Highlights

- A strong genetic variation in salinity tolerance exist amongst quinoa accessions;
- Both epidermal bladder cells (EBC) development and stomata patterning play an essential role conferring salinity tolerance trait in quinoa;
- Bladders density was increased in most accessions under saline condition while the bladder's diameter remained unchanged;
- The correlation analysis indicated a significant positive association between EBC diameter and salinity tolerance index (STI) on one hand and EBC volume and STI on the other hand, in a salt-tolerant group.

A large-scale screening of quinoa accessions reveals an important role of epidermal bladder cells and stomatal patterning in salinity tolerance

Ali Kiani-Pouya[a], Fatemeh Rasouli[a], Nadia Bazihizina[a,b], Heng Zhang[c], Rainer Hedrich[d] and Sergey Shabala[a,e*]

[a] Tasmanian Institute of Agriculture, College of Science and Engineering, University of Tasmania, Hobart, Australia; [b] Department of Agricultural, Environmental, Food and Forestry Science and Technology, University of Florence, Florence, Italy; [c] Shanghai Centre for Plant Stress Biology and CAS Centre for Excellence in Molecular Plant Sciences, Chinese Academy of Sciences, Shanghai, China; [d] Institute for Molecular Plant Physiology and Biophysics, University Wuerzburg, D-97070 Wuerzburg, Germany; [e] International Research Centre for Environmental Membrane Biology, Foshan University, Foshan, China

[*]Corresponding author; email: Sergey.Shabala@utas.edu.au; phone +61 3 6226 7539

Abstract

The presence of epidermal bladder cells (EBCs) in halophytes allows considerable amount of Na^+ being accumulated in these external structures, away from the metabolically active mesophile cells. Also, stomatal patterning may represent a primary mechanism by which plants can optimise its water-use efficiency under saline condition. This investigation was aimed to explore the varietal differences in a salinity tolerance of quinoa (*Chenopodium quinoa*) by evaluating a broad range of accessions and linking the overall salinity tolerance with changes in stomatal characteristics and EBC parameters. One hundred and fourteen accessions were grown under temperature-controlled glasshouse under non-saline and 400 mM NaCl conditions, and different physiological and anatomical characteristics were measured. Accessions were classified into three classes (sensitive, intermediate and tolerant) based on a relative dry weight defined as salinity tolerance index (STI). Results showed a large variability in STI indicating a strong genetic variation in salinity tolerance in quinoa. Bladders density was increased in a majority of accessions under saline condition while the bladder's diameter remained unchanged; this resulted in a large variability in a bladder's volume as a dependant variable. Stomata density remained unchanged between saline and non-saline conditions while the stomata length declined between 3% to 43% amongst accessions. Leaf Na^+ concentration varied from 669 μmol/gDW to 3155 μmol/gDW under saline condition and, with an exception of a few accessions, leaf K^+ concentration increased under saline conditions. Correlation analysis indicated a significant positive association between EBC diameter and STI on one hand and EBC volume and STI on the other hand, in a salt-tolerant group. These observations are consistent with the role of EBCs in sequestration of toxic Na^+ in the external structures, away from the cytosol. A negative association was found between EBC density and diameter in salt-sensitive plants. A negative association between STI and stomata length was also found in a salt-tolerant group, suggesting that these plants were able to efficiently regulate stomatal patterning to balance water loss and CO_2 assimilation under saline conditions. Both salt-sensitive and salt-tolerant groups had the same Na^+ concentration in the shoot under saline conditions; however, a negative association between leaf Na^+ concentration and STI in salt-sensitive plants indicated a more efficient Na^+ sequestration process into the EBCs in salt-tolerant plants.

Key words: quinoa, salinity tolerance, epidermal bladder cells, stomata, sodium, potassium

1. Introduction

While halophytes and glycophytes have similar salinity tolerance mechanisms at a basic level, halophytes have far superior salinity tolerance ability through developing numerous strategies to adapt to high saline conditions (Shabala and Mackay, 2011). These mechanisms include a range of anatomical and physiological traits (Flowers and Colmer, 2008; Munns and Tester, 2008; Shabala and Mackay, 2011)

One of the specialised features that distinguishes halophytes from glycophytes is the presence of the epidermal bladder cells (EBCs). EBCs have been found in about 50% of all halophyte species (Flowers and Colmer, 2008) and are located on the leaf surfaces, panicles and stem (Shabala, 2013). Given that EBCs are larger than epidermal cells, they are able to take up a considerable amount of Na^+ away from the photosynthetically active mesophyll cells (Shabala et al., 2014), making it an efficient strategy to confer salinity stress tolerance in halophytes (Ben Hassine et al., 2009). It was long suggested that EBC are essential in maintaining low concentration of Na^+ in leaves and particularly young leaves. Because of small and underdeveloped vacuoles in the mesophyll cells in younger leaves, they do not possess effective internal sequestration mechanisms and rely mainly on EBCs for salt sequestration (Bonales-Alatorre et al., 2013). In our previous work we have shown that a mechanical removal of EBC by gentle brushing results in a salt-sensitive phenotype in quinoa, thus providing the first direct evidence for the role of EBC in salinity tolerance (Kiani-Pouya et al., 2017). However, giving the pioneering nature of that study, many questions remain unanswered. Is EBC density genetically predetermined or can it be adjusted for saline conditions? Will salinity impact EBC cell size (and, hence, volume)? No answers to these questions are available in the literature.

Many unanswered questions are also related to the stomata patterning as a component of the salt tolerance mechanism. Stomata control the gas exchange between plant and its surrounding environment and serve as a primary gateway for transpirational water loss and CO_2 influx in plant (Lawson and Blatt, 2014). As a result of this process, biomass accumulation in plants is directly proportionate to the amount of assimilated CO_2 and eventually is dependent on the regulation of stomatal aperture (Shabala, 2013). Under saline conditions, both osmotic stress and toxic Na^+ level in the cytosol negatively affect stomatal parameters (Tavakkoli et al., 2012). Why are halophytes capable to optimise their stomata performance? Are there any special strategies in stomata operation that halophytes utilise under salinity stress? How does salinity stress regulate epidermal the fate of epidermal cells leading to either an increase or decrease in the stomata numbers?

Significant advances have been made in understanding mechanisms that control stomatal function and also the signaling pathways that regulate guard cells operation in glycophytes (Casson and Hetherington, 2010). Also advanced is our understanding of the basal genetic pathways that regulate stomatal development, specifically in Arabidopsis (Assmann and Jegla, 2016; Bergmann and Sack, 2007; Wang et al., 2007). In contrast, much less is known about stomata operation in halophytes (Hedrich and Shabala, 2018), and a question on how environmental variables and particularly salinity stress modulates the basal stomatal development pathway requires more investigations. In light of this, understanding the genes regulatory network that control stomatal patterning and thus gas exchange under saline condition could be critical to reduce water loss in salinity-grown plants. Additionally, optimised gas exchange would maintain a high photosynthetic rate for better plant performance under saline conditions (Deinlein et al., 2014; Kim et al., 2010).

The ABA hormone is involved in controlling the closing and opening of stomata in response to alteration in plant water balance (Chen and Gallie, 2004). Can stomatal development be also affected by stress-induced ABA increase? An association between stomatal density and ABA levels was shown in tomato (Okuma et al., 2011) and Arabidopsis (Watkins et al., 2017), where the mutants of these two plants which were defective in ABA biosynthesis produced higher stomatal numbers, supporting the above hypothesis.

Reduction in the stomatal conductance may occur via either physiological (e.g. changes in a stomatal aperture) or morphological (e.g. decrease in a stomatal density) pathways. It has been argued that alteration in the stomatal density may represent a primary mechanism by which plant can optimise water-use efficiency under salinity stress (Shabala et al., 2013). A comparison between halophyte *Thellungiella halophila* and its glycophyte counterpart Arabidopsis showed that salinity stress increased stomata density in Thellungiella leaves by about twofold (Inan et al., 2004). These results came in a contrast with the suggestion that reduced stomata density may reduce the residual (cuticular) transpiration through the closed stomata (Hasanuzzaman et al., 2018; Shabala, 2013) and, thus, be advantageous to plants. Thus, the question is: can these results from Thellungiella be extrapolated to all halophytes?

The aim of the current study was to evaluate effects of salinity on EBC and stomata patterning and development in quinoa plants and correlate the extent of variability in these traits with the genetic variation in a salinity stress tolerance amongst the large number of quinoa accessions.

2. Materials and methods

2.1 Plant materials and growth conditions

One hundred and fourteen quinoa accessions were grown from seeds in 15 cm diameter pots filled with standard potting mix under temperature-controlled glasshouse conditions. The standard potting mix was consisted of 90% composted pine bark; 5% coco peat; 5% coarse sand; gypsum at 1 kg/m^3; dolomite at 6 kg/m^3; ferrous sulphate at 1.5 kg/m^3; Osmoform Pre-mix at 1.25 kg/m^3 and controlled-release fertiliser, Scotts Pro at 3 kg/m^3. Day/night temperatures were 20 °C and 15.5 °C; mean humidity 74% and day length 16 h (incandescent lights were set at 6.00 to 9.00 and 16.00 to 22.00 hrs to give the day length hours). The experiment was carried out at the University of Tasmania in Hobart, Australia, between June and August 2017. Ten seeds were sown in each pot and germinating seedlings were then thinned to leave 3 uniform plants per pot a few days before salinity treatment commenced. Seedlings were watered for 14 days with tap water. Salt stress was commenced at 15th day after sowing and 50 mM NaCl was added to the irrigation water twice daily over 4 days to a final concentration of 400 mM. Plants then were maintained under salt stress for six weeks. At harvesting date, one of the youngest fully expanded leaves from the top was taken for scanning electron microscope images.

2.2 Sampling and measurements

For fresh weight (FW) measurements, plants were cut at the base and whole plant immediately weighed. Plants were then dried at 60 °C for 96 hrs to obtain the dry weight (DW).

To quantify the stomata and EBC density of leaves, fresh samples were carefully harvested without causing any damage to the surfaces of one of the youngest fully expanded leaves from 5 individual plants of saline- and non-saline-grown quinoa plants. Leaf sections of 5 x 5 mm were mounted and two images from different leaf zones were taken from the abaxial side of the leaves using scanning electron microscopy (FEI MLA650 ESEM, ThermoFisher Scientific, Oregon, United States) at the environmental mode. A Peltier cooling element maintained the specimen temperature close to 5 °C. Stomatal and EBC density (number of cells per unit of leaf area) was counted from stored SEM images. For those accessions with very high density of bladders, EBCs were removed before images were taken to enable unobstructed view. To determine the EBCs volume we presumed that the EBC is spherical and the volume was calculated based on EBC density per leaf area and EBC diameter. Stomata length and epidermal cell area were measured using the ImageJ analysis software. Stomata and bladder indexes were determined as the ratio of the number of stomata/bladders in a given area divided by the total number of stomata/bladders and epidermal cells in that area. Presented data are the mean ± SE of measurements of 10 different fields of view of the abaxial side of leaves from five individual plants.

Leaf Na^+ and K^+ determinations were conducted from digested leaf samples. One of the youngest fully expanded leaf of plants was harvested and about 0.1 g aliquot of ground dry weight of leaves was used for determination of Na^+ and K^+. Dried leaf samples were mixed with 7 ml of 70% HNO3 and digested in a Teflon digestion vessel using a microwave digester (MDS-2000 microwave digestion system, CEM Corporation). After digestion the solution was transferred to a 15 ml centrifuge tube and topped up with distilled water to a final volume of 15 ml. Then an appropriately diluted solution was used to measure Na^+ and K^+ content using the flame photometer.

2.3 Grouping of accessions for salt tolerance

In order to allow comparisons among accessions, the measurements of plants DW at 400 mM NaCl were divided by their means under non-saline condition to convert to relative values. The relative DW was then considered as a salinity tolerance index (STI) and values were used to group the accessions. All the quinoa accessions were arbitrarily classified into three classes for salinity tolerance index (sensitive, intermediate and tolerant). The class intervals of tolerance classes were defined as the difference between the lowest and the highest relative values of DW divided by three.

2.4 Data analysis

The statistical analysis was carried out by IBM SPSS Statistics 24 software (IBM corp. Armonk, NY, USA). All presented data are mean values of five to ten replicates and accompanied by the standard errors. Significance between different treatments was determined by one-way ANOVA analysis based on Least Significant Distance test. The correlation analyses were applied to determine association between different characteristics under saline condition. To do this, all the studied characteristics measured under saline condition were correlated with STI for each of salt-tolerant, intermediate and sensitive groups.

3. Results

3.1 Salt stress affects physiological characteristics in quinoa

Imposing 400 mM NaCl on quinoa plants significantly impacted all the studied physiological traits, revealing a large variation among accessions for all characteristics. The mean individual results of physiological characteristics are shown in the Supplementary Table S1. Salinity stress caused a significant reduction in fresh weight (FW) and dry weight (DW) of all accessions. The FW ranged from 1.36 to 8.25 g plant^{-1} under non-saline condition, and was significantly reduced under saline condition, where the FW varied from 0.62 to 2.92 g plant^{-1} (Suppl Table S1). In relative terms, FW of salt-grown plants were declined between 4% and 87% (Suppl Table S1). Similar to FW, all the accessions had the highest DW under non-saline condition, ranging from 0.14 to 0.75 g plant^{-1} (Suppl Table S1). DW significantly decreased under saline condition and ranged from 0.06 to 0.31 g plant^{-1}, showing relative variation between 7% and 84% (Fig. 1A-C and Suppl Table S1). Collectively, these results indicate a strong genetic variation for salinity tolerance among quinoa accessions.

With an exception of a few accessions, salinity stress significantly increased bladder density in all the quinoa plants and at a maximum amount it increased by more than 3.5-fold (Suppl Table S1). The regression analysis revealed no association between salinity tolerance index (STI) and bladder density for salt-tolerant, intermediate and sensitive groups (Suppl Fig. S1A-C). Bladder diameter remained unchanged in the majority of accessions under saline condition; however, it slightly increased or decreased in a few accessions (Suppl Table S1). In a salt-tolerant group, there was a significant association between STI and a bladder diameter under saline condition while there was not such a relation for intermediate and sensitive groups (Fig. 2). EBC volume, as a dependant variable of bladder density and diameter, had a great variation among accessions and ranged from 41% to 339% in relative terms (Suppl Table S1). Ina salt-tolerant group, there was a significant positive correlation between STI and bladder volume under saline condition, while in intermediate and sensitive groups there was no association between these parameters (Fig. 2). Accessions also showed a great variation for the bladder index, which ranged from 64% to 291% in relative terms (Suppl Table S1). There was no significant association between STI and the bladder index for all three groups (Suppl Fig. S1D-F).

Salinity stress also significantly affected stomata characteristics. On average for all accessions, stomata density remained unchanged between saline and non-saline conditions.

However, a large genetic variability was found for the stomata density amongst accessions, ranging from 67% to 159% in relative terms (Suppl Table S1; Suppl Fig. S2A, B), with some genotypes increasing and some decreasing stomata density. The regression analysis showed a significant positive correlation between STI and stomata density in a salt-tolerant group (Fig. 3).

However, the relative length of stomata declined by 3% to 43% in salt-grown plants (Suppl Table S1; Suppl Fig. 3A). This implies that quinoa plants manage to reduce stomatal gas exchange under saline condition by minimising the size of the pore. Salt-tolerant plants had a negative correlation between STI and stomatal length under saline condition while no association between these parameters was found in intermediate and sensitive groups (Fig. 3D-F). Relative changes in stomatal index ranged from 53% to 118% among accessions (Suppl Table S1; Suppl Fig. 3B) and there was no significant association between STI and stomata index in any group (Suppl Fig. 4A-C).

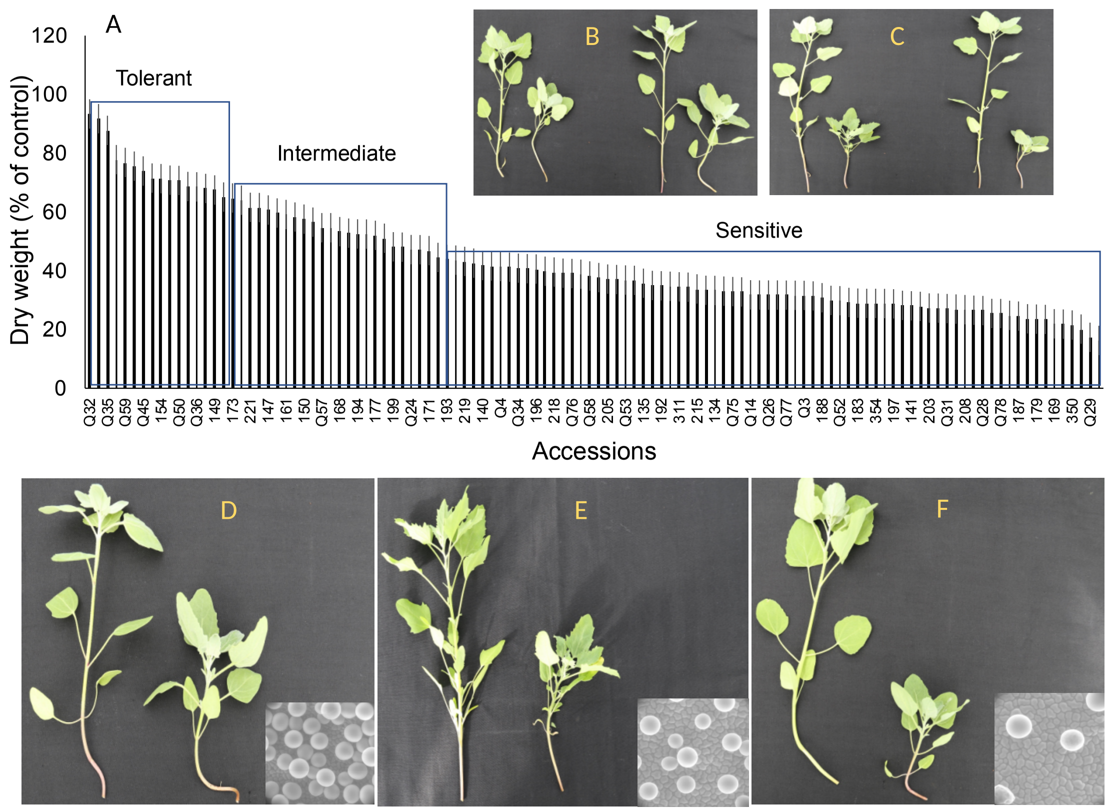

Figure 1- Genetic variability of salinity tolerance in quinoa. A - salinity tolerance index defined as a relative dry weight of studied accession (% of control). Based on this result, all accessions were classified into three major groups including tolerant, intermediate and sensitive groups according to their performance under 400 mM NaCl. B, C - representative images of salt-tolerant and salt-sensitive accessions, respectively; D to F – images of representative plants from salt-tolerant(D), intermediate (E), and salt-sensitive (F) groups grown under non-saline and 400 mM NaCl conditions. The insets are scanning electron microscope images of leaf surface showing bladder density in plant of each group.

