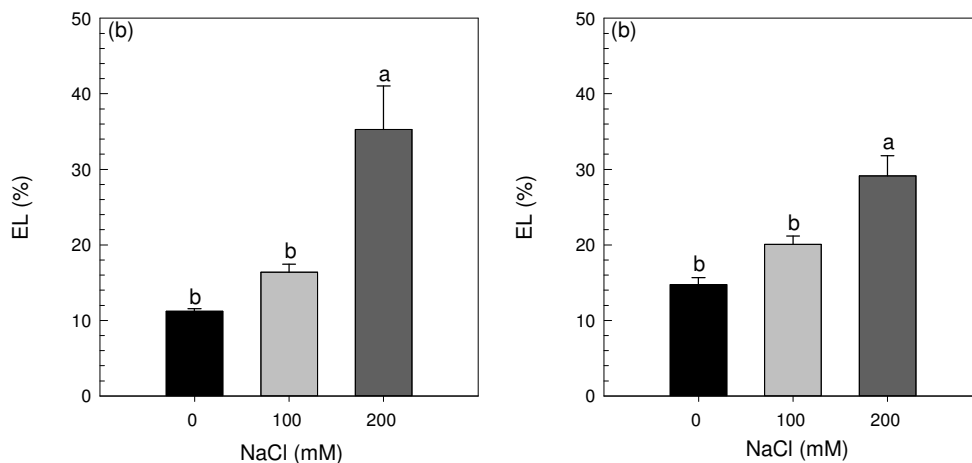


Figure 8. Variation in (a) leaf proline content and (b) electrolyte leakage (EL) of two *Z. mays* genotypes ('SY Verdemax' and 'SY Sincero') subjected to three salinity concentrations (0, 100 and 150 mM NaCl) for 60 days

Data are means of three different replicates. Different letters denote significant differences at $p \leq 0.05$

The release of electrolytes across leaf cell membranes (EL) was used to assess the degree of cell permeability under stressful conditions. There was a significant increase in EL with increasing salinity (Figure 8b), 'SY Verdemax' showing the highest values when challenged with 150 mM NaCl (+214.8 % as compared to the control).

Membrane stability index (MSI) has been measured as an indicator to evaluate cell membrane permeability under stress as a percentage of the control (100%; Kamanga *et al.*, 2023). MSI was not affected by 100 mM NaCl in both cultivars (94.18% and 93.72% in 'SY Verdemax' and 'SY Sincero', respectively). At 150 mM NaCl, significant differences were recorded between the two cultivars since MSI was equal to 72.95% in 'SY Verdemax' and 83.21% in 'SY Sincero' depicting that this later was less affected by salt stress.

Membrane injury (MI) was calculated based on MSI (Kamanga *et al.*, 2023), and results revealed that MI was equal to zero in control plants but salinity impacted significantly this parameter. In 'SY Verdemax', MI increased to 5.82 and 27.05 at 100 and 150 mM NaCl, respectively. In 'SY Sincero', MI was less affected as values varied between 6.28 and 16.79 at both salinity concentrations, respectively depicting less damage to leaf membrane in this cultivar.

Discussion

According to Soltabayeva *et al.* (2021), selecting tolerant genotypes to salinity should be performed based on morphological (*i.e.* root or/and shoot morphology), physiological and biochemical markers (*i.e.* chlorophyll content, accumulation of proline, membrane stability, photosynthetic activity). In this context, the current study was designed to identify some key traits underlying variation in salinity tolerance in *Z. mays* using biometric, physiological and biochemical parameters. Under salt treatment, significant phenotypic differences between plants cultivated in free-salt medium or exposed to 100 or 150 mM NaCl were recorded. Phenotype-related seedling shoot and root traits are considered as useful biometric criteria for screening wheat genotypes regarding their tolerance to nutrient deprivation and drought stress (Rossi *et al.*, 2024).

