Potassium is a potential toxicant for *Arabidopsis thaliana* under saline conditions

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Abstract

Background and aims: Most physiological and biochemical studies on salt stress are NaCl-based. However, other ions (*e.g.*, K^+, Ca^{2+}, Mg^{2+}, and SO_4^{2-}) also contribute to salt stress in special circumstances. In this study, salt stress induced by various salts was investigated for a better understanding of salinity.

Methods: *Arabidopsis thaliana* plants were stepwise acclimated to five iso-osmotic salts as follows: NaCl, KCl, Na_2SO_4, K_2SO_4, and $CaCl_2$.

Results and Conclusions: Exposure to KCl and K_2SO_4 led to more severe toxicity symptoms, smaller biomass, and lower level of chlorophyll than exposure to NaCl and Na_2SO_4, indicating that *Arabidopsis* plants are more sensitive to potassium salts. The strongly reduced growth was negatively correlated with the accumulation of soluble sugars observed in KCl- and K_2SO_4-treated plants, suggesting a blockage in the utilization of sugars for growth. We found that exposure to KCl and K_2SO_4 suppressed or even blocked sucrose degradation, thus leading to strong accumulation of sucrose in shoots, which then probably inhibited photosynthesis *via* feedback inhibition. Moreover, K^+ was more accumulated in shoots than Na^+ after corresponding potassium or sodium salt treatments, thus resulting in decreased Ca^{2+} and Mg^{2+} concentrations in response to KCl and K_2SO_4. However, K_2SO_4 caused more severe toxicity symptoms than iso-osmotic KCl, even when the K^+ level was lower in K_2SO_4-treated plants. We found that Na_2SO_4 and K_2SO_4 induced strong accumulation of tricarboxylic acid intermediates, especially fumarate and succinate which might induce oxidative stress. Thus, the severe toxicity symptoms found in K_2SO_4-treated plants were also attributed to SO_4^{2-} in addition to the massive accumulation of K^+.

Key words: fumarate / potassium salts / succinate / sucrose degradation / sucrose transport

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Supporting Information available online

1 Introduction

Salinity is one of the major threats to crop yield worldwide (*Munns* and *Tester*, 2008). The physiological and molecular mechanisms of salt stress in plants have been well documented (*Zhu*, 2001; *Munns* and *Tester*, 2008). Most of the results are derived from NaCl–stress experiments, since Na^+ and Cl^- often dominate in saline soils (*Rengasamy*, 2006). However, apart from Na^+ and Cl^-, other ions may also contribute to salt stress such as K^+ and SO_4^{2-} (*Chang* et al., 1983; *Rengasamy*, 2006). The principle sources of K^+ in soils are potassium fertilizers and K^+-rich minerals such as granite dust, greensand, muscovite, biotite, and feldspars. The unusual K^+ accumulation in soils might be attributed to heavy application of K^+ fertilizers (*Parnes*, 2013), and extreme weathering of K^+-rich minerals (*Hillel*, 2008). Many soils in eastern U.S. show an excess of K^+ because of over-application of organic residues (*Parnes*, 2013). Minerals such as micas and feldspars have significant amounts of potassium and this element is released by weathering to make it available for plants. If the weathering process is prolonged and the leaching system is incomplete, soils will reach high potassium concentrations such as the soils in northwest Missouri (*Hillel*, 2008). Thus, it is necessary to conduct experiments with salt stress induced by other salts (*e.g.*, Na_2SO_4 and KCl) for a more comprehensive understanding of salt stress.