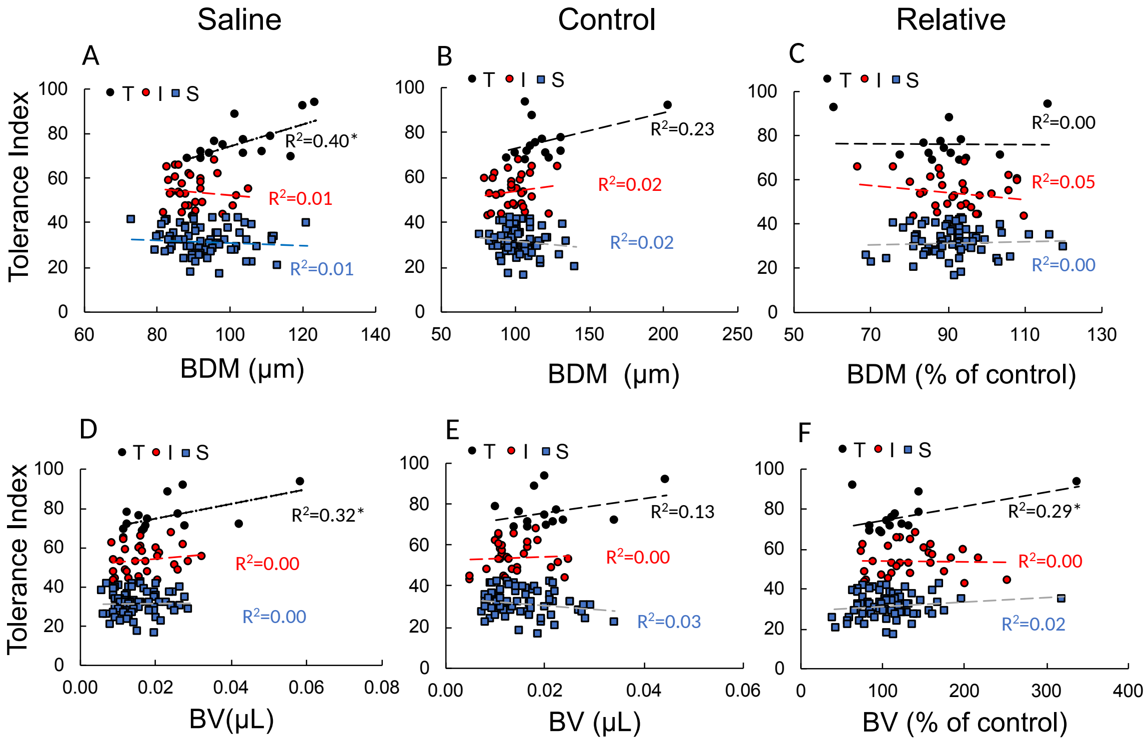

Figure 2- Regression analysis (1) between salinity tolerance index (STI; defined as a relative dry weight) and bladder diameter, and (2) between STI and bladder volume. A, D – saline conditions; B, E – control conditions; C, F – relative change (% control). BDM, bladder cell diameter; BV, bladder cell volume. T, I and S letters in the figures stay for salt-tolerant, intermediate and sensitive groups. Each point represents one accession (a mean of 10 replications).

In respect to epidermal cell area (ECA), quinoa accessions responded differently to salt stress where ECA either declined or increased under saline condition so the relative change varied between 40% and 123% among accessions (Suppl Table S1; Suppl Fig. S2C, D).

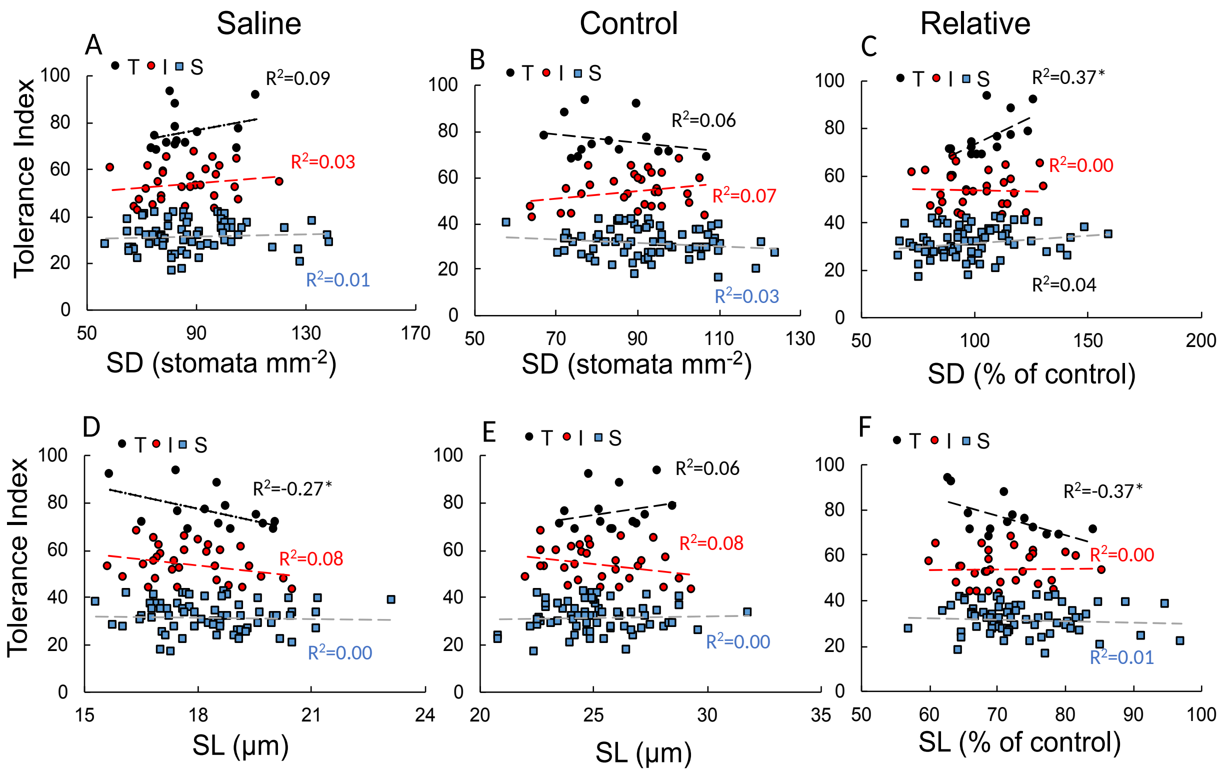

Figure 3- Regression analysis (1) between STI and stomatal density, and (2) between STI and stomatal length. A, D – saline conditions; B, E – control conditions; C, F – relative change (% control). SD, stomatal density; SL, stomatal length. T, I and S letters in the figures stay for salt-tolerant, intermediate and sensitive groups. Each point represents one accession (a mean of 10 replications).

Salinity stress caused a significant increase in leaf Na^+ concentration, with Na^+ content varying between 669 µmol/gDW and 3155 µmol/gDW amongst accessions under saline condition (Suppl Table S1). This result indicates significant genetic variation in quinoa's ability for Na^+ uptake (Suppl Table S1; Suppl Fig. 3C). With an exception of a few accessions, plants grown under saline condition showed higher K^+ content in their leaves compared with non-saline condition (Suppl Table S1; Suppl Fig. 3D). The K^+ concentration ranged from 89% to 258% in accessions grown under 400 mM salinity stress indicating that K^+ uptake was stimulated under saline condition.

3.2 Correlation analysis

All the accessions were assigned to three distinct classes based on the relative DW that defined as salinity tolerance indexes (STI). The major bulk of genotypes (70 accessions) was classified as salt-sensitive, while 30 and 14 accessions were categorised as intermediate and salt-tolerant, respectively. The STI of these three groups were considered as dependent variables and correlated with measured physiological characteristics under 400 mM NaCl (Tables 1-3).

In the salt-tolerant group, there was a significant correlation between the EBC dimeter and STI (R^2= 0.63; P < 0.05) and also between STI and the bladder volume, indicating that the larger EBCs played a positive role in salinity tolerance (Table 1). In salt-sensitive plants on the other hand, there was a negative correlation between STI and leaf Na^+ concentration (R^2= -0.29; P < 0.05) (Table 3). This may imply a compromised Na^+ sequestration ability (to move away Na^+ from the photosynthetic active leaves) and, thus, a negative impact on a biomass production. In this regard, in a salt-sensitive group there was a strong negative correlation between bladder density and diameter (R^2 = -0.40; P < 0.01). Taking into account the positive relation between bladder density and bladder index (R^2 = 0.68; P < 0.01) it could be suggested that in salt-sensitive plants higher bladder density resulted in smaller bladders (Table 3). Also, there was no significant association between STI and a bladder volume or density in a salt-sensitive group. Instead, results revealed that increasing bladder density had a negative correlation with the bladder diameter and stomatal index (Table 3).

While there was a very significant positive correlation (R^2 = 0.73; P < 0.01) between EBC index and a stomata index in a salt-tolerant group (Table 1), these two parameters were negatively correlated (R^2 = -0.32; P < 0.01) in a salt-sensitive group (Table 3). The simultaneous increase in the bladder and stomata cells density in a salt-tolerant group was achieved through reducing the epidermal cell size (Suppl. Fig. S2).

Table 1- Correlation between physiological characteristics and salinity tolerance index (relative dry weights) in a salt-tolerant cluster under saline condition

	STI	FW	BD	BDM	BV	BI	SD	SL	SI	ECA	Na^+	K^+
STI	1											
FW	0.79**	1										
BD	0.17	0.46	1									
BDM	0.63*	0.5	0.1	1								
BV	0.57*	0.70**	0.80**	0.65*	1							
BI	-0.25	0.11	0.41	0.55*	-0.03	1						
SD	0.3	-0.08	-0.31	0.54*	0.06	-0.40	1					
SL	-0.55*	-0.21	0.15	-0.05	-0.02	0.26	-0.26	1				
SI	-0.34	0.001	0.23	-0.42	-0.06	0.73**	-0.04	0.18	1			
ECA	-0.29	0.07	-0.005	-0.41	-0.19	0.37	0.71**	0.05	0.26	1		
Na^+	0.10	0.06	0.05	0.02	0.12	0.06	0.01	-0.17	0.21	0.32	1	
K^+	0.40	0.34	0.2	0.29	0.3	0.08	0.42	-0.28	0.02	-0.34	0.09	1

Abbreviations:

STI: relative dry weight (% of control); FW: relative fresh weight (% of control); BD: bladder density (cell mm^{-2}); BDM: bladder diameter (µm); BV: bladder volume (µl); BI: bladder index; SD: stomatal density (cell mm^{-2}); SL: stomatal length (µm); ECA: epidermal cell area ($µm^2$); Na^+: leaf Na^+ concentration (µmol/gDW); K^+: leaf K^+ concentration (µmol/gDW).

Table 2- Correlation between physiological characteristics and salinity tolerance index in plants from the intermediate cluster under saline condition

	STI	FW	BD	BDM	BV	BI	SD	SL	SI	ECA	Na^+	K^+
STI	1											
FW	0.64**	1										
BD	0.11	0.32	1									
BDM	-0.11	-0.18	0.15	1								
BV	0.15	0.19	0.82**	0.61**	1							
BI	0.23	0.39*	0.64**	0.28	0.64**	1						
SD	0.18	0.15	0.48**	-0.12	0.39	-0.132	1					
SL	-0.29	-0.28	-0.60**	-0.11	-0.59**	-0.125	-0.67**	1				
SI	0.001	0.42*	-0.06	0.02	-0.08	0.14	-0.008	0.04	1			
ECA	-0.17	-0.12	-0.59**	0.18	-0.42*	0.07	-0.84**	0.76**	0.31	1		
Na^+	-0.05	0.2	-0.1	0.04	-0.004	-0.018	-0.24	0.06	0.20	0.13	1	
K^+	0.02	0.09	0.09	-0.27	-0.171	0.21	-0.07	0.05	-0.02	0.06	-0.37*	1

Abbreviations:

STI: relative dry weight (% of control); FW: relative fresh weight (% of control); BD: bladder density (cell mm^{-2}); BDM: bladder diameter (μm); BV: bladder volume (μl); BI: bladder index; SD: stomatal density (cell mm^{-2}); SL: stomatal length (μm); ECA: epidermal cell area ($μm^2$); Na^+: leaf Na^+ concentration (μmol/gDW); K^+: leaf K^+ concentration (μmol/gDW).

Table 3- Correlation between physiological characteristics and salinity tolerance index in plants from salt-sensitive cluster under saline condition

	STI	FW	BD	BDM	BV	BI	SD	SL	SI	ECA	Na^+	K^+
STI	1											
FW	0.80**	1										
BD	0.09	0.25*	1									
BDM	-0.09	-0.08	-0.40**	1								
BV	0.07	0.22	0.68**	0.31**	1							
BI	-0.04	0.21	0.68**	-0.41**	0.46**	1						
SD	0.07	0.04	0.08	0.14	0.09	-0.38**	1					
SL	-0.04	-0.11	-0.45**	0.35**	-0.24*	-0.28*	-0.30*	1				
SI	-0.15	-0.08	-0.34**	0.38**	-0.14	-0.32**	0.48**	0.24*	1			
ECA	-0.18	-0.13	-0.59**	0.17	-0.40**	-0.01	-0.64**	0.59**	0.17	1		
Na^+	-0.29*	-0.01	0.11	-0.14	0.13	0.40**	-0.41**	-0.11	-0.19	0.27*	1	
K^+	-0.14	-0.13	0.08	-0.13	-0.05	0.06	0.05	-0.18	-0.10	-0.14	-0.14	1

Abbreviations:

STI: relative dry weight (% of control); FW: relative fresh weight (% of control); BD: bladder density (cell mm^{-2}); BDM: bladder diameter (µm); BV: bladder volume (µl); BI: bladder index; SD: stomatal density (cell mm^{-2}); SL: stomatal length (µm); ECA: epidermal cell area (μm^2); Na^+: leaf Na^+ concentration (µmol/gDW); K^+: leaf K^+ concentration (µmol/gDW).

A significant negative correlation between ECA and the bladder density was reported for the intermediate (R^2= -0.58; $P < 0.01$) and sensitive (R^2= -0.59; $P < 0.01$) clusters while no such correlation was found in the salt-tolerant group (Table 1-3).

A negative correlation between bladder index and stomatal parameters (stomatal density (R^2 = -0.38; $P < 0.01$), stomatal length (R^2 = -0.28; $P < 0.05$) and stomatal index (R^2 = -0.32; $P < 0.01$)) were also found in salt-sensitive plants. This data suggests that the increasing bladder density affected stomatal characteristics which in turn finally affected plant performance under saline conditions (Table 3).

4. Discussion

4.1 EBCs played an important role in salinity tolerance in quinoa

In a salt-tolerant group, the significant positive correlations between bladder diameter and STI in one hand and bladder volume and STI on the other hand (Table 1) indicate that higher external Na^+ sequestration capacity conferred by the larger bladder volume played a positive role in salinity tolerance in quinoa. The mechanistic basis for this is an increased capacity for compartmentalisation of significant amounts of toxic Na^+ in EBCs, as shown before in *Mesembryanthemum crystallinum* L. (Barkla et al., 2018) and quinoa, where bladderless plant possessed a salt-sensitive phenotype (Kiani-Pouya et al., 2017).

To better understand the contribution of EBCs towards salinity tolerance in quinoa, we have further selected 5 accessions with the highest and lowest bladder volume grown under 400 mM NaCl for detailed analysis (Fig. 4A-F). Plants with higher EBC volume had a significantly higher DW, bladder density, and bladder diameter than a group with low bladder volume (Fig. 4B-D). Also, plants with high EBC volume had about 5.5 times more EBC sequestration capacity compared to plants with low EBC volume (Table 4) indicating that tolerant plants had higher external Na^+ storage on their leaves where EBC act as a major sink for the toxic ions such as Na^+ and Cl^-. Using measured volumes of EBC (Table 4) and assuming that the thickness of leaf lamina is about 120 µm, the corresponding volume of the leaf lamina was about 0.12 µl. Thus, in accessions with a high bladder volume, about 40% of the total aerial volume was represented by EBCs while this value for plants with low EBC volume was about 10%. This 4-fold difference resulted in EBCs making a significant contribution towards the total aerial volume in salt-tolerant plants (Table 4) and therefore, provided them with a storage capacity for toxic Na^+ and Cl^-. In line with this, we have already calculated that Na^+ and Cl^- concentrations of quinoa EBC could be estimated around 850 mM and 1 M, respectively (Kiani-Pouya et al., 2017). Given that plants with high EBC volume had the same Na^+ concentration in their leaves as plants with a low EBC volume (Fig. 4F) and the fact that plant with high EBC volume had higher salt tolerance, it could be speculated that the majority of toxic Na^+ may be transported into the EBCs thus conferring the salinity tolerance of this group.