In our study, maize plants displayed leaf injury symptoms including chlorosis, wilting, a decline in leaf size and leaf rolling. Salinity was shown to trigger toxicity symptoms including leaf burn, leaf scorch and wilting

and in extreme cases dry leaf tissues and senescence (Saddiq *et al.*, 2021; Liu *et al.*, 2023). Similar morphological aspects were described in *Juglans microcarpa* which exhibited yellowing, withering, curling, and falling of leaves under exposure to salt stress. Further, increasing NaCl concentration and exposure time led to severe damage including leaf withering and shedding (Ji *et al.*, 2022). These symptoms could be due to salt-induced injuries to photosynthetically active leaves resulting in chlorosis, necrosis and premature leaf senescence (Hanin *et al.*, 2016; Saddiq *et al.*, 2021). Consistent with our study, NaCl-related leaf lesions were shown to be more prominent in rice salt stress-sensitive genotypes (Rodríguez Coca *et al.*, 2023) and could be used for discriminating salt tolerance degree and genotypic variability.

Affected plant height under abiotic stress reflects changes in plant growth and development and thus, is considered as a fundamental morphological parameter when studying plant response to adverse environmental issues including salinity (Rodríguez Coca *et al.*, 2023). Our findings indicated that shoot height was significantly impaired by both salinity levels in 'SY Verdemax' and 'SY Sincero' confirming previous findings focused on *Z. mays* challenged with salinity stress (Sezer *et al.*, 2021). Our data corroborated the recent findings of Xu *et al.* (2024) who found that salt stress had a significant effect on plant height of rice genotypes with the more severe decrease characterizing salt-sensitive genotypes.

Leaves are particularly important organs for plant survival and growth enabling these autotrophic organisms to adapt to environmental conditions. Such adaptations include a reduction in leaf size and number. In our study, the phenotypic expression of leaves (i.e. leaf number and leaf surface area) of 'SY Verdemax' and 'SY Sincero' was significantly hampered by salinity. Leaf number was slightly reduced by 100 mM NaCl and significantly decreased by 150 mM NaCl especially in 'SY Verdemax'. Our data are in line with previous findings conducted in the same plant species under both salinity and alkalinity stresses (Fatima *et al.*, 2021). This could be explained by the fact that NaCl stress inhibits leaf primordium formation (Rodríguez Coca *et al.*, 2023). Likewise, leaf surface area decreased with increasing salinity in both genotypes. Salinity stress was shown to restrict leaf expansion in different durum wheat genotypes (Chamekh *et al.*, 2014). In rice cultivars, both leaf area and leaf area indices were inhibited by salinity (Haque *et al.*, 2021). Drought stress also impaired leaf area in wheat cultivars (Rossi, *et al.*, 2024).

Reduced leaf size and number consequently to salinity-induced water stress is among the adaptive strategies used by plants to avoid excessive transpiration, reduce water loss, optimize water use efficiency and enabling its survival under such circumstances (da Cunha Cruz *et al.*, 2023).

Roots play a key role in coping with abiotic stresses in cereals, and root length and volume are two pertinent criteria to assess genotypic salinity tolerance (Rossi, *et al.*, 2024). Genotype-dependent reduction in root traits including root surface area, root volume and root specific length was documented among different maize genotypes (Wang *et al.*, 2020). Our data also pointed that root length was not affected by both salinity levels in 'SY Sincero', whereas it was significantly inhibited by high salinity in 'SY Verdemax'. This corroborates recent findings in maize showing that the salt-sensitive genotype exhibited the more pronounced reduction in root length as compared to the salt-tolerant one (Rizk *et al.*, 2024). Plant exposure to salt stress induced quick cell wall response notably polysaccharide deposition and pectin modifications both affecting cell elasticity and expansion (de Lima *et al.*, 2014; Gall *et al.*, 2015). One might speculate that under our experimental conditions, salt stress increased root lignin content of the cultivar 'SY Verdemax' and reduced arabinoxylan content which explain in part the reduction of root length (Oliveira *et al.*, 2020). Root volume was only affected by 150 mM NaCl in the salt-tolerant cultivar ('SY Sincero') while it was drastically decreased by both salinities in the salt-sensitive one ('SY Verdemax'). Plants challenged with salt stress exhibited root phenotypic plasticity by modulating both root system architecture and growth (i.e. restriction of root hair density and elongation; Dinneny, 2019; Zou *et al.*, 2022). The reduction in root volume under saline conditions could be a result of decreased availability of photosynthates from source organs or caused by water stress and ion toxicity imposed by the buildup of salts around the roots (Shafi *et al.*, 2010).