Plants suffer salt stress in three phases (*Munns*, 1993; *Munns* and *Tester*, 2008; *Schubert*, 2011). First, after the application of salt treatment, transient decreases in turgor and growth rate occur in Phase 0 (the first few minutes or hours) (*Schubert*, 2011). Second, plants then show stunted growth which is attributed to salinity-induced osmotic stress (Phase 1) (*Munns*, 2002). The osmotic effect induced by salt stress in Phase 1 is similar to that caused by drought stress, thus it is not salt-specific (*Chazen* et al., 1995). Finally, ion toxicity symptoms develop resulting from ion accumulation over time (Phase 2). Generally, ion toxicity symptoms mainly occur in old leaves as they are transpiring and accumulating ions for a longer time period than young leaves (*Munns*, 2002).

During Phase 2, the Na^+ accumulation interferes with K^+ homeostasis and the imbalance of K^+ is responsible for a

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large proportion of Na^+ toxicity (*Kronzucker* et al., 2013). Proper potassium fertilization can alleviate the damages caused by NaCl stress (*Wakeel* et al., 2011). However, K^+ does not always benefit organisms and it can be harmful when taken up in excess. In the human body, excessive K^+ in the blood leads to tingling, decreased reflexes, and muscle weakness (*Viera* and *Wouk*, 2015). Previous researchers observed that both NaCl and KCl reduced the biomass of plants at relatively high concentrations, but plants treated with NaCl such as *Triticum aestivum* (*Adiloglu* et al., 2007) and *Brassica rapa* (*Reich* et al., 2017) showed higher reductions in biomass. For *Arabidopsis thaliana*, an important model plant in plant biology, it is unknown whether potassium salts are toxic. This leads to our first hypothesis that high concentrations of sodium salts and potassium salts can reduce the growth of *Arabidopsis* plants and that plants are more sensitive to salt stress induced by sodium salts compared to potassium salts.

Apart from Na^+ toxicity, Cl^- toxicity is another important topic in salinity research. Many important fruits (*e.g.*, strawberry) and vegetables (*e.g.*, tomato, bean, and soybean) cannot tolerate Cl^- levels above 40 mg g^{-1} dry weight (*White* and *Broadley*, 2001; *Hütsch* et al., 2018). However, sulfate salts can also exceed the tolerable level of plants in some marine soils as well as in areas that are affected by secondary salinization induced by saline irrigation water (*Chang* et al., 1983). Thus, a comparison of plant responses to chloride salts and sulfate salts is necessary. Sulfate salts (*e.g.*, Na_2SO_4) have a higher inhibitory effect on plant growth than chloride salts (*e.g.*, NaCl) in *Prosopis strombulifera* (*Llanes* et al., 2013; *Reginato* et al., 2014), *Thellungiella salsuginea* (*Leonova* et al., 2009), *T. botschantzevii* (*Leonova* et al., 2009), *Triticum aestivum* (*Hampson* and *Simpson*, 1990), and *Brassica rapa* (*Aghajanzadeh* et al., 2017; *Reich* et al., 2017). In those plants, Na_2SO_4 induced higher reductions in germination rate, shoot height, leaf number, and biomass, even when the SO_4^{2-} concentration was much lower than the Cl^- concentration in the NaCl-treated plants. This leads to our second hypothesis that sulfate salts have a higher inhibitory effect on the growth of *Arabidopsis* plants than chloride salts.

In order to test our hypotheses, *Arabidopsis* plants were stepwise acclimated to five iso-osmotic salts (NaCl, KCl, Na_2SO_4, K_2SO_4, and $CaCl_2$) to avoid differences caused by osmotic stress. Plants were harvested when the toxicity symptoms occurred at least in one treatment to make sure that plants were starting to enter Phase 2. Biomass, chlorophyll concentration, and sugar concentrations were determined to test the growth of *Arabidopsis* plants under various salt treatments. Moreover, mineral nutrient composition of plants treated with different salts were determined to evaluate whether Na^+ or K^+ was more toxic in *Arabidopsis*, as well as to investigate the contribution of Cl^- and SO_4^{2-} to the toxicity symptoms.