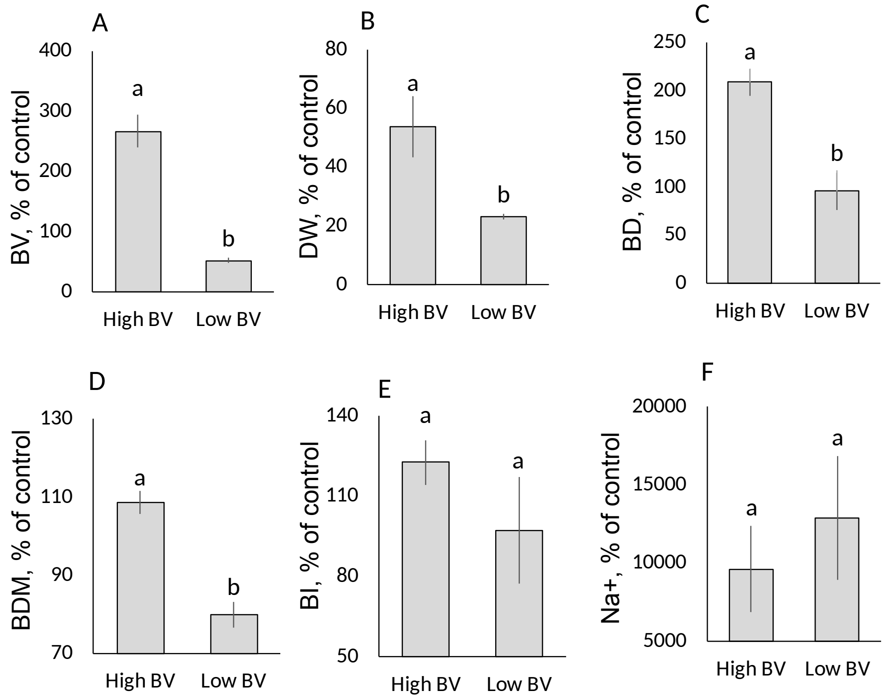

Figure 4- Physiological characteristics of five quinoa accessions grouped based on the highest and lowest bladder volume. Bars show the average pooled data of five quinoa accessions. A - bladder volume, BV; B - dry weight, DW; C - bladder density, BD; D - bladder diameter, BDM; E - bladder index, BI; F - Na^+ concentration. The chosen accessions with higher BV were Q32, 195, 193, Q57, 127 and those with lower BV were Q5, 144, Q65, Q79, and 157. Mean ± SE (n = 5; 25 replications in total). Data labelled with different lower-case letters are significantly different at $P < 0.05$.

The bladder diameter had a major contribution towards salinity tolerance in quinoa; hence, increasing the size and quantity of EBCs may be beneficial to improving salinity tolerance through compartmentalization of Na^+ into EBCs. There is not much information on the mechanisms controlling EBC size in quinoa. Studies on Arabidopsis (Churchman et al., 2006) and *M. crystallinum* L. (Barkla et al., 2018) showed that, to a large extent, the trichome size is determined by the number of endoreduplications. It has also been revealed in *M. crystallinum* that salinity stress induced endopolyploidy in EBCs and leaves of this plant, with one or two additional rounds of endoreduplication occurring in salt-grown plants (Barkla et al., 2018). This increase in a cell size may contribute to salinity tolerance through increasing the external store volume for Na^+ sequestration. Endopolyploidy involves the tight control of molecular mechanisms that initiate and then maintain endoreplication in the cell, allowing endocycling cells to replicate their DNA during the synthesis (S) phase but arresting progress to the mitosis phase, cycling instead between the S and gap (G) phases (Barkla et al., 2018). Cyclin-dependent kinases (CDKs), a conserved class of serine/threonine kinases, along with their regulatory subunit cyclins (CYCs) drive unidirectional and irreversible progression from one cell cycle phase to the next by phosphorylating target proteins (Kumar and Larkin, 2017). If similar mechanisms are involved in quinoa, they could be exploited to modify the bladder size through manipulating one or a few genes associated with cyclin production, to further improve external Na^+ storage capacity by controlling EBC size.

Table 4- Bladder-related information of five quinoa accessions grouped based on the highest and lowest bladder volume when grown under 400 mM NaCl conditions. It was assumed that the thickness of leaf lamina was about 120 µm. Mean ± SE (n = 5). *Significant and P< 0.01.

	Bladder density (EBC mm^{-2})	Bladder diameter (µm)	Bladder volume on both sides (µL)	% of total aerial volume
High EBC volume	66±5.9 *	104±4.1 *	0.077±0.01 *	38.2±3.24 *
Low EBC volume	16.9±1.8	90.3±0.8	0.014±0.001	10.5±0.51

4.2 Salt-sensitive plants failed to coordinate bladder size and density

The superior performance of plants under saline condition depends on numerous anatomical and physiological mechanisms (Ozgur et al., 2013; Shabala and Mackay, 2011). The cell elongation declines under saline conditions, first because of osmotic stress and then due to Na^+ build up (Munns and Tester, 2008; Zhu, 2002). Salt-sensitive plants showed a negative correlation between the bladder density and bladder diameter (Table 3). Given that EBCs play an important role in salinity tolerance in quinoa, the failure of this group to produce larger bladder cells resulted in a salt-sensitive phenotype. As it has been discussed in the previous section, this may be potentially explained by the number of endoreduplications occurring in salt-sensitive and tolerant groups.

Not much is known about the molecular mechanisms of EBCs patterning and formation in quinoa but based on the existing knowledge in Arabidopsis, the trichome formation is the result of an interaction between neighbouring epidermal cells (Glover, 2000; Larkin et al., 1996). This process is regulated by a number of positive and negative regulators such as GLABRA1 and R2R3 MYB transcription factors (Pesch and Hulskamp, 2009) and is also under hormonal control.

On the contrary to the salt-sensitive group, salt-tolerant plants were able to concurrently keep constant density of both stomata and bladder cells under saline condition, mainly through reducing ECA (Table 1). The relation between decreasing ECA and salinity tolerance was further confirmed by analysis of 5 accessions with the highest and lowest ECA (Fig. 5A-H). As the relative ECA of group with highest area was increased to 119%, the ECA of group with the lowest was markedly reduced to 49.2% (Fig. 5A). Plants with a larger cell area significantly had less DW and bladder volume, bladder and stomata densities (Fig. 5B, C, E, F). This finding indicates that ECA had an association with all the important salt-responsive characteristics and thus could be considered as an important salt-responsive characteristic in quinoa. For instance, lower ECA resulted in higher bladder and stomata densities which correlated positively with biomass production. Furthermore, the group with bigger ECA also had bigger stomata length and higher leaf Na^+ concentration; as both play a negative role in salinity tolerance, they likely contributed to the salt-sensitive phenotype (Fig. 5G-H; Suppl. Fig. S5).

An increase in the stomata density was associated with a decrease in ECA (Fig. 5F). This strategy was rather different from those reported for other halophytes. For instance, it has been reported that stomatal density reduced under hypersaline condition in *Atriplex halimus* (Boughalleb et al., 2009), *Kochia prostrata* (Karimi et al., 2005) and *Suaeda maritima* (Flowers and Colmer, 2008). The reasons for this discrepancy should be a subject of a separate investigation.

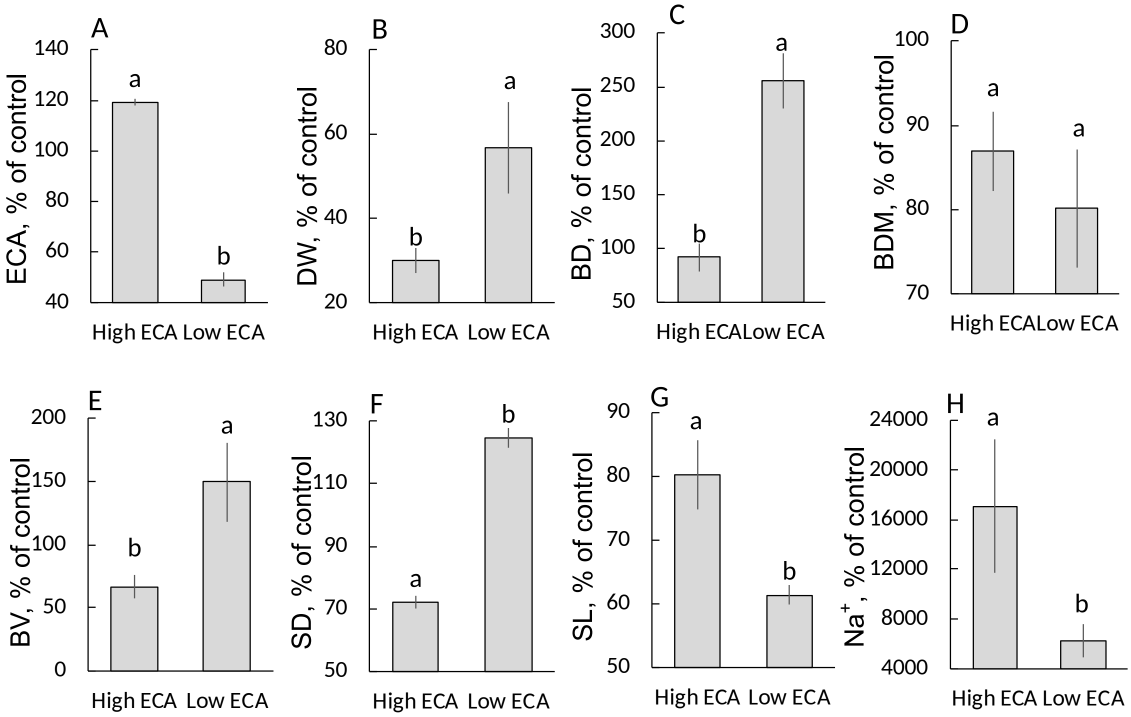

Figure 5- Physiological characteristics of five quinoa accessions grouped based on the highest and lowest epidermal cell area. Bars show the average pooled data of five quinoa accessions. A - epidermal cell area, ECA; B - dry weight; C - bladder density, BD; D - bladder diameter, BDM; E - bladder volume, BV; F - stomata density, SD; G - Stomata length, SL; H - Na^+ concentration. The chosen accessions with higher ECA were 155, 146, 188, 157, Q65 and those with lower ECA were 193, Q68, 217, 208, and 173. Mean ± SE (n = 5; 25 replications in total). Data labelled with different lower-case letters are significantly different at $P < 0.05$.

4.3 Salt-tolerant plants effectively coordinate stomata length and density

Stomatal transpiration accounts for about 95% of the total water loss (Hedrich and Shabala, 2018) playing a significant role in water use efficiency in plants. Transpirational water loss through stomata are controlled by stomata parameters such as density, structure and aperture (Hetherington and Woodward, 2003) and the results of this investigation revealed that quinoa plants regulate this process through stomata length but not by stomata density. Indeed, while stomata density was not altered under either saline and non-saline conditions, stomata length (as a proxy for stomata aperture) declined on average by 30% in all accessions.

Salt-tolerant plants, however, employed a different strategy. The negative correlation between STI and stomata length in the salt-tolerant group means that tolerant plants reduced guard cell aperture as a strategy to manage their water loss (Table 1). However, this mechanism has a cost for plants, as reduction in the stomatal conductance results in a reduction of photosynthetic rate and thereby decreasing plant biomass production that eventually leads to yield loss (Centritto et al., 2003). A further analysis revealed that salt-tolerant quinoa plants were able to increase stomata density as a compensation mechanism for reduced stomata length (Fig. 6D). As a result of this strategy, the gas exchange was efficiently controlled in a way that it balanced leaf water loss and CO_2 assimilation under saline condition enabling plants to better deal with salt stress. Analysis of 5 accessions with the highest and lowest stomatal length revealed that the group with the smaller stomata length had significantly higher DW, bladder and stomatal densities (Fig. 6B-D) indicating that smaller guard cell aperture is compensated by the higher stomata density. Reducing ECA was a primary reason of the increased of other cell types densities e.g. bladder or stomata. In this regard, while ECA increased by 8% in plants with high stomatal length, the cell area decreased by 46% in group with smaller stomata length (Fig. 5E).

The stomatal lineage is dynamic and flexible, altering stomatal production in response to environmental change, with numerous transcriptional regulators, cell-to-cell signaling and polarity proteins involved (Adrian et al., 2015; Lee and Bergmann, 2019). Like our knowledge of EBCs development, all available information comes from studies on Arabidopsis. Comparing transcriptional profiles of the above key genes between contrasting quinoa accessions may be an important step for targeting stomatal density as a salinity tolerance strategy in plant breeding programs.

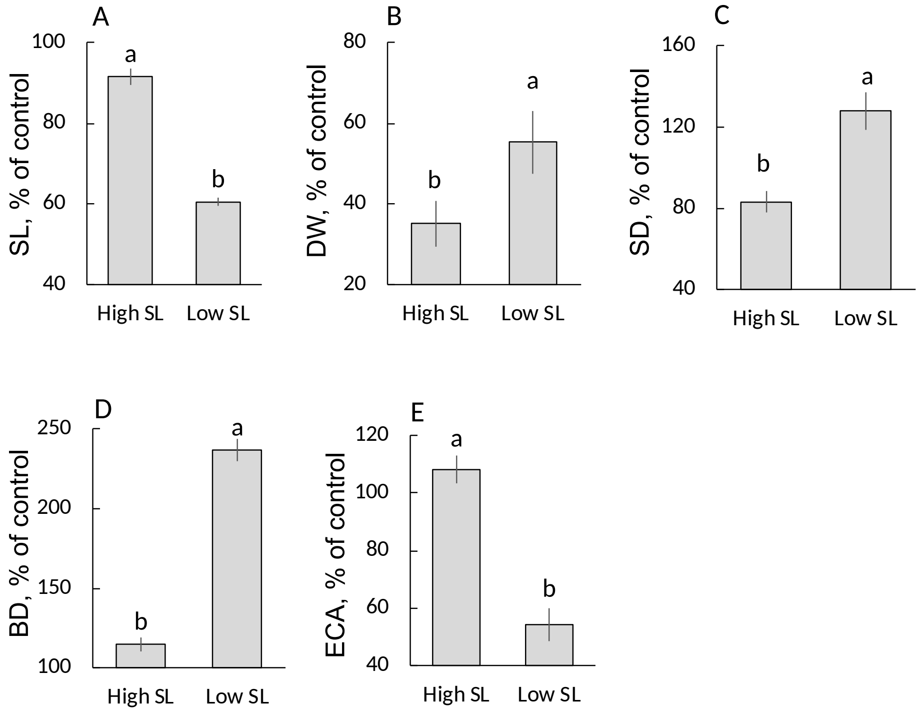

Figure 6- Physiological characteristics of five quinoa accessions grouped based on the highest and lowest stomata length. Bars show the average pooled data of five quinoa accessions. A - Stomata length, SL; B - dry weight, DW; C - stomata density, SD; D - bladder density, BD; E - epidermal cell area, ECA. The chosen accessions with higher SL were Q65, Q58, Q54, 146, 178 and those with lower SL were Q32, 136, 173, 217, and 208. Mean ± SE (n = 5; 25 replications in total). Data labelled with different lower-case letters are significantly different at $P < 0.05$.

4.4 Na^+ adversely affected salt-sensitive plants

It has been argued that prevention of Na^+ delivery to the leaves, and particularly young leaves, is a fundamental characteristic of Na^+ sequestration at the whole-plant level in different plant species (Munns, 2002). However, in addition to this general characteristic, halophytes are able to effectively compartmentalise Na^+ into vacuoles to prevent the toxic effects of Na^+ (Flowers and Colmer, 2008). Both salt-sensitive and salt-tolerant groups had the same leaf Na^+ concentration (on average 1649 µmol/gDW and 1700 µmol/gDW in salt-sensitive and tolerant group, respectively) suggesting that the ability of salt-tolerant and sensitive plants in preventing Na^+ entry to the shoot was the same. Also, there was a negative relation between leaf Na^+ concentration and STI in salt-sensitive plants (Table 3), which suggests that this group could not cope with high concentration of Na^+ that resulted in a lower biomass production (Table 3). Given that Na^+ sequestration into EBCs is one of the most important mechanisms for salinity tolerance in quinoa, this result further confirms the role of EBCs as salt dumpers for the sequestration of toxic ions away from the cytosol.

5. Conclusion

The findings of the current study revealed that in salt-tolerant quinoa genotypes a combination of higher bladder density and larger EBCs resulted in a higher EBC volume, increasing plant's external capacity for storage of toxic Na^+ and Cl^-. This result shows the important role of EBC in salinity tolerance in quinoa. Furthermore, although salt-tolerant plants had a negative association between STI and stomata length, they were also able to increase stomata density as a compensation strategy for the reduced stomata size. This mechanism indicates the superior ability of salt tolerant plants in regulating stomatal patterning to efficiently balance water loss and CO_2 assimilation under saline conditions.

Conflict of interest

The authors declare that they have no conflict of interest

Author contributions

AKP carried out the research, data analysis and wrote the manuscript. FR contributed to elements analysis and taking the image using ESEM. NB contributed to image analyses. HZ and RH contributed to analysing the data and reviewed the manuscript. SS designed the experiment, contributed to data analysis, and wrote the manuscript. All authors read and approved the manuscript.