The root length to shoot length ratio increased significantly upon plant exposure to 150 mM NaCl in 'SY Verdemax', suggesting that shoots were more sensitive to salt stress than roots at this concentration. This could be partly ascribed to the induced ionic imbalance resulting from the excessive accumulation of Na⁺ and Cl⁻ which impacts cell wall properties (i.e. restricting cell wall elasticity) and therefore hinders shoot elongation (Shao *et al.*, 2021; Colin *et al.*, 2023).

These alterations in shoot and root morphology resulted in a significant decrease in plant biomass production notably in the salt-sensitive cultivar which had the highest stress susceptibility index (SSI). Indeed, cell dehydration and shrinkage induce a reduction in shoot development and elongation (Rodríguez Coca *et al.*, 2023). Besides, several physiological pathways including nutrient transport, stomatal conductance and the activity of a wide range of enzymes involved in several metabolic pathways notably photosynthesis decrease upon salt exposure leading to a decrease in plant growth (Balasubramaniam *et al.*, 2023). It is worth noting that 'SY Sincero' accumulated more biomass in leaves in benign conditions as compared to 'SY Verdemax' and was shown to be less affected by salinity. Our data corroborated those of Temme *et al.* (2019, 2020) who found that the most sunflower genotypes exhibiting high vigor in terms of biomass production under control conditions tended to remain the best performers under salt stress.

Chla, chl_b, chl_{a+b} and carotenoids were negatively affected by salt stress especially 150 mM NaCl in 'SY Verdemax' while in 'SY Sincero' the effect was less important with chl_b, Chl_{a+b} and carotenoids being unaffected which could be due to a restriction of macro and micronutrient uptake notably magnesium (Shahzad *et al.*, 2019; Zirek and Ozlem, 2020) or to an inhibition of chlorophyll biosynthesis as well as an increase of their degradation (Qiu *et al.*, 2017), which is in line with our findings as the percentage of chlorophyll degradation increased with increasing salinity especially in 'SY Verdemax'. It has been reported that the ability of any plant species to withstand salt stress depends on its capacity to maintain chlorophyll in its leaves. Thus, salt-tolerant genotypes showed less chlorophyll loss as compared to sensitive ones (Ghosh, *et al.*, 2011). Our data showed that 'SY Sincero' was able to retain chlorophyll under salt stress, a behavior not detected in 'SY Verdemax'. Similar findings were obtained by Xu *et al.* (2024) who demonstrated that salt-tolerant rice genotypes exhibited higher chlorophyll contents than sensitive ones and were able to maintain higher photosynthetic activity and biomass production. The reductions in chlorophyll synthesis explained the chlorosis phenomenon observed in leaves of 'SY Verdemax' and the decline in plant growth rate (Nawaz *et al.*, 2023).

Carotenoid concentration decreased significantly in 'SY Verdemax' subjected to salt stress while it was not affected in 'SY Sincero'. The decrease of carotenoid content in the sensitive variety suggested the inaptitude of the sensitive variety to consume excess light energy.

Salinity imposes reductions in leaf characteristics that weakened the leaf photosynthetic efficiency (Huanhe *et al.*, 2024). The tolerance degree of any plant species to salt stress depends on its aptitude to maintain an adequate rate of photosynthesis to sustain its growth under such harsh conditions (Munawar *et al.*, 2021). Our results showed an impact of salinity on photosynthesis assimilation rate, stomatal conductance and transpiration and consequently the photosynthetic rate with significant differences between both cultivars. It has been shown that salinity affected differently photosynthetic gas exchange, in a plant species and salinity stress magnitude dependent manner (Hameed *et al.*, 2021). The disruption of cell ionic balance (i.e. depletion of K⁺ and Ca²⁺) led to stomatal closure, a decline in the transpiration rate, and an inhibition of photosynthetic enzymes with devastating effects on photosynthesis leading to premature senescence of leaves (Huanhe *et al.*, 2024). Similar effects of salinity on gas exchange parameters were reported in other cereals such as wild and cultivated barley, wheat and rice (Ashraf *et al.*, 2023; Saoudi *et al.*, 2023; Huanhe *et al.*, 2024).

In our study, there was a significant increase in Na⁺ content in the different organs following *Z. mays* exposure to 100 or 150 mM NaCl. The increase in Na⁺ contents with increasing salinity in maize was reported by Shahzad *et al.* (2019). One may hypothesize that salinity decreases the external osmotic pressure notably as

a consequence of the strong accumulation of Na^+ in shoots (Mahmood *et al.*, 2024). Besides, at 150 mM NaCl, leaves accumulated more Na^+ than roots which is a direct consequence of (i) a passive Na^+ diffusion via the injured membranes and (ii) a decrease in root exclusion mechanism efficiency (Fricke *et al.*, 2004; Qu *et al.*, 2012). ‘SY Verdemax’ displayed the highest shoot Na^+ content while ‘SY Sincero’ has the greater Na^+ root concentrations which was concomitant with an increase/decrease of Na^+ translocation index in shoots (TIS) of ‘SY Verdemax’ and a ‘SY Sincero’, respectively. Our data are in line with those of Vetterlein *et al.* (2004) who studied the response of two maize cultivars, Pioneer 3906 (Na^+ excluder cultivar) and Across 8023 (Na^+ includer cultivar) to salt stress and found that Across 8023 accumulated higher amounts of sodium in shoots as compared to Pioneer 3906. It has been reported that salt-tolerant cultivars displayed high root Na^+ content and hence preventing Na^+ flux to shoots (Ashraf *et al.*, 2023). As shown by Zeeshan *et al.* (2020), subjecting wheat and barley genotypes to salt stress resulted in better accumulation of Na^+ and K^+ in roots rather than shoots justifying the ability of the studied genotypes to limit the translocation of both ions from roots to shoots. Our results revealed that ‘SY Sincero’ was more efficient in restricting the upward movement of Na^+ suggesting its high ability to prevent excessive Na^+ buildup in active leaves via either lowering Na^+ loading in xylem or retrieval of those ions from xylem (Shahzad *et al.*, 2022). This assumption was recently confirmed by Elkelish *et al.* (2019) and Saddiq *et al.* (2021) who found that salt-tolerant genotypes have a better ability to maintain low Na^+ in their leaves. Our data corroborated previous findings focused on wheat and rice (Saddiq *et al.*, 2018; Mohanty *et al.*, 2023).

Chloride is also a toxic and growth inhibitor (Shahzad *et al.*, 2019). It was accumulated especially in leaves of both cultivars and in roots of ‘SY Verdemax’ challenged with 150 mM NaCl. This increase in Cl^- contents could be due to its passive influx through the biomembranes and its translocation to the photosynthetic organs (Le *et al.*, 2021). Salt tolerant crop plants maintain less Cl^- concentration in their tissues via an exclusion mechanism (Ebrahimi and Bhatla, 2011). Moreover, the restriction of chloride translocation from roots to shoots is a trait of chloride tolerance in maize (Zhang *et al.*, 2019).

Salinity can induce nutrient deficiencies, with harmful impacts to plant growth (Farooq *et al.*, 2022). The evaluation of Na^+/K^+ ratio is an important parameter to evaluate the impact of salt stress on K^+ uptake. Our data pointed significant increase in Na^+/K^+ demonstrating a negative effect of sodium on potash uptake. This could be due to the antagonistic relationship between Na^+/Cl^- and macronutrients (Javed *et al.*, 2022), resulting in nutrient deficiency which explain in part the phenotypic symptoms observed under our experimental conditions. Xu *et al.* (2024) focused on rice supported our findings since ‘SY Sincero’ showed the lowest Na^+/K^+ and was shown to be more tolerant to salinity stress. According to Vijayalakshmi *et al.* (2014) and Chaurasia *et al.* (2022), lower root Na^+/K^+ and $\text{Na}^+/\text{Ca}^{2+}$ ratio could be used as a selection criterion for screening tolerant wheat genotypes to salt stress. In agreement with our findings, several wheat and barley genotypes with low Na^+/K^+ or $\text{Na}^+/\text{Ca}^{2+}$ ratios are more efficient in discriminating K^+ or Ca^{2+} over Na^+ and consequently exhibited high tolerance to salinity (Iqra *et al.*, 2020; Zeeshan *et al.*, 2020; Chaurasia *et al.*, 2022).