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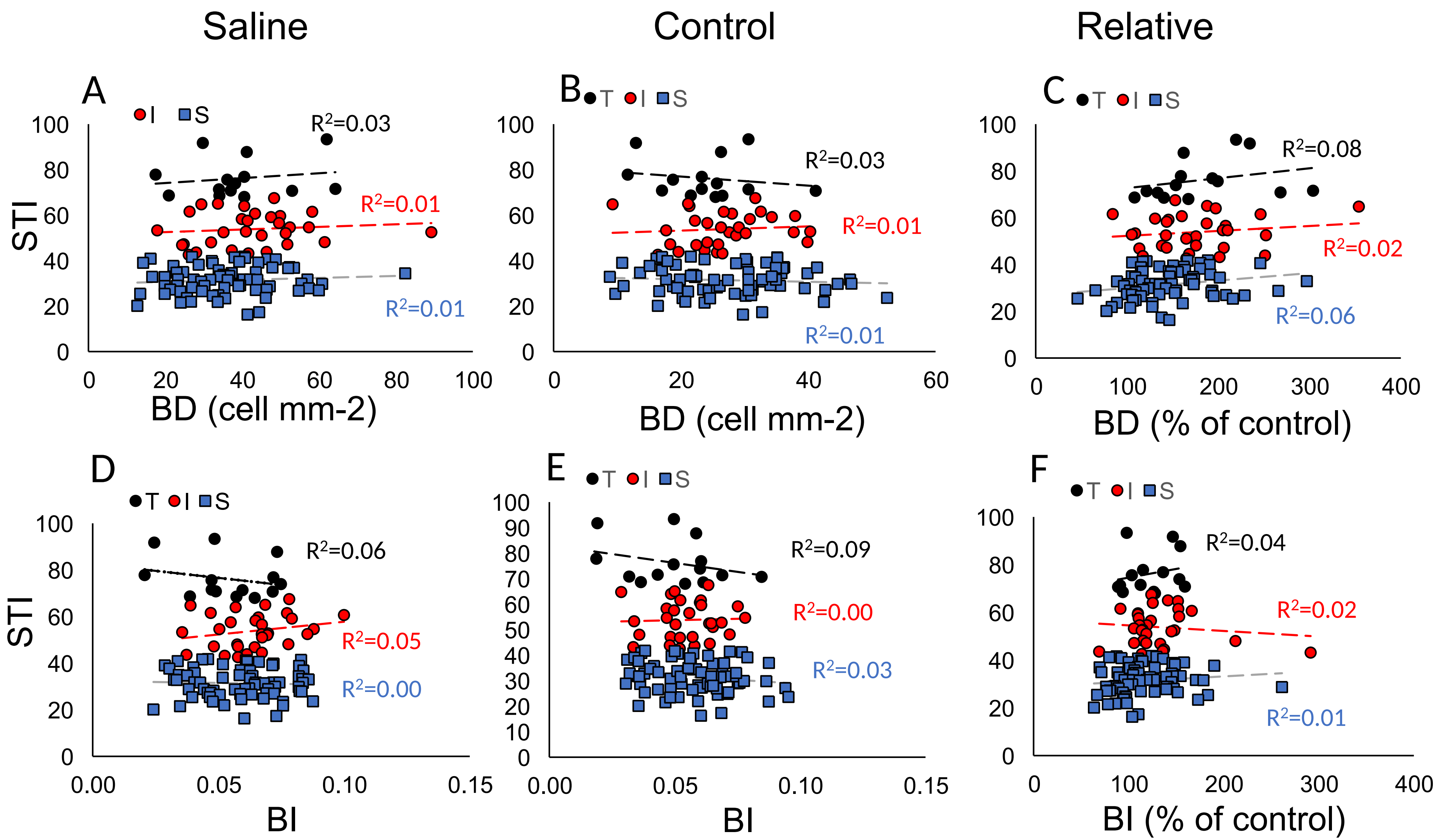
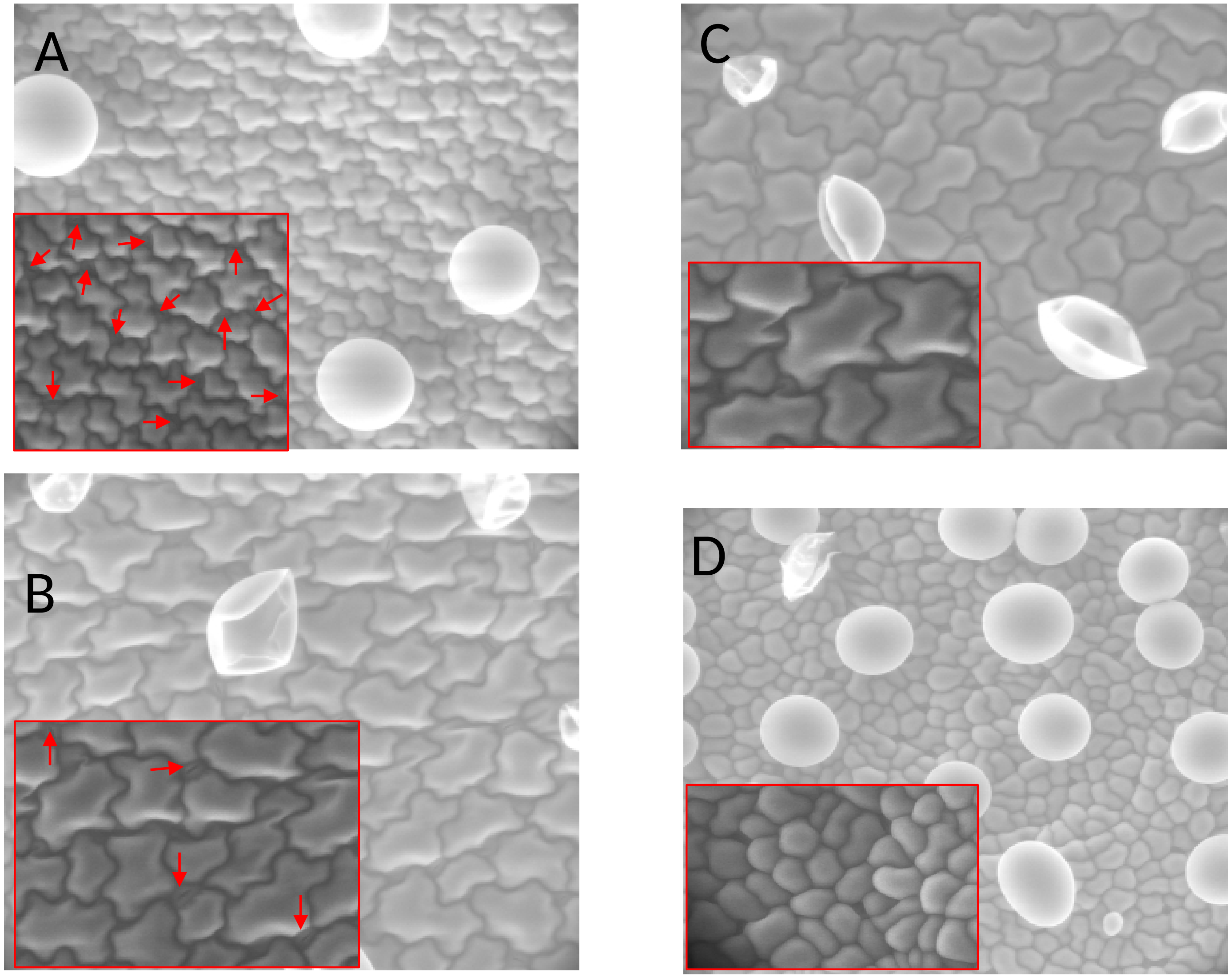
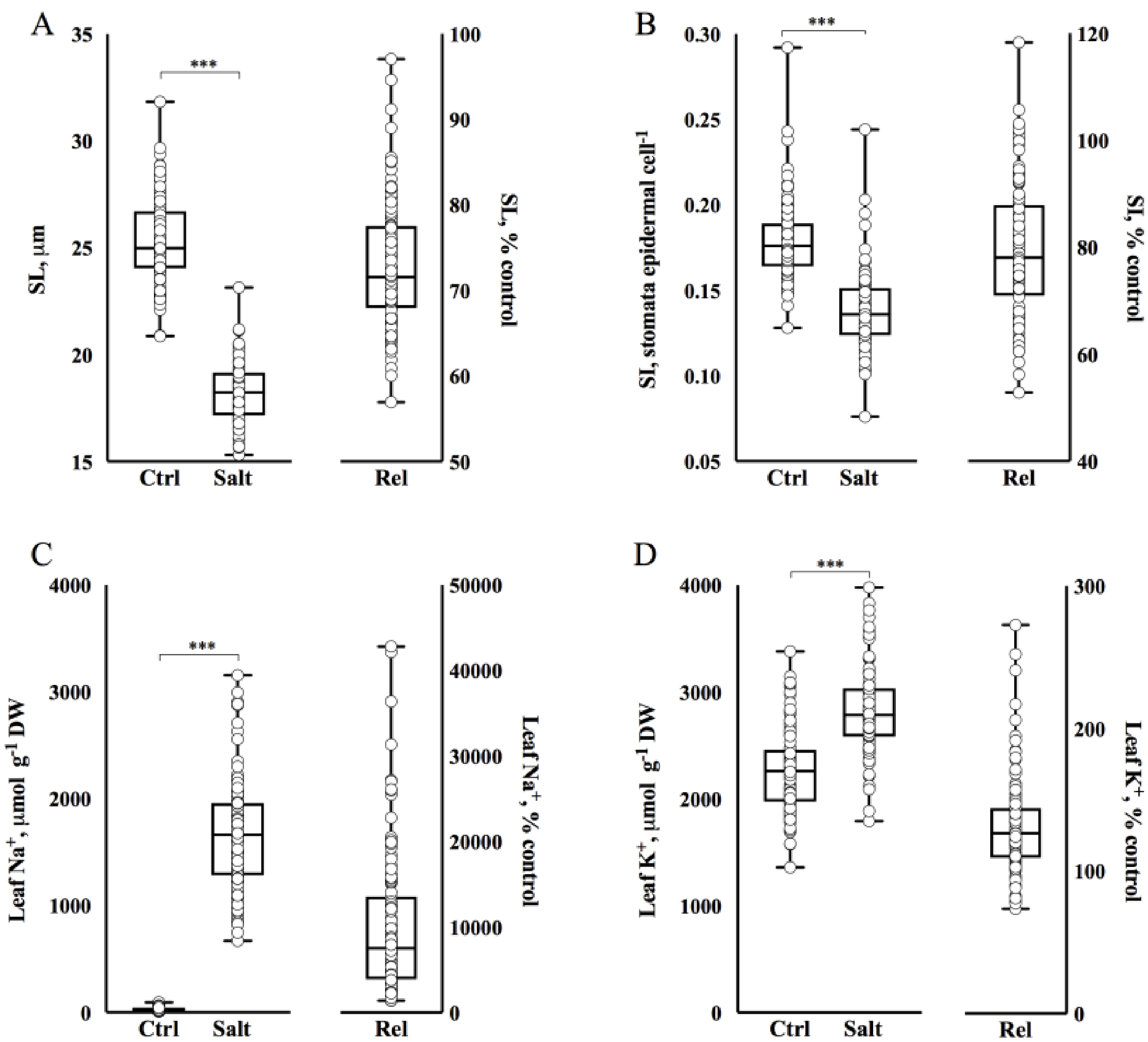


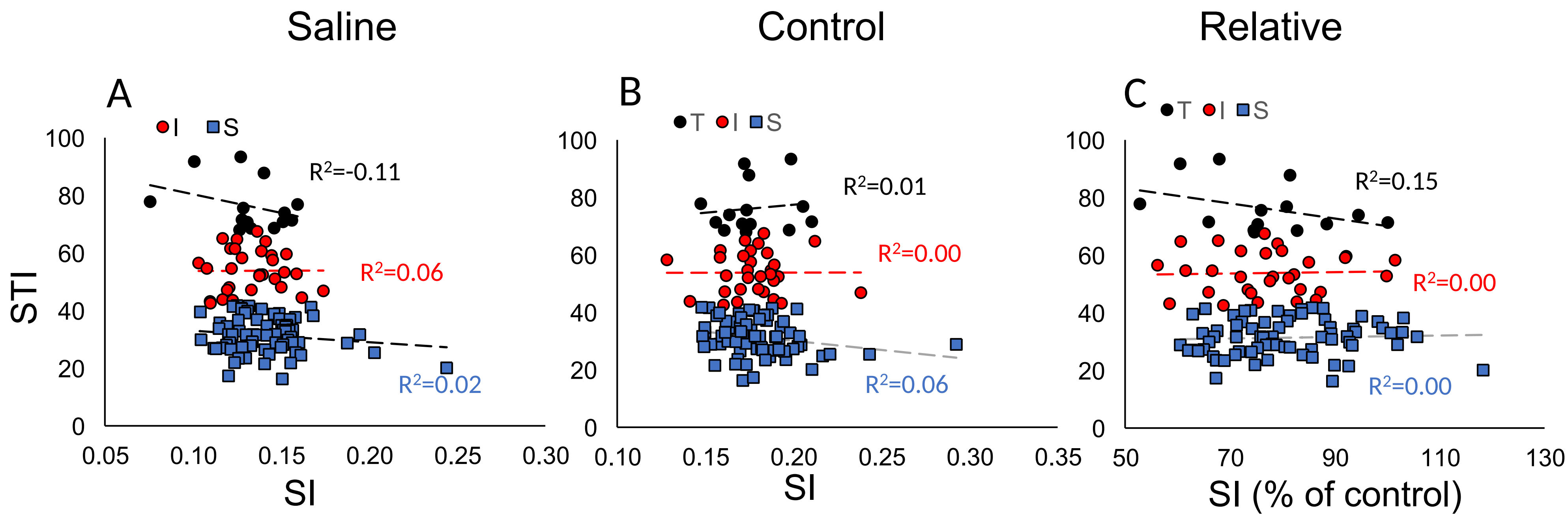
Supplementary Fig. S1- Regression analysis (1) between salinity tolerance index and bladder density, and (2) between STI and bladder index. A, D – saline conditions; B, E – control conditions; C, F – relative change (% control). BD, bladder density; BI, bladder index. T, I and S letters in the figures stay for salt-tolerant, intermediate and sensitive groups. Each point represents one accession which is a mean of 10 replications.



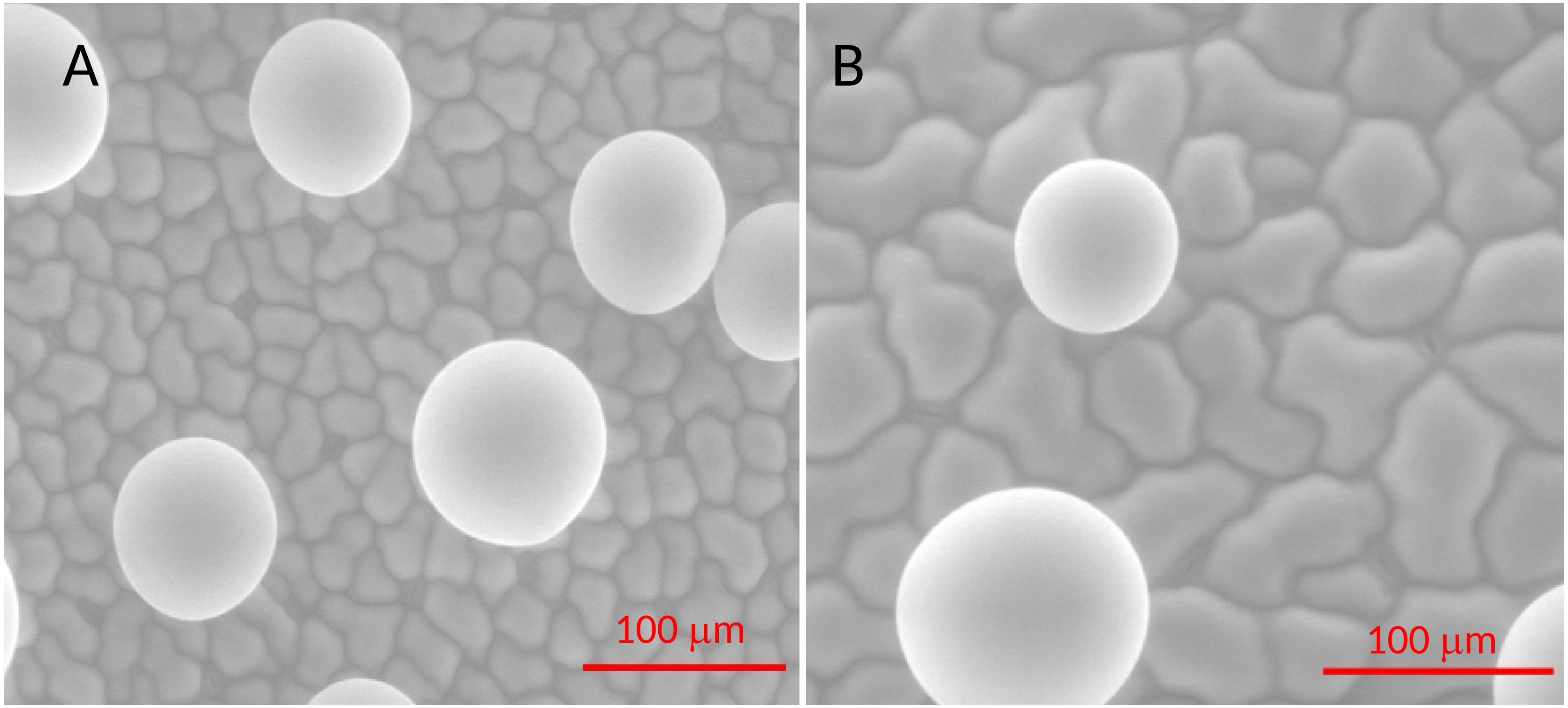
Supplementary Fig. S2- Scanning electron microscope images of leaf surface of a plant with A) high stomata density (accession 197); B) low stomata density (accession 141) under saline condition (The red arrows in the inset show stomata in an area of 0.063 mm^2 of the image); C) images of leaf surface of a plant with high epidermal cell area (accession Q28) and D) low epidermal cell area (accession 208) under saline condition (The inset show epidermal cells in an area of 0.026 mm^2 of the image).



Supplementary Fig. S3- Genetic variation in stomatal characteristics and Na^+ and K^+ concentrations in leaves. A - stomatal length, SL; B - stomatal index, SI; C – leaf Na^+ ; D – leaf K^+ . Each dot in the box plot representing a mean value of a single accession under control (Ctrl), saline (Salt) and in relative term (Rel). The middle line in the box plot denotes the median. *** shows significant difference ($P < 0.001$)



Supplementary Fig. S4- Regression analysis between salinity tolerance index and bladder index. A – saline conditions; B – control conditions; C – relative change (% control). SI, stomata index. T, I and S letters in the figures stay for salt-tolerant, intermediate and sensitive groups. Each point represents one accession which is a mean of 10 replications.



Supplementary Fig. S5- Scanning electron microscope images of the leaf surface of a plant with (A) low epidermal cell area and smaller stomatal length (accession 208) and (B) high epidermal cell area and bigger stomatal length (accession Q28) under saline condition

Table 1s- Mean values of all physiological characteristics under non-saline and saline conditions with corresponding relative values

Accession		FW	DW	BD	BDM	BV	BI	SD	SL	SI	ECA	Na^+	K^+
127	Ctrl	4.3±0.13	0.35±0.014	16.4±0.9	82.7±4.8	0.005±0.001	0.052±0.005	64.2±3.6	29.4±1.3	0.16±0.005	2094±224	63±2	3049±301
	Salt	1.2±0.01	0.15±0.003	26.1±1.5	89.9±3.2	0.009±0.001	0.058±0.008	69.2±3.4	20.5±0.4	0.11±0.01	1410±169	887±105	3177±41
	Rel	27.7±1.1	42.56±2.126	165±15.4	110.2±7.5	201.8±29.5	113.8±15.314	112.6±10.1	70.4±3.9	68.75±6.733	73±15	1398±124	108±11
132	Ctrl	3.6±0.37	0.35±0.028	17.9±1.3	110.5±7.6	0.013±0.002	0.063±0.01	57.8±3.6	28.9±1.4	0.16±0.008	2290±240	30±6	2096±53
	Salt	1.4±0.11	0.14±0.014	32.1±1.3	82.5±4.6	0.01±0.001	0.072±0.018	71.1±6.8	18.7±0.6	0.13±0.007	1474±124	2029±370	2737±126
	Rel	39.3±5.73	39.82±2.721	190.6±18.7	76.4±8.1	72.3±3.605	113.39±19.981	128.2±13.9	65.2±3.4	83.69±5.903	67±7	7845±2357	131±8
133	Ctrl	2±0.11	0.22±0.012	30.8±3.7	103.5±5.5	0.017±0.001	0.047±0.007	91.2±6	24.6±1.1	0.13±0.01	1616±114	23±5	2263±315
	Salt	1.3±0.17	0.13±0.008	39.9±1.7	83.5±3.9	0.012±0.001	0.065±0.006	78.5±2.1	18.2±0.2	0.13±0.005	1338±59	1264±267	2843±217
	Rel	62.3±9.6	58.26±6.221	143.5±15.1	80.9±2.3	75.429±5.361	153.12±27.111	90±6.9	74.9±3.5	101.49±6.252	85±8	6143±1591	134±18
134	Ctrl	3.4±0.1	0.35±0.005	22.4±1.6	98.7±3.5	0.011±0.001	0.061±0.009	80±3.1	24.7±0.5	0.15±0.008	1559±48	27±4	1984±72
	Salt	1±0.05	0.12±0.005	36.7±2.2	80.1±4.8	0.011±0.001	0.083±0.006	69.4±2.1	20.5±0.3	0.15±0.008	1652±67	978±114	3050±68
	Rel	30.2±1.51	33.26±1.247	170.7±15.5	82.1±7.6	107.4±9.194	146.43±16.624	88.3±5	83±2.1	102.89±10.241	107±7	4035±697	154±5
135	Ctrl	5.1±0.18	0.44±0.019	17±0.9	100.3±3.6	0.009±0.001	0.042±0.005	72.4±3.1	28.8±1	0.17±0.019	1740±107	48±6	2137±103
	Salt	1.4±0.13	0.16±0.014	33.9±5.1	91±1.8	0.013±0.001	0.041±0.004	80.1±4.8	19.1±1.3	0.12±0.009	1469±101	1069±59	2960±87
	Rel	26.4±2.41	35.74±2.789	191.3±32.1	91.4±4.7	124.2±1.7	106.05±18.773	107±5.3	66.5±5	71.26±11.85	85±6	2345±294	140±8
136	Ctrl	2.4±0.22	0.22±0.026	13.6±1.3	103.2±2.8	0.008±0.001	0.04±0.006	80.4±4	27.3±0.8	0.15±0.012	2130±214	32±4	1905±46
	Salt	0.7±0.04	0.07±0.003	22.9±2.1	84.7±5.5	0.009±0.001	0.038±0.006	122.9±11.2	16.8±0.7	0.14±0.017	1241±158	1263±80	2539±198
	Rel	30.5±3.64	34.69±3.643	172.4±13	82.4±6	104.9±11.9	107.7±26.4	159.2±10.1	61.9±3.5	99.11±16.241	63±13	4224±513	134±12
137	Ctrl	2.6±0.18	0.26±0.008	34.9±4.6	95.5±6.8	0.014±0.001	0.065±0.007	108.9±2.9	24.7±1.1	0.15±0.005	1513±223	16±4	1811±192
	Salt	0.7±0.04	0.08±0.005	31.7±2	87.5±1.8	0.011±0.001	0.065±0.004	72.2±2.3	20.1±0.7	0.13±0.011	1508±91	1977±173	2771±227
	Rel	29.2±3.16	31.61±2.014	102.2±12.5	93.8±7.9	72.3±5.9	104.5±10	67.1±1.8	81.7±3.2	87.5±6.26	105±9	15123±3286	158±19
138	Ctrl	2.8±0.21	0.25±0.022	17±1	110.6±4.4	0.012±0.002	0.05±0.002	85.5±4.4	22.6±0.9	0.15±0.011	1729±141	43±13	1963±145
	Salt	1.1±0.19	0.11±0.023	26.9±1.6	102.5±2.9	0.014±0.001	0.044±0.005	81.9±5.6	17.6±0.8	0.13±0.007	1377±111	1847±301	3074±151
	Rel	38.8±4.01	41.59±8.609	166.3±16.9	93.4±5.4	100.1±7.3	87.5±8.1	96.9±12.5	78.7±5.3	87.78±5.885	83±10	6104±1805	161±18
140	Ctrl	4±0.44	0.44±0.054	21.6±1.3	97.4±4.6	0.011±0.001	0.038±0.003	80.6±3.1	24.6±0.6	0.15±0.012	1436±42	15±2	1700±87
	Salt	1.7±0.27	0.18±0.024	40.5±2.4	90.4±4.3	0.017±0.001	0.046±0.008	86±4.4	18.7±0.4	0.13±0.018	1112±168	1863±83	3074±151
	Rel	43.7±12.02	41.74±10.721	188.8±5.5	94±7.5	170.4±22.1	124.3±26.3	109.4±8.8	75.9±1.1	85.66±14.094	78±12	13384±1529	184±19
141	Ctrl	4.6±0.13	0.38±0.012	19.4±1.5	96.3±7.9	0.009±0.002	0.065±0.011	72.2±1.6	27.6±0.5	0.15±0.011	2043±49	13±2	2086±108

	Salt	1±0.05	0.11±0.005	35.4±3.5	91.8±5.3	0.015±0.003	0.082±0.007	56.9±2.5	18.4±0.7	0.12±0.01	1479±119	1684±159	2751±114
	Rel	22.8±1.26	28.02±0.942	192.5±23.7	96.6±6.3	131.1±12.7	147.5±35.5	79.1±3.7	66.9±2.9	81.44±9.982	73±7	14036±1998	134±12
144	Ctrl	4.2±0.21	0.47±0.034	24.6±2.9	117.7±1.7	0.019±0.002	0.048±0.007	79.8±4.3	26.8±1.3	0.18±0.008	1778±153	12±2	1859±52
	Salt	1±0.09	0.11±0.009	35.6±2.4	87.7±3.6	0.013±0.002	0.076±0.007	82.7±3.1	17.2±1	0.13±0.009	1352±228	2903±445	2561±68
	Rel	23.9±3.06	23.41±3.358	161.1±21.4	74.5±3.2	59.2±5.9	173.1±30.1	111.5±8.1	64.6±5	68.93±5.886	79±15	25493±4348	138±5
146	Ctrl	4.3±0.22	0.4±0.024	28.7±1.3	97.5±2.3	0.014±0.001	0.056±0.002	95.5±3.4	23±0.3	0.16±0.008	1402±42	9±1	2240±83
	Salt	1.4±0.06	0.15±0.01	32.3±1.8	81.4±2.3	0.009±0.001	0.082±0.005	65.1±2.2	20.4±0.4	0.15±0.009	1686±93	1845±127	2867±108
	Rel	31.1±2.96	38.81±5.965	115.3±9.1	83.8±3.4	65.5±7.6	146.2±5.4	69.1±3.7	89±1.9	95.14±9.778	120±7	20497±1395	129±8
147	Ctrl	2.4±0.18	0.24±0.016	28±1.5	105.2±4.9	0.017±0.001	0.06±0.002	89.3±8.3	24.1±1.3	0.19±0.016	1950±268	10±0	2792±161
	Salt	1.3±0.05	0.14±0.005	43.3±2.6	89.3±2.8	0.016±0.002	0.1±0.009	59.3±1.2	19.2±0.2	0.14±0.007	1615±62	1649±529	3574±146
	Rel	54.8±5.84	60.64±3.232	160±14.5	85.9±6	108.2±10.3	166.4±13.9	72.7±7.8	80.2±3.3	76.83±6.153	90±13	16163±4326	130±9
148	Ctrl	3.7±0.21	0.4±0.033	21.3±1.3	95.8±6.3	0.011±0.001	0.049±0.005	92.7±3	24.8±0.2	0.18±0.008	1591±69	14±2	2043±100
	Salt	2.2±0.16	0.25±0.015	40.5±2.2	83±1.3	0.012±0.001	0.057±0.003	105.4±3.5	18±0.6	0.14±0.006	1052±73	1348±365	2598±113
	Rel	58.5±3.76	63.99±5.184	197.2±16.2	88.2±6	135.8±17.1	125.4±19.9	114.3±3.8	72.6±2.3	79.08±4.828	67±6	10141±2068	128±6
149	Ctrl	1.6±0.08	0.17±0.007	31.7±1.8	103±5.5	0.018±0.003	0.063±0.008	100.5±4	22.7±0.4	0.18±0.015	1363±108	20±3	1821±117
	Salt	1±0.09	0.11±0.009	48.3±3.6	96.1±5.6	0.025±0.002	0.078±0.015	89.9±6.6	16.4±0.4	0.14±0.009	1200±84	1260±110	3178±119
	Rel	62.1±2.81	67.47±6.995	152.8±8	94.8±9.3	141.6±19.8	123.8±17.3	90.4±6.6	72.1±1.4	76.59±7.785	89±4	7106±1411	178±16
150	Ctrl	2.6±0.23	0.27±0.028	22.2±1.1	98.8±5.7	0.011±0.002	0.05±0.003	84.5±2.2	24.8±0.4	0.18±0.011	1736±89	14±2	1782±57
	Salt	1.3±0.11	0.15±0.016	41.4±3.7	92.1±3	0.017±0.002	0.055±0.007	97.7±2.6	17±0.7	0.15±0.008	1090±81	898±204	3699±416
	Rel	53.1±5.69	57.53±7.001	187.3±14.4	94.5±6.2	158.8±9.4	110.5±11.1	115.9±2.7	68.7±2.3	85.04±9.815	64±6	6955±2273	206±20
151	Ctrl	3.1±0.21	0.28±0.02	23.7±1.7	107.4±11.9	0.012±0.001	0.064±0.013	90.1±5.2	24±0.5	0.19±0.01	1773±107	15±2	2379±102
	Salt	1.2±0.1	0.12±0.011	37.3±3.8	90.8±7	0.016±0.001	0.067±0.005	74.8±4.6	18.8±1	0.16±0.012	1636±197	1605±197	2745±550
	Rel	37.6±4	44.49±4.959	168.1±25.8	88±11	108.3±11.1	137.3±43.6	84.7±6.4	78.4±3	86.42±6.95	92±8	11066±1098	119±27
153	Ctrl	4.1±0.18	0.31±0.036	21.6±1.1	91.6±2.5	0.009±0.001	0.044±0.007	72±2.9	26.7±0.8	0.17±0.014	2094±189	21±4	2375±160
	Salt	0.9±0.08	0.1±0.01	35.8±1.8	88.8±4.8	0.011±0.001	0.063±0.005	91.6±10.7	17.6±1	0.16±0.009	1166±96	1460±141	3316±394
	Rel	22.6±1.82	33.33±2.293	168.5±8.7	97.2±5.8	148.4±15.9	154.7±17.7	142.3±9	66.4±4.6	93.97±7.405	58±7	8079±1894	145±26
154	Ctrl	2±0.1	0.21±0.014	30.6±3	108.5±5.9	0.024±0.003	0.069±0.008	85.8±4	25.4±1.4	0.16±0.007	1631±110	13±1	1855±28
	Salt	1.2±0.06	0.14±0.009	34±0.9	92.2±12.2	0.013±0.001	0.06±0.006	79.5±5.6	16.5±0.5	0.16±0.01	1714±178	2350±281	2783±142
	Rel	59.7±5.07	71.32±5.288	121.5±12.8	85.7±12.8	85.3±11.6	91±13	98.9±8.9	65.9±4.5	100.1±4.49	109±16	20040±3474	150±7
155	Ctrl	2.6±0.17	0.28±0.018	34.3±3.3	86.4±3.3	0.011±0.001	0.074±0.014	85.6±4.3	26.1±1.6	0.16±0.017	1456±182	7±0	2026±48
	Salt	0.9±0.12	0.1±0.017	34.2±1.6	84±2	0.011±0.001	0.086±0.01	65.5±4.9	17.9±0.4	0.15±0.005	1661±204	2630±113	2775±53
	Rel	35.8±6.52	33.02±5.798	116.5±21.2	98.1±5.6	97.9±10.3	139.5±33.3	77.7±6	69.4±3.2	100.68±12.239	123±27	36366±2032	137±3

157	Ctrl	3.9±0.11	0.29±0.006	28.5±2.1	103.9±2.6	0.017±0.002	0.071±0.005	105.9±5.8	26.8±0.6	0.22±0.012	1595±133	53±9	2649±296
	Salt	0.7±0.08	0.08±0.008	13.5±1	92.2±12.2	0.007±0.001	0.047±0.011	67.9±3.7	19.1±0.4	0.16±0.018	1812±199	2709±459	2992±369
	Rel	16.7±1.67	25.43±2.515	45.8±5.3	88.8±12.1	40.8±10	66.8±17.7	66.6±8	71.5±3	71.01±5.301	118±19	5742±1337	126±31
158	Ctrl	2.6±0.15	0.26±0.015	23.3±1.8	131.2±13.2	0.034±0.009	0.043±0.003	76.3±3.4	26.8±0.7	0.21±0.03	1994±71	6±1	2972±53
	Salt	1.5±0.13	0.18±0.016	64.2±8.1	109.2±17.4	0.043±0.017	0.047±0.002	83.4±6.9	20.1±1	0.13±0.012	1152±159	1949±268	3122±375
	Rel	58±2.99	71.52±8.06	303.8±55.6	91.2±20.6	126±12	112.6±10.9	110±8.4	75.3±5	65.95±11.307	57±7	31331±4991	106±15
159	Ctrl	2.9±0.3	0.31±0.027	27.6±3.1	91.9±4.4	0.011±0.001	0.064±0.008	87.5±2.7	27±0.5	0.19±0.005	1618±89	25±2	1809±31
	Salt	1.4±0.04	0.16±0.006	35.1±1.8	84±2	0.011±0.001	0.067±0.006	85.4±6.1	18.5±0.2	0.14±0.005	1361±119	2048±223	3306±256
	Rel	50±6.03	52.44±3.242	142.7±19.9	92±4.1	112.8±7	113.7±19.9	99.5±9.1	68.5±1.4	72.04±2.425	86±10	8016±451	184±16
161	Ctrl	2.2±0.24	0.24±0.021	34.3±2.2	85.7±3.5	0.011±0.001	0.075±0.007	90.1±3.4	22.8±0.5	0.16±0.006	1445±102	19±2	2031±103
	Salt	1.2±0.09	0.14±0.01	47.5±3.5	92.4±3	0.02±0.002	0.079±0.004	78.7±4.7	18.6±0.8	0.14±0.006	1292±144	1796±36	3055±76
	Rel	59±9.81	59.12±6.979	145.4±16.2	108.4±5.3	199.7±22	109.6±12.9	89.4±8.1	81.7±3.7	91.98±5.872	92±13	9656±748	151±6
168	Ctrl	1.4±0.08	0.14±0.016	17.7±1.8	106.1±6.4	0.012±0.001	0.034±0.003	94.6±2.8	24.3±1.1	0.19±0.01	1514±93	46±6	1906±166
	Salt	0.7±0.04	0.07±0.007	17.9±2.1	86.2±11.6	0.009±0.001	0.036±0.004	90.3±3.5	16.6±0.6	0.15±0.005	1162±66	1655±98	2215±308
	Rel	50.4±1.45	53.28±2.348	108.9±13.7	84.1±14.4	89.8±15.2	105.5±5.4	96.4±3.8	69±4.8	82.21±5.61	79±8	3855±521	121±21
169	Ctrl	4.7±0.47	0.42±0.045	20.7±2.4	90.9±7.7	0.008±0.001	0.059±0.01	89±2	24.9±1	0.17±0.007	1614±151	69±9	1998±171
	Salt	0.7±0.05	0.09±0.006	26.7±2.6	90.7±2	0.011±0.001	0.052±0.008	91.2±3	17.6±0.4	0.12±0.015	1158±94	1673±180	2752±81
	Rel	15.7±1.22	21.95±2.333	127.7±13.2	103.8±11.9	137.5±10.6	98.1±19.4	102.5±2.9	71.1±3.3	74.77±9.461	74±8	2526±385	142±12
171	Ctrl	2.6±0.11	0.21±0.012	22.4±1.8	105.9±5.9	0.015±0.002	0.052±0.007	95.9±2.6	24.4±0.6	0.24±0.018	1946±142	71±10	1986±233
	Salt	0.9±0.11	0.1±0.007	24.4±1.8	101±2.4	0.013±0.001	0.064±0.003	77.6±3.9	18.5±0.2	0.17±0.007	1628±118	1490±92	2866±193
	Rel	34.9±5.1	46.84±4.108	113.5±10.8	96.7±6.1	99.6±8.2	133.3±19	80.9±3.2	76.1±2.5	74.03±4.01	86±10	2186±208	154±21
172	Ctrl	2.2±0.09	0.18±0.009	18.8±1.4	114.1±1.8	0.015±0.001	0.05±0.008	83.2±2.3	23.8±1	0.17±0.009	1750±111	82±7	3000±144
	Salt	1.2±0.1	0.13±0.006	36.1±3.8	96±3.9	0.016±0.001	0.047±0.003	91±3	17.5±0.7	0.13±0.012	1029±78	1127±26	2343±110
	Rel	54.1±6.45	75.58±4.674	199.3±20.3	84.1±2.2	112.8±6.5	103.4±14.8	110.5±5.8	74.1±4.7	75.95±10.846	60±7	1427±140	79±6
173	Ctrl	2.5±0.09	0.18±0.008	9.3±0.6	129.2±3.9	0.011±0.001	0.029±0.003	78±4.5	27.7±0.5	0.21±0.013	2228±162	69±12	3078±221
	Salt	1±0.06	0.12±0.01	29.4±2	86±6.3	0.012±0.001	0.039±0.004	96.4±5.3	16.8±0.6	0.12±0.011	888±53	1163±184	2378±92
	Rel	39.7±3.08	64.75±6.458	354±48.1	67.1±6	119.2±4.3	151.8±35.8	128.8±11.9	60.9±2.1	60.61±8.187	41±4	2028±621	79±5
176	Ctrl	2.2±0.14	0.21±0.018	15.1±1.9	111.1±5	0.011±0.001	0.036±0.012	92.3±5.6	23.9±0.3	0.18±0.007	1551±83	37±10	1691±152
	Salt	0.6±0.04	0.07±0.006	22.1±1.4	88.1±5.9	0.006±0.001	0.031±0.011	132.6±3.6	15.3±0.2	0.16±0.01	904±41	938±107	3182±214
	Rel	29.3±1.41	37.66±6.188	163.5±20	78.9±2.4	71.2±7.6	190±145.4	148.8±10.1	63.4±1.1	88.13±7.429	61±5	3638±1085	195±22
177	Ctrl	3.8±0.2	0.4±0.033	30.2±1.9	87.9±2.6	0.011±0.001	0.05±0.005	76.3±3.8	23.8±0.5	0.17±0.017	1511±29	36±10	1881±153
	Salt	1.8±0.11	0.2±0.014	51.3±3.8	86.6±1.9	0.018±0.001	0.069±0.007	88.6±2.7	17.5±0.8	0.14±0.007	1044±126	1670±171	2785±109