Increase in salts in soils lowers the soil water potential of plant cells. This reduces water uptake by plants and consequently causes cellular dehydration (Gupta *et al.*, 2021). As shown in our results salinity reduced leaf water contents in leaves of both cultivars with an effect more important in ‘SY Verdemax’ which is concomitant with the visible morphological aspects of wilting and dehydration. Such findings could be due to a decline in water uptake as a result of osmotic stress via an efflux of water from roots leading immediately to stomata closure. Under such conditions, several metabolic pathways must maintain their functioning to ensure plant survive keeping in mind that such processes need adequate temperature rate. The latter is maintained via transpiration which removes water from different plant tissues leading to decrease in their water content. The dehydration of plant organs hinders cellular expansion (Khodarahmpour, 2012) and reduces their growth which is in line with our findings.

Under salt stress, ion imbalance and water deficiency in the plant cell cause osmotic stress (Zhao *et al.*, 2021). Our data revealed a decrease in leaf water potential in both cultivars as salinity increased with the highest reductions recorded in 'SY Verdemax'. Indeed, salinity induced generally an osmotic stress by lowering leaf water potential and turgor pressure (Arif, *et al.*, 2020). The decrease of both soil water and leaf water potentials by salinity disturbs plant water relations and reduces the turgor of plant, resulting in osmotic stress (Navada *et al.*, 2020). The lesser reduction in LW ψ in the salt-tolerant cultivar ('SY Sincero') reflects its ability to maintain an equilibrium between transpiration and water uptake and ensure its osmotic adjustment *via* the accumulation of some inorganic ions or compatible solutes, both essential for maintaining leaf water potential (El-Hendawy *et al.*, 2017). Our data confirmed previous findings focused on other plant species revealing that genotypes presenting the lowest reductions are the most tolerant to salt stress (Zarei *et al.*, 2016; El-Hendawy *et al.*, 2017). LWUE and LIWUE were not affected by moderate salinity but decreased significantly at 150 mM NaCl in both cultivars with the salt-sensitive cultivar showing the highest reduction. LSM expressed on basis of FW decreased at both salinities in the sensitive cultivar and remained unaffected in the tolerant one suggesting the failure of 'SY Verdemax' in maintaining its photosynthesis potential. Nevertheless, when expressed on basis of DW, LSM was slightly increased at 150 mM NaCl in 'SY Verdemax' and was enhanced by both salinities in 'SY Sincero'. The increase in LSM under salt stress was also reported in *Lawsonia inermis* and is considered as an adaptive strategy to overcome salt stress in plants (Fernández-García *et al.*, 2014).

Cell membrane permeability is a crucial trait to evaluate the degree of abiotic stresses including salinity. EL and MSI are widely used as common useful markers to predict indirectly the damages caused by salinity to cell membranes (Nijabat *et al.*, 2020; Savage *et al.*, 2024; Pai and Sharma, 2024). In our study, we found that EL and MI increased significantly especially at high salinity with an effect more obvious in 'SY Verdemax'. By contrast, MSI was declined at 150 mM NaCl especially in the sensitive variety. Indeed, salinity was shown to cause damages to membrane integrity leading to an influx of electrolytes across the biological membranes. We can speculate that salinity led to membrane protein denaturation and inactivation of several enzymes resulting in disruption of membrane integrity and permeability, leakage of electrolytes across the membrane along with other negative impacts affecting cell viability and consequently, reducing leaf area, chlorophyll content and plant growth (Nijabat *et al.*, 2020). According to Saddiq *et al.* (2021), the decrease in plant growth upon salt stress is linked with high cell membrane injury and induction of leaf senescence as a result of Na⁺ toxicity. In 'SY Sincero' and 'SY Verdemax', such effects were associated with a decrease in membrane stability index and a greater increase in cell permeability which is in line with the previous findings of Collado *et al.* (2010), Youssef *et al.* (2018) and Shereen *et al.* (2022).