	Rel	48.1±6.27	52.04±6.121	175.5±15.3	99±4.2	160±12.3	145±20.2	117.9±5.2	73.8±4	81.2±6.31	69±7	6774±2411	151±12
178	Ctrl	3.4±0.3	0.4±0.036	40.3±2.3	83.3±3.8	0.013±0.001	0.069±0.011	95.3±2.7	22.7±0.7	0.16±0.011	1207±51	20±3	1925±165
	Salt	1.8±0.11	0.2±0.015	41±2.3	84.6±3.4	0.015±0.001	0.07±0.005	91.8±3.4	19.4±1	0.16±0.01	1161±102	1853±111	2714±162
	Rel	54.4±3.12	52.76±5.299	105.2±9.1	102.1±4.9	122.4±17.2	114.7±21.1	96.5±2.6	85.5±4.6	99.87±9.179	96±9	10249±1502	145±15
179	Ctrl	4.2±0.18	0.35±0.012	20.3±0.7	91.6±8.8	0.009±0.001	0.052±0.006	91.8±4.7	24.2±0.9	0.2±0.016	1696±129	41±9	3145±224
	Salt	0.6±0.07	0.08±0.016	25.6±1.4	90±1.3	0.01±0.001	0.048±0.004	87.1±5.4	18.5±0.5	0.13±0.008	1320±98	1806±190	2928±149
	Rel	15.3±1.41	23.52±4.077	128±8.6	103.1±12.7	119±20.4	95.1±8.1	99±11.2	76.6±2.5	67.4±4.422	79±5	5186±1037	96±11
183	Ctrl	3.9±0.13	0.31±0.01	35.6±1.3	85.7±3.5	0.011±0.001	0.075±0.007	106.1±2.9	22.8±0.5	0.16±0.006	1445±102	28±4	2737±182
	Salt	0.8±0.03	0.09±0.003	23.1±1.2	102.3±1.7	0.013±0.001	0.061±0.008	76.5±3.9	18.4±0.9	0.16±0.008	1629±152	1937±227	2825±92
	Rel	20.4±0.9	28.95±0.986	65.5±4.1	120.4±6.7	113.8±12.9	83.9±14.4	72.8±4.7	80.8±3.3	101.96±7.339	115±14	7018±511	105±8
187	Ctrl	5.3±0.35	0.48±0.021	30.2±2.1	90±11.5	0.012±0.001	0.067±0.014	78.3±2.9	24.8±0.7	0.19±0.011	1765±130	15±4	2285±38
	Salt	1.1±0.03	0.12±0.006	32.3±2.7	90±4.5	0.013±0.001	0.059±0.009	66.2±3.5	19.3±0.8	0.16±0.02	1570±194	1979±154	2484±195
	Rel	20.1±0.84	24.53±1.88	106.4±10.5	106.9±14.5	106.8±13	97.4±16	86.5±6.9	77.9±2.6	85.7±7.596	89±9	15227±2737	109±9
188	Ctrl	3.9±0.29	0.4±0.031	33±2.1	99.7±3.6	0.017±0.001	0.048±0.006	110.4±6.1	22.7±0.7	0.18±0.013	1289±125	18±4	1847±134
	Salt	1.2±0.12	0.12±0.012	29.3±2.9	92.3±4.8	0.013±0.001	0.064±0.005	77.6±4.6	16.8±0.3	0.16±0.01	1461±103	1524±265	2332±182
	Rel	31±3.51	30.8±3.561	96.7±15.6	93.1±6.1	70.7±8.8	145.1±24	72±5.3	74.4±2.3	89.4±4.598	119±15	10784±3869	128±11
189	Ctrl	3±0.18	0.34±0.02	37.9±1.7	79.8±4.4	0.011±0.001	0.061±0.003	105.2±4.3	23.5±0.4	0.17±0.012	1263±27	31±7	1838±111
	Salt	1.9±0.05	0.2±0.006	49.9±3.1	85.4±1.5	0.016±0.001	0.066±0.007	94±5.1	17.7±0.4	0.15±0.01	1005±92	2166±167	2521±118
	Rel	65±3.44	59.61±3.887	130.7±12.6	108.6±7.2	153.4±19	109.8±11.2	90.2±5.1	75.3±2.2	92.16±11.81	80±8	7837±1014	140±12
190	Ctrl	4.6±0.11	0.46±0.022	29.8±2	106.6±3.5	0.019±0.002	0.06±0.005	110±3.3	22.5±0.5	0.17±0.011	1389±67	34±7	1957±119
	Salt	0.7±0.08	0.08±0.007	41.4±2.9	97.6±1.2	0.02±0.002	0.06±0.004	81.3±5	17.3±0.6	0.15±0.014	1171±41	2036±133	2812±257
	Rel	15.6±1.4	16.28±1.311	146.4±16.2	92±3.5	116.1±9.7	103.8±12.9	75.1±6.2	77.1±3.6	89.55±10.174	85±6	7107±1343	136±10
191	Ctrl	1.9±0.1	0.19±0.012	17±1.7	121.1±2.9	0.017±0.001	0.032±0.003	97.9±4.3	27±0.9	0.17±0.007	1393±133	35±5	1707±82
	Salt	1±0.04	0.13±0.006	37±2.7	94.5±2.6	0.018±0.001	0.049±0.006	86.5±4.1	18.6±0.7	0.15±0.005	1294±127	1084±108	2725±155
	Rel	55.8±4.11	70.8±2.072	268.2±57.3	78.1±1.7	110.3±6.5	159.2±22.6	89.8±6.1	69.2±3.1	88.46±0.905	94±7	3389±642	160±5
192	Ctrl	4.5±0.33	0.46±0.038	30.6±1.9	103.6±3.8	0.021±0.001	0.069±0.008	95.9±4.6	24.3±0.8	0.19±0.015	1550±87	18±2	2098±177
	Salt	1.3±0.06	0.16±0.008	43.5±2.6	96.3±3	0.02±0.002	0.058±0.006	107.1±2	17.6±0.7	0.15±0.007	1030±26	843±172	2934±259
	Rel	30.3±2.99	34.87±2.79	146.7±12	93.7±5.6	116.6±13.3	88.3±13.1	114±6	72.8±2.7	79.35±5.647	67±4	5114±1186	144±18
193	Ctrl	4.7±0.33	0.48±0.035	19.6±2	84.2±3.3	0.005±0.001	0.048±0.007	71.1±3.5	25.4±0.8	0.14±0.006	1711±141	22±3	1777±65
	Salt	1.9±0.2	0.21±0.022	46.4±3.1	82.2±2.5	0.013±0.001	0.061±0.004	86.7±4.1	16.7±0.7	0.12±0.008	953±86	1582±273	3830±140
	Rel	42.3±7.39	43.82±1.66	251.2±21.2	98.5±6.2	255±32.7	135.9±18.4	123±5.4	66.1±3.4	82.76±4.914	56±3	7545±1130	217±13
194	Ctrl	3.2±0.2	0.37±0.028	37.7±3.8	105.3±3.3	0.025±0.002	0.065±0.01	102.6±7.7	22.9±0.7	0.18±0.012	1425±139	17±3	1358±140

	Salt	1.6±0.06	0.19±0.01	89.2±7.6	87.8±4.4	0.029±0.002	0.085±0.005	104.3±3.8	15.6±0.5	0.14±0.002	799±108	669±66	3509±129
	Rel	51±3.84	52.48±6.105	252.2±23.1	83.4±3	133.9±13.3	148.1±26	105.4±6.6	68.3±2.1	78.19±4.935	57±6	4480±1091	273±35
	Ctrl	4.2±0.23	0.49±0.028	39.9±2.1	76.2±2.2	0.009±0.001	0.057±0.005	107.4±2.7	23.7±0.4	0.16±0.005	1243±66	26±4	2030±92
195	Salt	1.5±0.16	0.16±0.015	82.4±8.6	84.6±2.3	0.028±0.002	0.082±0.005	99.4±3.1	17±1	0.15±0.015	872±139	2080±112	2473±95
	Rel	37.3±5.94	34.39±4.819	201.7±23.5	111.4±4.4	321±46	145.5±11	92.7±2.3	71.6±3.6	93.55±9.825	69±9	8552±1021	123±7
	Ctrl	3.1±0.42	0.39±0.052	23.7±2	90.3±3	0.009±0.001	0.051±0.006	86.7±5.1	24.9±0.6	0.18±0.011	1694±112	24±5	2039±183
196	Salt	1.4±0.09	0.15±0.008	48.7±3.4	73±4.5	0.011±0.001	0.066±0.004	101.1±4.7	16.9±1	0.14±0.003	1084±85	1812±179	2799±31
	Rel	47.6±7.35	40.56±5.143	246±59.1	80.6±3	130±15.6	136.3±18.7	122.1±11.4	67.9±4.5	79.16±4.27	66±8	9333±2494	142±13
	Ctrl	8.3±0.5	0.75±0.074	18.8±1.3	110.5±4.6	0.012±0.001	0.036±0.009	102.8±3.8	25.2±0.6	0.2±0.008	1556±79	12±1	2058±22
197	Salt	1.7±0.15	0.21±0.017	47.2±3.6	89.6±3.3	0.016±0.001	0.057±0.005	138.8±6.7	18.3±0.7	0.19±0.02	1023±112	823±102	2794±141
	Rel	21.5±2.08	28.71±2.483	265.9±29.3	81.7±4.6	157.7±1.1	261.3±131.6	138.3±11.2	72.6±3.7	93.32±12.228	67±10	7275±1344	136±8
	Ctrl	2.6±0.05	0.28±0.009	39.9±3.6	99.7±5.7	0.021±0.002	0.072±0.01	102.8±1.6	22.1±0.6	0.18±0.008	1280±66	9±1	1575±98
199	Salt	1.2±0.04	0.14±0.005	61.4±3.9	92.6±3	0.026±0.002	0.078±0.006	97±3.1	16±0.3	0.15±0.012	864±36	2169±260	2979±140
	Rel	46.3±1.4	48.12±1.757	175.6±21.4	95.4±8.2	177.6±9.4	115.2±14.6	94.7±3.9	72.8±2.1	83.44±5.8	68±2	25991±3933	191±13
	Ctrl	4.5±0.44	0.32±0.048	23.5±1.6	102.7±5.5	0.012±0.001	0.061±0.005	86.9±2.6	26.5±1	0.18±0.017	1886±243	43±4	2429±50
203	Salt	0.7±0.04	0.08±0.004	21.3±2.2	101.7±4.4	0.013±0.001	0.046±0.009	78.3±3.7	18.6±0.7	0.15±0.01	1432±155	1878±290	2446±100
	Rel	16.5±1.16	27.28±4.858	99.9±10.2	99.4±3.1	123.5±10	80.8±20.9	90.6±4.6	70.8±4.1	85.57±6.761	81±14	4591±858	101±4
	Ctrl	5.1±0.46	0.41±0.046	36.2±1.9	97.2±5	0.017±0.001	0.056±0.005	104.3±2.4	23.5±0.6	0.18±0.007	1415±42	37±5	2438±56
205	Salt	1.2±0.21	0.15±0.023	52.4±4.1	90.7±3.7	0.02±0.002	0.062±0.006	100.7±4.9	17±0.3	0.15±0.008	978±78	827±143	2869±148
	Rel	24.9±3.82	37.14±5.998	145.8±10.5	93.6±2.8	114.8±7.6	109.9±7.6	97±5.3	72.8±2.8	80.93±4.469	69±6	2213±205	118±5
	Ctrl	4.8±0.3	0.4±0.028	24.4±2	94.9±4.6	0.01±0.001	0.048±0.004	92.9±5.2	28.2±0.5	0.19±0.019	1616±171	37±8	2114±92
208	Salt	1±0.06	0.11±0.009	54.7±3.9	79.7±0.6	0.014±0.001	0.059±0.004	118.6±4	16±0.3	0.11±0.01	707±63	1935±203	3527±128
	Rel	21.2±2.39	26.75±1.201	228.8±26.8	84.9±4.7	144.9±15.6	127.4±18.5	131.8±9.5	56.9±1.3	63.93±11.669	45±4	9425±5330	170±10
	Ctrl	5.3±0.53	0.49±0.047	46.6±2.5	87.1±3.7	0.017±0.001	0.07±0.006	95.9±3.2	24.8±0.8	0.16±0.011	1265±101	48±6	2277±45
209	Salt	1.4±0.15	0.15±0.018	57±2.4	83.6±3.6	0.016±0.001	0.065±0.011	91±4.4	18.8±0.5	0.12±0.01	1259±189	1505±166	2720±114
	Rel	26±2.54	31.69±3.104	130.8±6.5	96.9±6.7	100±9.3	95.7±19.7	96±6.3	76.1±3.3	78.11±9.224	104±20	3508±927	120±5
	Ctrl	3.1±0.19	0.27±0.013	25.7±2.3	109.6±8.7	0.017±0.002	0.059±0.007	79.1±2.4	28.4±0.5	0.2±0.024	1894±83	22±4	2482±46
211	Salt	0.6±0.07	0.08±0.007	26.9±2.2	92.1±4	0.011±0.001	0.048±0.008	73.1±3.6	20±0.7	0.15±0.006	1507±160	1646±148	2490±232
	Rel	20.9±1.78	28.19±1.974	109.4±10.6	85.7±6.4	66.4±2.5	89.4±25	92.6±4.4	70.3±1.9	80.44±13.382	80±9	8376±1436	100±9
	Ctrl	2.8±0.54	0.24±0.038	25.7±2	91.3±6.7	0.012±0.001	0.058±0.007	73.7±3.5	28.2±1.3	0.17±0.013	1744±147	26±1	3379±218
213	Salt	0.9±0.1	0.1±0.009	28±2.3	87.1±1.7	0.01±0.001	0.037±0.003	67.9±2.9	19.2±0.5	0.12±0.009	1334±134	2202±76	2456±174
	Rel	35.7±7.94	43.57±7.029	117.4±14.6	98.1±9.2	82.1±5.5	69±11.1	93.1±4	68.7±3.6	75.3±9.117	79±10	8610±444	73±5

214	Ctrl	3.1±0.25	0.25±0.011	26.3±1.5	97.9±3.8	0.011±0.001	0.047±0.005	94.9±3.7	26.1±0.5	0.19±0.012	1494±105	20±2	2832±125
	Salt	1.1±0.07	0.14±0.009	52.4±3.1	92.1±3.8	0.021±0.002	0.05±0.005	120.7±4.1	16.9±0.5	0.12±0.009	835±46	1390±114	2873±101
	Rel	38.1±5.06	54.61±4.532	210.2±24.2	94.8±6.1	185.7±20.7	111.4±14.6	130.6±10.5	64.9±2.8	66.61±7.328	57±6	7501±1288	102±6
215	Ctrl	4.9±0.52	0.42±0.045	22±2.2	93.4±6.8	0.009±0.001	0.051±0.004	76.5±3	27.9±0.9	0.18±0.016	1787±190	52±6	2453±71
	Salt	1.1±0.03	0.14±0.013	35.1±1.2	81±1.5	0.01±0.001	0.052±0.004	85.2±2.5	18.5±0.7	0.11±0.005	1178±81	1344±66	2949±71
	Rel	22.9±2.44	33.77±2.334	173.4±17.2	88.6±6.5	114±6.8	104.8±14.2	112.8±5.3	66.4±2.2	67.56±7.426	68±7	2687±268	120±4
216	Ctrl	3.7±0.23	0.3±0.019	24.1±1.6	104.9±10.4	0.015±0.001	0.036±0.007	91.8±5	25.5±1.6	0.17±0.014	1493±132	39±2	2623±101
	Salt	1.2±0.04	0.14±0.005	31.9±2.1	90.8±4	0.013±0.001	0.057±0.005	78±4.1	19.7±0.6	0.12±0.013	1316±109	1431±129	2870±86
	Rel	33.9±2.21	48.01±3.788	138.3±13.8	90.4±11.3	78.9±12.1	212.4±78.4	86.3±5.5	78.2±4.6	73.42±10.904	90±7	3687±403	111±7
217	Ctrl	2.8±0.15	0.23±0.018	24.1±1	98.3±3.2	0.012±0.001	0.056±0.004	78.5±2.6	28.3±0.6	0.19±0.014	1747±56	47±5	2594±37
	Salt	1.1±0.08	0.13±0.007	49.6±3.7	87.3±3.1	0.021±0.001	0.067±0.003	88.2±3.1	17±0.4	0.1±0.006	892±62	2060±214	2657±163
	Rel	41.1±4.2	56.52±6.057	208±9.3	89.1±4.2	162.6±15.1	123.4±9.9	113.3±5	60±1.2	56.18±6.328	51±2	4426±407	103±7
218	Ctrl	4±0.95	0.36±0.097	30.4±3.6	101.5±8.3	0.015±0.001	0.049±0.006	89.3±4.6	25.9±0.5	0.17±0.014	1482±122	72±4	2198±72
	Salt	1.1±0.13	0.12±0.014	39.2±3.3	86.8±3.9	0.013±0.001	0.052±0.007	86±4.4	18.2±0.7	0.1±0.007	975±62	1224±85	2610±123
	Rel	29.2±3.58	39.53±5.209	150.7±24.2	87.5±7.9	86.6±8.9	114.5±21	98.9±9.3	70.6±4.2	62.9±5.521	68±9	1712±126	119±5
219	Ctrl	3.9±0.53	0.33±0.045	26.5±3.9	123.1±10.8	0.024±0.001	0.033±0.01	106.7±5	26.2±0.9	0.19±0.023	1548±158	32±4	2339±75
	Salt	1±0.02	0.13±0.002	41.6±4.3	98.3±3.8	0.021±0.001	0.053±0.007	97±4.8	17.5±0.4	0.11±0.011	957±133	1019±22	2995±185
	Rel	28.4±4.32	43.16±6.311	201.4±37.5	81.6±5.7	80.8±3.5	291.4±123.5	94.4±9.1	67±2.8	58.48±5.146	66±12	3559±701	129±11
220	Ctrl	2.5±0.35	0.21±0.019	25.9±1.7	101±2.5	0.013±0.001	0.057±0.01	93.6±4.5	26.7±1.2	0.18±0.007	1544±158	24±2	2675±51
	Salt	0.8±0.05	0.1±0.005	51.7±2.4	88±2.3	0.018±0.001	0.058±0.007	105.9±3	16.9±0.4	0.12±0.008	893±54	1737±263	2215±213
	Rel	33.9±2.43	47.13±2.988	206±13.1	87.3±3.1	135.1±5.3	118.5±31.7	114.7±4.2	63.9±3.8	65.93±5.956	59±4	7490±1224	83±7
221	Ctrl	2.2±0.19	0.19±0.013	32.6±2.7	86.6±7.3	0.01±0.001	0.052±0.007	93.8±2.6	24.5±1	0.16±0.013	1300±87	71±5	2351±90
	Salt	1±0.09	0.12±0.008	26.3±3	89.1±3.6	0.009±0.001	0.047±0.007	72.7±3.1	18.3±0.4	0.12±0.01	1336±51	2223±287	3499±85
	Rel	47.8±4.16	61.54±4.29	84.3±9.1	106.4±11.8	77.2±12.2	91.4±8.4	78.4±4.8	75.2±3.1	79.9±11.297	104±5	3118±361	149±3
222	Ctrl	4.1±0.29	0.36±0.026	31.3±2.5	94.7±2.9	0.013±0.001	0.06±0.003	124±1.7	24.3±1.1	0.2±0.013	1348±124	44±4	2440±36
	Salt	0.9±0.03	0.1±0.004	46.4±3.6	93.7±2.5	0.02±0.002	0.047±0.004	97.3±2.3	17.4±0.7	0.13±0.01	1179±311	1652±178	2659±68
	Rel	21.2±1.59	27.26±2.422	135.4±10.8	99.2±2.8	163.6±3.7	80.3±10.8	78.7±2.6	71.5±0.8	65±6.299	84±13	3809±440	109±3
223	Ctrl	4.4±0.13	0.37±0.014	30.2±3.1	92±6.4	0.014±0.001	0.057±0.005	85.2±2.4	27.4±0.9	0.18±0.007	1640±90	37±5	2821±241
	Salt	1.3±0.1	0.15±0.01	46.6±4	83±3.9	0.01±0.001	0.061±0.001	99.4±2.8	17.8±0.8	0.13±0.015	1102±209	1313±135	2624±180
	Rel	29.6±2.51	40.66±3.828	180.5±19.3	92.5±9.1	90.1±12.5	109.9±8.8	117.9±5.9	65.3±3.8	72.8±9.363	71±18	3881±692	95±9
311	Ctrl	3.9±0.12	0.34±0.015	35.8±1.4	83.5±1.3	0.011±0.001	0.059±0.003	107.4±2.3	25.3±0.8	0.16±0.01	1240±90	38±2	2470±44
	Salt	1.1±0.09	0.12±0.008	37.3±3.8	96.8±11.2	0.02±0.002	0.064±0.005	101.3±2.2	17.2±0.9	0.12±0.002	1164±211	1796±217	2579±108