Proline is a beneficial osmoticum playing important roles in plants. Generally, proline content increases upon salinity stress exposure (Datir *et al.*, 2020; Nguyen *et al.*, 2021). Our results showed a decrease in proline content in both cultivars with an effect more important in 'SY Verdemax'. This result can be explained by (i) another osmolyte is involved in the response of both cultivars to salt stress (Kasim and Dowidar, 2006; Mittler, 2006), (ii) the ability of both varieties to use some amount of Na⁺ as "cheap" compatible osmolyte to minimize the high energy cost of osmolyte biosynthesis (Solis *et al.*, 2021). Similar results were shown by Abdel-Farid *et al.* (2020) who found a decrease in proline content in tomato and cucumber subjected to salt stress.

Overall, 'SY Sincero' was more efficient in tolerating salinity stress rather than 'SY Verdemax' due to a strict control of Na⁺ translocation to shoots to protect the photosynthetic machinery and chlorophyll synthesis and the maintenance of its biological membrane integrity. The main mechanisms developed by 'SY Sincero' to overcome salt stress were summarized in Figure 9.

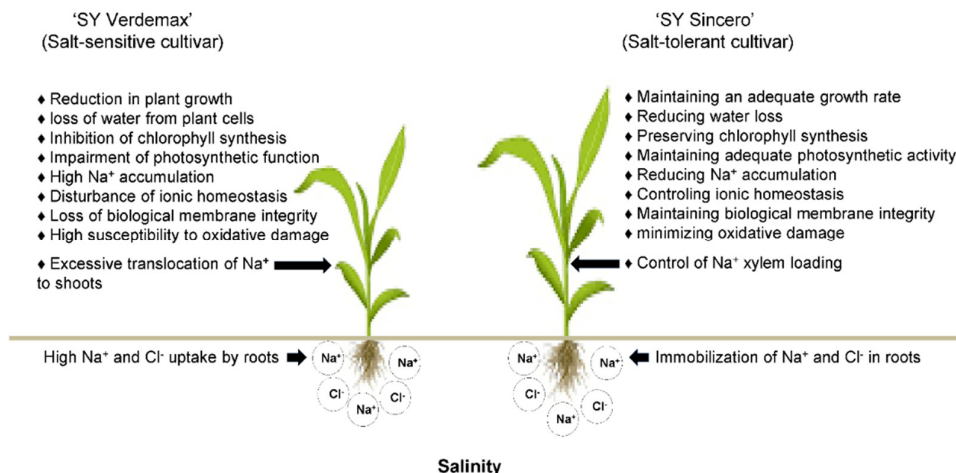


Figure 9. Schematic illustration emphasizing the contrasting behavior of *Z. mays* 'SY Verdemax' and 'SY Sincero' cultivars toward salinity stress (100 or 150 mM NaCl)

Conclusion

Using several ecophysiological criteria, our study pointed out that 'SY Sincero' is a relative salt-tolerant maize cultivar, a behavior strongly correlated with the ability to avoid Na⁺ buildup to shoots. This mechanism is vital when the plant is exposed to long-term salinity as it contributes to preserve chlorophyll synthesis and an adequate photosynthetic activity. Besides, 'SY Sincero' showed a better control of cell turgor, stomatal dynamics and less membrane damage. Efficiently using these adaptive traits confers 'SY Sincero' a major advantage when cultivated in areas affected by soil and/or salinization, and opens new perspective for breeding maize genotypes to improve the productivity of salt-affected areas.

Authors' Contributions

Conceptualization: AD; Data curation: HH, RH; Formal analysis: HH; Funding acquisition: NMA; Investigation: HH; Methodology: HH, AD; Project administration: AD; Resources: AD, HH; Supervision: AD; Validation: AD; Roles/Writing - original draft: HH and Writing - review & editing: AD, NMA.

All authors read and approved the final manuscript.

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Conflict of Interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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