	Rel	27.4±2.92	34.51±2.522	109.1±12.9	116.9±15.8	198.7±18.3	110.4±11.8	94.7±2.5	68±2.6	74.22±4.996	93±12	4782±677	104±4
	Ctrl	2.7±0.34	0.26±0.016	16.6±1.9	95.3±3.8	0.007±0.001	0.043±0.008	70.5±5	27.2±0.9	0.17±0.006	2285±272	94±13	1884±105
319	Salt	0.8±0.15	0.07±0.01	29.5±1.5	82.4±4.9	0.009±0.001	0.063±0.014	67±3.4	19.3±1	0.12±0.005	1549±179	3155±258	2680±252
	Rel	25.9±3.69	26.54±5.56	194.9±18	87.5±7.4	139.4±23.3	151.7±26.4	101.8±11.8	71.9±6	71.76±2.989	74±14	3790±822	141±8
	Ctrl	3.9±0.12	0.34±0.011	26.1±1.4	99.7±2.3	0.013±0.001	0.053±0.008	104.3±2.7	23.2±0.4	0.19±0.007	1488±65	61±5	2896±148
321	Salt	0.9±0.07	0.1±0.008	39±3.4	88.4±3.8	0.014±0.001	0.07±0.009	78.7±5.5	18.5±0.4	0.15±0.007	1312±92	1669±100	3170±283
	Rel	22.5±2.17	28.86±2.619	153.9±16.1	89±4.9	102.3±7.5	141.4±21.8	75.5±5	80.1±2.2	76.93±4.115	88±4	2851±352	109±8
	Ctrl	5.7±0.26	0.49±0.025	23.7±1.5	117.4±7	0.019±0.003	0.046±0.005	84.1±4.2	25.6±1.1	0.16±0.012	1449±106	37±4	2404±76
350	Salt	0.9±0.05	0.1±0.003	24±3.2	105.1±5	0.015±0.001	0.035±0.005	81.5±6.1	19.1±1.2	0.14±0.006	1406±270	1919±179	3321±216
	Rel	16.7±1.14	21.52±1.498	103.5±12.1	91.1±7.8	80.13±9.526	78.18±13.264	96.6±4.8	74.8±4.3	92.64±7.736	96±15	5299±592	139±10
	Ctrl	4.7±0.24	0.39±0.021	31±2.7	89.2±3	0.011±0.001	0.063±0.009	98.7±4.2	24.8±1	0.15±0.003	1324±33	53±10	2097±108
354	Salt	1±0.07	0.11±0.007	30.2±1.4	84.4±1.1	0.009±0.001	0.044±0.003	89±3.9	18.6±0.6	0.12±0.007	1144±91	1308±89	2523±107
	Rel	21.2±1.67	28.86±1.648	103.3±9.6	95.2±4.1	85±2.7	76.3±12.7	91.3±5.2	75.7±3.7	78.87±3.993	87±8	3028±836	121±8
	Ctrl	2.2±0.24	0.16±0.023	21.1±2.3	111.9±9.9	0.014±0.001	0.05±0.006	88.4±5.6	26.3±1.1	0.17±0.006	1655±243	22±4	2602±56
366	Salt	0.7±0.07	0.1±0.006	33.7±4.6	85.3±14.8	0.016±0.002	0.069±0.013	79.8±4.6	17.7±0.8	0.12±0.011	1202±176	1227±89	3017±195
	Rel	35±5.41	65.04±8.415	187.7±28.7	76.3±12.9	122.6±12.4	141.3±26.2	92.4±5.9	67.7±4.1	67.76±6.322	76±14	6709±1757	116±8
	Ctrl	2.9±0.21	0.28±0.023	27.4±1.3	94±10.5	0.009±0.001	0.068±0.008	74.2±2.6	27.4±1.1	0.19±0.014	1903±85	63±2	2703±101
367	Salt	0.8±0.07	0.09±0.008	36.2±0.9	86.3±2.4	0.012±0.001	0.068±0.006	74.4±3.2	19.2±0.7	0.14±0.004	1370±58	1616±359	2762±221
	Rel	26.8±3.07	31.4±2.224	135.9±9.2	95.1±7.8	121.1±14.6	111.5±26.2	100.8±4	70.4±3.5	76.34±5.883	72±4	2552±502	102±8
	Ctrl	2.6±0.22	0.24±0.016	25.2±1.3	118.1±4.2	0.022±0.002	0.052±0.006	88.6±2.8	25.1±0.6	0.19±0.015	1706±24	31±9	2289±342
Q3	Salt	0.7±0.06	0.07±0.004	43.9±1.9	104.7±4.4	0.023±0.002	0.084±0.015	86.9±2.7	17.2±0.5	0.14±0.024	1243±119	2298±109	3537±390
	Rel	28±2.64	31.57±2.594	173±14.5	89±4.3	131.9±7.7	178.7±47.5	98.8±4	69±2.9	71.21±10.636	73±8	12935±5134	168±30
	Ctrl	3.2±0.38	0.28±0.032	35.1±2.5	105±3.5	0.021±0.001	0.072±0.007	92.9±2.4	25±0.8	0.19±0.003	1631±55	11±1	1990±42
Q4	Salt	1.2±0.06	0.11±0.009	38±4.4	95.6±8.2	0.017±0.002	0.083±0.018	75.5±3.3	16.1±1.2	0.12±0.02	1372±176	1748±269	2227±150
	Rel	39.9±4.36	41.41±8.547	121.5±17.8	90.8±6.6	78.2±4.9	129.2±40.9	81.7±4.2	64.5±3.9	65.3±10.922	84±10	15390±1956	112±8
	Ctrl	3.5±0.18	0.32±0.014	31±1.5	109.4±2.9	0.021±0.002	0.071±0.002	92.7±2	24.9±0.9	0.22±0.008	1631±86	9±1	1580±74
Q5	Salt	0.9±0.06	0.08±0.007	33.8±0.9	91.8±2.8	0.013±0.001	0.068±0.009	85.2±4.6	17.1±0.8	0.14±0.006	1413±128	1504±84	3763±142
	Rel	27.1±2.61	24.81±2.581	109.5±6.8	84.3±4.5	60.8±7.7	96.5±14.5	92.1±5.2	69.1±4.9	66.83±4.891	88±9	17230±1375	241±17
	Ctrl	4.5±0.27	0.41±0.031	39.5±2.3	109.6±1.5	0.027±0.001	0.064±0.007	110±2.6	22.6±0.7	0.18±0.019	1324±50	7±1	2060±40
Q6	Salt	1.2±0.11	0.1±0.012	57.3±3.2	95.6±3.3	0.029±0.002	0.083±0.011	94.4±2.1	15.8±0.7	0.13±0.008	1091±53	2875±257	2938±112
	Rel	28±3.24	27.84±4.752	152.4±15.1	87.3±3.6	126.5±10.2	139.5±27.5	86.3±2.7	70.2±4.4	75.26±6.347	83±4	42153±6733	143±6
Q7	Ctrl	5.3±0.45	0.49±0.042	34.1±2.1	104.7±3.5	0.02±0.001	0.076±0.005	98.5±4.3	23.5±0.5	0.17±0.011	1438±60	6±0	1994±44

	Salt	1.4±0.11	0.14±0.01	39.5±2.6	97.5±2.8	0.02±0.001	0.062±0.009	86±4.1	18.5±1	0.13±0.007	1276±191	1215±119	2434±134
	Rel	27.8±3.02	29.19±3.78	117.9±8.4	93.6±4.6	99.5±7	86±18.3	89.9±7.4	78.8±3.7	78.05±4.739	89±12	22755±3388	123±9
	Ctrl	3.9±0.45	0.31±0.034	35.1±1.1	105.1±3.2	0.022±0.002	0.077±0.007	88.6±3.1	25.3±0.3	0.2±0.012	1590±68	7±0	2286±60
Q11	Salt	1.3±0.06	0.12±0.005	40.7±3.3	99.2±3.3	0.02±0.002	0.061±0.009	98.1±4.3	17.7±0.6	0.17±0.009	1195±95	1265±111	2641±34
	Rel	35.4±3.98	41.18±4.119	117.2±10.3	94.5±2.7	107.1±7.5	79.5±9.2	111.9±6.6	70.1±2.7	83.64±5.924	76±7	18398±1732	116±4
	Ctrl	4.4±0.37	0.35±0.037	17.7±2	111.2±3.9	0.012±0.001	0.035±0.005	84.9±4.7	24.1±1	0.16±0.006	1575±138	16±1	2368±55
Q14	Salt	1±0.08	0.1±0.012	23.3±2.8	98.7±4.8	0.016±0.002	0.04±0.004	105.9±7.9	16.5±1	0.15±0.009	1253±186	1345±179	3189±98
	Rel	23.3±4.44	31.77±7.347	143.1±20.5	90.4±6.8	128.8±7.9	126.9±27.9	125.3±13.3	68.7±3.3	92.34±5.923	82±13	8291±633	135±6
	Ctrl	5±0.33	0.43±0.029	22.2±1.5	122.1±7.1	0.021±0.002	0.038±0.003	109.1±2.9	25.5±1	0.17±0.009	1261±73	24±2	2047±53
Q20	Salt	1.4±0.05	0.14±0.009	19.8±2.4	112.6±1.7	0.015±0.001	0.033±0.007	100.3±5.3	19.6±0.6	0.15±0.012	1224±52	951±140	2585±123
	Rel	29.6±2.83	32.77±3.918	89.1±7.9	93.4±5.2	83.36±8.835	89.99±19.546	93±6.6	77.6±3.5	89.27±6.018	99±8	3886±421	127±6
	Ctrl	2±0.08	0.16±0.009	11.6±0.9	131.5±21.1	0.01±0.003	0.019±0.002	67±2.8	28.6±0.3	0.15±0.014	2065±91	55±6	2265±75
Q21	Salt	1.1±0.08	0.12±0.013	17.5±1.3	111.5±5.5	0.013±0.001	0.021±0.001	83±4.9	18.8±0.9	0.08±0.011	1419±163	1513±111	2428±62
	Rel	54.1±5.35	77.79±11.805	159±20.4	94±14.4	145.2±7	115.1±13	123.8±5.4	65.7±3.5	52.82±9.617	69±8	2929±404	108±5
	Ctrl	3.8±0.31	0.33±0.028	36±2.5	95±8.1	0.014±0.001	0.065±0.008	83.4±3.6	25.2±1.4	0.17±0.015	1536±193	17±2	2593±87
Q22	Salt	1±0.05	0.11±0.008	52±3.4	88.1±2.1	0.018±0.001	0.063±0.005	87.1±2.8	17.5±0.3	0.13±0.012	1025±76	1575±149	2781±147
	Rel	26.4±3.22	36.69±6.022	148.3±11	95.4±8.1	136.9±15.5	101.2±13.3	106.1±5.6	70.2±3.3	76.62±5.316	69±6	9825±1481	108±9
	Ctrl	2.8±0.06	0.21±0.012	18.3±1.4	95.7±3.9	0.008±0.001	0.048±0.007	63.8±3.2	28.8±0.9	0.16±0.018	2190±95	50±7	2809±76
Q24	Salt	0.9±0.09	0.1±0.011	24.8±1.5	89.1±2.4	0.009±0.001	0.048±0.005	69.4±3.9	20.3±0.4	0.13±0.011	1651±149	1630±161	2792±56
	Rel	30.7±3.55	47.17±5.947	143.4±15.2	93.9±5.2	113.8±12.1	105.7±11.7	112.5±10.4	70.7±3	87.28±12.173	76±8	3553±595	101±2
	Ctrl	3.8±0.24	0.31±0.033	32.8±1.3	83.7±2.9	0.01±0.001	0.074±0.004	82.1±4.3	26.2±0.8	0.18±0.008	1713±98	39±10	2305±60
Q26	Salt	0.8±0.05	0.09±0.005	42±3.9	83.7±4.3	0.014±0.001	0.074±0.008	77.8±7	18.7±1.2	0.12±0.01	1335±172	2556±133	1791±81
	Rel	21.5±2.03	31.71±3.852	125.2±14.4	100±4.1	134.3±13.8	100.1±9.2	98.1±12.1	72±6.7	66.98±6.784	81±13	8788±2344	77±5
	Ctrl	4.8±0.23	0.37±0.028	21.1±1.6	112.2±2.9	0.016±0.002	0.057±0.005	76.3±2.8	25.8±1.1	0.19±0.015	1945±124	64±14	1959±72
Q28	Salt	0.8±0.03	0.1±0.005	23.9±2	94.9±1.7	0.012±0.001	0.051±0.006	65.8±5.9	21.1±1.3	0.14±0.004	1822±226	1413±119	2773±240
	Rel	17.5±0.44	26.43±1.085	115.3±9.5	84.7±3	76.8±5.7	94±16.5	87±8	82.2±5.4	74.08±6.398	93±8	2971±877	144±19
	Ctrl	5.8±0.46	0.49±0.046	32.8±2	95.9±4.5	0.015±0.001	0.069±0.005	89.5±5.8	26.5±0.7	0.18±0.009	1569±135	18±2	1891±280
Q29	Salt	0.8±0.03	0.08±0.005	44.4±5.1	89.2±3	0.016±0.001	0.073±0.016	85.5±5	17±1.1	0.12±0.018	1230±159	2020±160	2624±256
	Rel	13±0.48	17.32±1.227	138±16.1	93.8±4.6	105.8±8.2	110.3±26.9	97.6±6.8	64.2±3.9	67.34±8.904	82±14	12454±2561	157±31
	Ctrl	4.6±0.37	0.38±0.036	30.6±2.2	98.8±3	0.015±0.001	0.067±0.007	93.8±3.3	25.9±0.7	0.18±0.013	1563±102	55±4	1724±325
Q30	Salt	0.9±0.05	0.1±0.005	59.9±3.5	83.8±3.3	0.019±0.001	0.072±0.003	91.8±2.4	17.9±0.2	0.11±0.004	972±39	1287±159	3607±167
	Rel	19.1±1.66	26.93±2.033	208.6±22.2	85.1±4.1	118.1±7.3	112.8±12	99.2±5	69.4±1.5	62.07±3.185	63±5	2394±332	252±61

Q31	Ctrl	4.1±0.14	0.36±0.012	42.7±3.8	107.6±2	0.028±0.004	0.094±0.01	95.7±3.1	22.3±1.3	0.19±0.016	1432±88	7±1	2378±50
	Salt	1.1±0.14	0.1±0.006	43.5±3.7	100.8±1.8	0.026±0.001	0.069±0.003	78.3±3.5	17.9±0.6	0.12±0.007	1238±74	2992±272	2123±95
	Rel	26.7±3.38	27.08±0.855	105.4±7.1	93.9±3.1	88.3±6.9	76.9±9.6	82.2±4	80.9±3.1	62.7±6.487	87±3	42786±6055	90±5
Q32	Ctrl	1.6±0.21	0.15±0.011	30.6±2	107.2±4.3	0.02±0.003	0.05±0.002	77.2±2.7	27.9±0.5	0.2±0.026	1977±40	11±1	2384±40
	Salt	1.5±0.14	0.14±0.013	62±6.9	123.6±4.9	0.059±0.001	0.048±0.003	81.1±4.8	17.5±0.5	0.13±0.009	1411±165	1870±130	2816±60
	Rel	96.2±10.53	93.33±9.252	219.5±32.2	116.2±7.4	339.4±32.8	98±6.4	105.5±6.3	62.8±2.7	67.96±8.433	71±8	17958±1233	118±4
Q33	Ctrl	4.3±0.15	0.36±0.019	30.6±4.5	102.9±4.6	0.016±0.002	0.055±0.007	101.1±2.6	23±1.4	0.17±0.007	1419±72	17±3	2356±80
	Salt	1.4±0.08	0.12±0.007	24.6±2.3	103±5.1	0.013±0.001	0.034±0.008	103.3±6.3	17.8±0.8	0.15±0.009	1132±131	1254±61	2653±50
	Rel	31.8±1.38	34.95±2.73	105.2±22.6	104.4±5	78.4±9.3	71.3±20.3	103.5±8.2	81.2±3.1	89.14±6.632	84±11	8614±1684	113±3
Q34	Ctrl	3.1±0.19	0.24±0.012	16.2±1.2	101.4±5.8	0.01±0.002	0.037±0.004	85.6±3.8	24.7±1.5	0.18±0.008	1657±80	14±2	2408±53
	Salt	1±0.06	0.1±0.006	16.2±1.3	90.3±8.8	0.008±0.002	0.034±0.006	71.6±6.6	18.8±0.9	0.13±0.01	1514±228	2041±213	2837±296
	Rel	33.7±2.2	40.85±3.509	105.7±12.9	84.6±9.7	90.1±5.4	92.5±14.9	85.8±9.8	77.5±6.8	74±8.269	93±15	15666±2203	118±13
Q35	Ctrl	2±0.27	0.16±0.016	26.3±1.2	112.6±5.1	0.018±0.002	0.059±0.013	72±4	26.2±1.3	0.17±0.01	1757±184	36±8	2702±55
	Salt	1.4±0.1	0.14±0.01	41.2±2	101.5±4.6	0.024±0.003	0.073±0.005	83±1.2	18.5±0.4	0.14±0.012	1251±20	1935±128	2953±159
	Rel	75.6±10.12	87.74±13.669	162±14.6	90.7±4.8	145.9±15.2	154.4±37.4	116.4±6.2	71.2±2.8	81.45±8.495	75±9	6690±1550	109±6
Q36	Ctrl	3±0.3	0.23±0.025	26.5±2.3	95.4±3.5	0.014±0.002	0.061±0.003	75.5±3.5	24.2±1.2	0.16±0.004	1617±101	27±3	2530±69
	Salt	1.5±0.19	0.15±0.021	34.1±3	88.5±2.4	0.012±0.001	0.057±0.004	74.2±3.4	18.9±0.7	0.13±0.01	1417±153	2190±101	2820±80
	Rel	54.8±10.68	68.52±12.507	140.4±20.4	93.4±4.8	99.1±6	93.8±7	101.3±8.5	79.1±6	82.8±6.411	91±14	8578±1114	112±3
Q37	Ctrl	3.2±0.57	0.25±0.038	21.6±1.8	123.4±4.7	0.02±0.001	0.037±0.006	107.1±4.2	26±0.7	0.2±0.013	1527±106	41±12	2359±89
	Salt	1.5±0.17	0.15±0.015	20.9±2.1	117.1±2.5	0.017±0.001	0.039±0.008	105±3.5	20±0.4	0.15±0.013	1175±70	1765±69	2594±78
	Rel	52.6±10.41	68.62±13	108.3±18.3	95.3±3.2	86.7±11	126.4±39	99.1±4.6	77.3±2.6	74.55±5.912	78±7	5344±988	110±4
Q38	Ctrl	4.4±0.33	0.34±0.026	33.4±1.1	100.4±2.3	0.018±0.001	0.079±0.009	93.1±4.1	24.7±0.4	0.19±0.01	1597±97	8±1	2634±93
	Salt	1.5±0.16	0.13±0.018	44.2±4.2	104.3±1.7	0.027±0.002	0.071±0.011	80.2±2.1	19.6±1.8	0.13±0.004	1310±59	2148±323	2356±84
	Rel	34.5±5.19	39.14±7.948	135.4±16	104.1±3.1	162.8±29.7	100±22.3	88.1±5.7	79.6±7.9	70.72±4.439	82±2	27150±3104	90±4
Q40	Ctrl	6.6±0.46	0.64±0.061	46.8±2.4	106.3±3.9	0.029±0.002	0.078±0.011	97.7±2.8	22.6±0.6	0.16±0.01	1248±77	10±1	2411±66
	Salt	1.9±0.19	0.17±0.026	55.4±5.8	96.8±1.7	0.025±0.002	0.073±0.005	78.9±3.2	18.1±0.7	0.1±0.011	1149±110	1929±197	3222±96
	Rel	30.3±4.81	29.88±5.838	123.3±14.9	91.6±3.8	93.2±11.2	103.7±19.7	81.1±3	80.3±3.9	66.03±9.639	93±10	19264±3488	134±4
Q42	Ctrl	3±0.25	0.3±0.065	28.7±2.1	111.7±4.5	0.023±0.001	0.065±0.015	86.9±4.8	26.1±0.7	0.19±0.007	1790±138	12±2	2299±99
	Salt	1.5±0.14	0.13±0.011	45.1±2.6	102.3±3.8	0.026±0.001	0.067±0.009	72.4±4.1	17.3±0.4	0.15±0.008	1335±84	2885±290	1885±175
	Rel	50.3±2.37	51.04±8.611	164.9±14.7	91.7±2	119.6±12.6	118.6±20.9	85.4±6.2	66.7±2.9	77.63±3.439	76±7	27033±4612	82±7
Q45	Ctrl	2.1±0.28	0.19±0.017	25.7±1.7	110.6±3.6	0.02±0.002	0.06±0.012	78.7±3.6	27.4±0.5	0.16±0.008	1845±107	10±1	2306±94
	Salt	1.5±0.13	0.13±0.008	38.2±3	98.5±1	0.018±0.002	0.075±0.005	75.5±3	19.6±0.3	0.15±0.011	1470±95	1200±125	3221±117

	Rel	75.3±12.32	73.91±8.89	153.5±13.7	89.4±3.2	106.9±11.9	153.3±40.7	98.7±7.8	71.6±2.2	94.51±10.463	82±9	12257±1883	141±8
	Ctrl	6.1±0.54	0.55±0.066	41.4±2.3	101.3±2.8	0.022±0.001	0.088±0.006	90.3±2.1	23±0.7	0.16±0.01	1442±95	8±1	1977±77
Q49	Salt	1.9±0.19	0.19±0.028	47.9±3.5	99.7±1.8	0.025±0.003	0.059±0.006	103.1±4.5	16.9±1.1	0.16±0.008	1073±104	1485±261	2427±113
	Rel	31.5±4.46	36.96±7.219	117.1±7.9	98.9±4	115.6±10.3	69.5±10.4	114.5±5.2	73.5±4.3	98.21±9.809	76±9	20159±4534	124±10
	Ctrl	2.7±0.05	0.27±0.01	41.2±2.7	100±3	0.022±0.001	0.085±0.008	95.1±5.3	23.6±0.9	0.18±0.006	1561±122	17±4	1869±201
Q50	Salt	1.7±0.14	0.19±0.019	53±1.9	103.9±3.8	0.028±0.001	0.072±0.01	82.8±4.4	19.7±0.5	0.13±0.011	1298±91	1008±132	3028±111
	Rel	63.6±4.64	70.68±6.478	133.6±12	104±3.6	134.7±4.8	88.9±17.6	89.1±6.2	84.1±2.8	75.29±7.785	84±6	7228±1830	171±22
	Ctrl	5.4±0.65	0.51±0.068	26.7±2.7	110.7±6.2	0.019±0.001	0.06±0.009	96.2±6.6	24.9±0.9	0.18±0.015	1481±116	12±5	2202±82
Q51	Salt	2.9±0.31	0.31±0.052	58.2±4.1	96.9±1.6	0.028±0.003	0.077±0.009	99.2±3.6	17±0.6	0.12±0.01	1039±47	1956±292	2470±161
	Rel	54.4±8.64	61.46±11.88	246.3±41.2	88.9±6.2	159.9±17.1	152.2±43.8	106.4±6.9	68.9±4.5	72.1±7.863	72±8	26070±8950	120±5
	Ctrl	5.1±0.4	0.47±0.026	44.6±3.6	107.1±3.7	0.028±0.003	0.087±0.008	87.5±3.8	24.2±1.5	0.17±0.008	1479±109	11±2	2179±54
Q52	Salt	1.6±0.13	0.14±0.008	60.8±4.5	94.6±3.4	0.027±0.003	0.082±0.009	100.9±2.5	16.5±0.2	0.15±0.01	1100±35	1732±289	2655±150
	Rel	32.4±5.28	29.79±1.256	142.6±11.9	88.5±2.6	104.2±12.6	99.4±16.2	117.6±6.5	69.3±4.9	92.82±7.781	76±6	19722±4732	122±8
	Ctrl	4.6±0.64	0.38±0.046	34.9±2.2	101.3±3.5	0.019±0.001	0.07±0.008	105.2±7.2	23.5±1	0.19±0.02	1550±98	13±2	2354±86
Q53	Salt	1.4±0.11	0.12±0.01	53.5±3.2	92.5±0.9	0.024±0.001	0.084±0.01	109.1±2.3	16.8±0.4	0.14±0.007	1022±33	1813±126	2838±131
	Rel	35±5.23	36.83±8.321	155.6±9.8	91.9±4.2	121.8±15.3	127.3±21.7	109.4±9.5	71.8±3.6	72.27±6.172	67±3	15668±2753	121±7
	Ctrl	4.9±0.33	0.49±0.042	52.4±2.9	101.4±3.2	0.028±0.001	0.095±0.01	102.8±4.4	20.9±0.6	0.17±0.006	1249±72	11±1	2344±53
Q54	Salt	1.2±0.07	0.11±0.008	46.1±2.5	94.2±3.3	0.02±0.001	0.088±0.009	81.7±3.5	19±0.5	0.13±0.014	1367±81	1800±141	3169±72
	Rel	25.5±2.3	23.62±3.012	89±3.9	93.4±4.9	73.6±9.7	97.2±16.7	81±5.2	91.2±3.6	77.2±9.822	111±10	15810±1442	135±4
	Ctrl	4.2±0.28	0.35±0.034	30.6±2	116.4±2.8	0.025±0.002	0.065±0.009	94±4	25±0.6	0.18±0.005	1589±98	13±4	2837±145
Q56	Salt	1.5±0.15	0.11±0.007	40.3±3.1	95.2±2.2	0.019±0.002	0.072±0.01	73.9±3.9	20.5±1	0.13±0.01	1514±119	1966±216	2624±92
	Rel	37.7±3.98	31.71±3.684	135.4±11.2	82±2.7	76.6±8	118.9±25.9	79.3±4.5	81.9±3.4	75.84±6.633	96±9	19911±5282	94±7
	Ctrl	3.9±0.65	0.3±0.054	29.1±1.7	101.8±4.2	0.016±0.001	0.078±0.012	72.4±2.2	27.2±0.5	0.17±0.007	1951±61	11±2	2589±71
Q57	Salt	1.4±0.06	0.14±0.009	57.3±4	105.3±1.6	0.032±0.003	0.088±0.017	76.3±1.9	17.4±0.8	0.11±0.003	1228±58	1249±13	2088±60
	Rel	40.1±6.8	54.63±10.277	205±21.5	106.5±6	219.5±11.5	119.2±26.7	105.8±2.6	64.4±2.3	61.54±2.961	63±4	12641±2073	81±2
	Ctrl	7±0.47	0.64±0.064	19.2±2.4	119.1±5.3	0.016±0.001	0.031±0.008	108.2±5.8	25.1±1.3	0.17±0.013	1327±150	11±1	2000±96
Q58	Salt	2.1±0.18	0.23±0.034	28.7±2.8	106.1±1.7	0.017±0.002	0.04±0.007	99.4±6.3	23.1±3.7	0.17±0.018	1240±191	1251±23	2464±130
	Rel	31.8±4.85	38.2±8.539	179.9±29.2	90±5.3	111.9±8.2	148.6±30.6	93.8±6.8	94.6±18.5	103.09±17.17	97±17	11848±1580	125±11
	Ctrl	5.1±0.58	0.41±0.054	23.3±2.6	119.3±9.2	0.023±0.001	0.061±0.011	92.5±5.1	25.3±0.9	0.21±0.015	1803±178	28±5	2320±51
Q59	Salt	2.8±0.36	0.3±0.041	40.5±3.5	104.1±3.5	0.026±0.002	0.072±0.005	105.6±4.5	18.2±0.8	0.16±0.011	1228±125	2100±92	3330±208
	Rel	56.3±4.7	76.83±12.585	193.5±25.8	88.7±5.4	117.3±11.6	136.2±25.7	116±5.7	72.3±4.1	80.81±11.184	70±9	12280±6148	144±13
Q64	Ctrl	3.8±0.33	0.31±0.023	25.4±2	107.3±2	0.017±0.001	0.054±0.007	73.9±2.9	25.8±0.8	0.17±0.013	1821±109	10±2	2732±197

	Salt	1.7±0.15	0.21±0.02	40.5±2.4	92.5±1.6	0.017±0.001	0.064±0.003	75.7±3.8	17.8±0.3	0.13±0.005	1376±98	1465±268	2795±187
	Rel	48.2±6.65	67.98±9.942	167.2±14.1	86.3±2.6	100.5±8.1	127.7±18.4	103±4.7	68.9±1.1	74.65±6.318	76±4	16780±4393	103±4
Q65	Ctrl	3.7±0.22	0.29±0.031	42.5±2.2	117.4±3.9	0.034±0.001	0.087±0.003	93.6±4.5	20.9±0.6	0.17±0.003	1376±52	19±5	2425±22
	Salt	0.7±0.05	0.06±0.006	33.6±2.3	106.1±5.1	0.022±0.001	0.076±0.011	69.2±2.8	20.2±0.6	0.16±0.014	1577±67	1763±37	3061±105
	Rel	19.6±1.7	21.82±3.495	83.3±9.7	70.6±17.8	59±2.6	86.3±11.7	75.4±4.3	97.1±3.7	89.94±8.255	115±8	12136±2773	126±5
Q68	Ctrl	2.3±0.16	0.18±0.011	12.9±0.6	203.2±16.6	0.045±0.006	0.019±0.003	89.9±2.3	24.9±0.6	0.17±0.015	1758±102	23±4	2222±42
	Salt	1.6±0.07	0.16±0.012	29.8±2.2	120.3±2.7	0.028±0.002	0.024±0.002	111.9±3.7	15.7±0.6	0.1±0.014	926±76	1526±33	3977±79
	Rel	71.5±6.8	91.72±8.732	234.5±20.3	60.9±5.3	64.3±4.2	146.5±28	125.9±7.2	63.1±2.6	60.5±9.446	54±6	7925±1987	179±6
Q75	Ctrl	6.5±0.26	0.51±0.029	8.8±1.2	121±5.7	0.008±0.001	0.032±0.006	72.9±2.7	31.8±0.9	0.2±0.014	2177±121	50±17	3087±98
	Salt	1.5±0.1	0.16±0.011	16.6±1.1	111.7±2.8	0.012±0.001	0.032±0.005	75.7±1.9	21.1±0.7	0.13±0.008	1360±88	1368±175	2700±131
	Rel	23.1±1.52	32.87±2.478	297±93.5	93±4.2	169.8±14.1	122.6±33.5	105.2±4.9	66.7±3.7	64.8±5.774	63±5	5405±1996	88±6
Q76	Ctrl	6.3±0.41	0.52±0.036	10.8±1.3	132.9±4.6	0.015±0.001	0.034±0.008	110±3.5	25±0.7	0.18±0.008	1644±141	22±2	2052±39
	Salt	2±0.13	0.2±0.013	14.2±1.8	121.2±4.7	0.014±0.001	0.029±0.008	87.6±3.7	21.2±1.1	0.15±0.01	1666±313	1093±19	2454±52
	Rel	32±2.95	39.03±4.72	162.3±35.3	90.6±8.2	97.7±0.1	158.2±41.2	83.6±3.8	85±5	81.42±4.854	105±23	5321±661	120±5
Q77	Ctrl	6.7±0.41	0.64±0.033	19.8±1.4	135.1±7.2	0.025±0.002	0.036±0.007	120.5±4.2	24.4±0.6	0.2±0.024	1408±68	39±10	1911±83
	Salt	2±0.39	0.19±0.04	27.4±1.3	111.9±4.8	0.021±0.002	0.043±0.004	138.6±11.5	20±0.6	0.19±0.017	1159±83	1416±123	2659±88
	Rel	31.3±8.75	31.68±8.72	149.1±18.8	83.9±6.3	85.4±6.2	170.8±69.8	115.2±8.8	82±1.1	105.68±22.091	83±5	4416±894	140±7
Q78	Ctrl	6.2±0.42	0.5±0.035	9.7±0.8	130.9±5.5	0.01±0.001	0.038±0.008	90.3±3.2	29.7±0.5	0.24±0.019	2285±184	44±6	2253±359
	Salt	1.1±0.03	0.13±0.003	19.8±2	90.8±7.1	0.006±0.001	0.04±0.008	127.7±6.1	19.1±0.7	0.2±0.021	1291±198	1675±271	2667±145
	Rel	18.8±1.03	25.39±1.168	216±25.4	69.3±8.1	92.1±9	183.5±104	140.8±5.5	64.7±3.1	83.91±6.375	60±15	4381±1325	124±14
Q79	Ctrl	5.4±0.22	0.44±0.024	16.4±0.6	141±5.2	0.022±0.001	0.036±0.007	119.4±6.5	24.1±0.4	0.21±0.011	1477±33	54±6	1805±116
	Salt	1.1±0.04	0.09±0.003	12.7±1.5	113.1±6.1	0.008±0.001	0.024±0.005	128.5±7.1	20.5±0.8	0.24±0.018	1551±133	1957±97	2478±112
	Rel	20.1±1.27	20.11±1.228	77.5±8.4	81.5±2.5	43.8±4.2	63.5±15.5	109.7±7.2	85.1±2.9	118.28±13.399	105±9	3790±451	140±13
Q80	Ctrl	5.7±0.37	0.44±0.027	11±0.9	115.1±5	0.008±0.001	0.031±0.006	106.9±7.6	28.6±1.4	0.29±0.045	1998±194	42±11	2002±151
	Salt	1.1±0.04	0.12±0.004	19.8±1	107.7±1.7	0.014±0.001	0.038±0.003	103.3±6.3	19.6±0.5	0.16±0.013	1241±31	747±62	2897±43
	Rel	19.8±1.42	28.84±2.121	193.5±20.4	95.5±6.2	177.3±13.5	140.1±20.3	103.4±11.7	69.6±5	60.52±12.693	66±10	2255±575	147±8

Abbreviations:

DW: dry weight; FW: fresh weight; BD: bladder density; BDM: bladder diameter; BV: bladder volume; BI: bladder index; SD: stomatal density; SL: stomatal length; ECA: epidermal cell area; Na^+: leaf Na^+ concentration; K^+: leaf K^+ concentration

Authors statement

The authors declare that they have no conflict of interest