2 Material and methods

2.1 Plant material and growth conditions

Arabidopsis thaliana (L.) (ecotype: Col-0) was used throughout the study. Plants were cultivated in a growth chamber with 21°C and light (200 μmol m^{-2} s^{-1}) for 8 h and 18°C without light (0 μmol m^{-2} s^{-1}) for 16 h. The hydroponic culture consisted of 1 mM KH_2PO_4, 0.25 mM K_2SO_4, 1 mM $MgSO_4$, 2 mM $Ca(NO_3)_2$, 50 μM KCl, 5 μM $MnSO_4$, 1 μM $ZnSO_4$, 1 μM $CuSO_4$, 0.1 μM $NiSO_4$, 0.7 μM $(NH_4)_6Mo_7O_{24}$, 30 μM H_3BO_3, and 100 μM FeNaEDTA. Four-week-old seedlings were stepwise acclimated to five iso-osmotic salt treatments. For each treatment, 15.00 mM NaCl, 15.34 mM KCl, 11.23 mM Na_2SO_4, 11.70 mM K_2SO_4, and 10.61 mM $CaCl_2$ were applied every 24 h until reaching final concentrations of 105.00, 107.38, 78.61, 81.90, and 74.27 mM, respectively. Experiments were conducted in seven biological replicates (*i.e.*, seven 3-L pots). For each pot, there were three plants. The nutrient solution was changed every 3 d. Plants were harvested after 12 d of treatment with 105 mM NaCl, iso-osmotic KCl, Na_2SO_4, K_2SO_4, and $CaCl_2$. Four biological replicates (*i.e.*, four pots) were harvested to determine the dry weight, chlorophyll (N-tester), ion concentrations, and sugar concentrations. In these experiments, the entire rosette leaves were harvested. The other three biological replicates (*i.e.*, three pots) were harvested for the GC-MS and qRT-PCR analyses. Mature rosette leaves from 9th leaf to 14th leaf were harvested because these leaves showed toxicity symptoms under salt stress especially after exposure to KCl and K_2SO_4. The most severely affected young leaves were not harvested because they were totally bleached under stress in some treatments.

2.2 N-tester values

After 12 d of treatment with the salts described above, all the rosette leaves were tested by the hand-held Yara N-tester (Yara, Norway), except the cotyledons and the first and second-produced leaves because they were too small to take a measurement. Thirty random-point measurements on the rosette leaves were pooled in one read and four reads were obtained for each treatment. Yara N-tester allows estimating chlorophyll concentration without damaging the plants (*Faust* and *Schubert*, 2016).

2.3 Quantification of ion concentrations

Shoots and roots were harvested separately and dried at 80°C for three days in an oven. Then, the dried samples were ground to powder in a coffee grinder. To determine Na^+, K^+, Ca^{2+}, and Mg^{2+} concentrations, 200 mg of shoot dry matter (or 100 mg of root dry matter) were weighed into a ceramic alumina crucible, then dry-ashed at 550°C for 12 h in a muffle furnace. After cooling down of samples, 2.5 mL 5 M HNO_3 and 2 mL double-deionized water were added and briefly heated to dissolve the ash. The mixed solution was filtered into a 50-mL volumetric flask with hot double-deionized water, and diluted to 50 mL with double-deionized water after cooling down. Samples were automatically diluted by Varian SPS5 and injected into the atomic absorption spectrophotometer (SpectrAA220 FS, Varian, Mulgrave, Victoria, Australia) (*Pitann* et al., 2013).

To determine Cl^- and SO_4^{2-} concentrations, 50 mg of shoot dry matter (or 50 mg of root dry matter) were weighed into a test tube, 3 mL double-deionized water were added and

boiled in a water bath at 100°C for 3 h. Samples were filtered into a 25-mL volumetric flask, cooled, and filled up to 25 mL with double-deionized water. Samples were automatically injected by a 788 IC filtration sample processor into the ion chromatograph (761 Compact IC, Metrohm). The determined ion concentrations in shoots and roots were listed in Tab. S1.

Ion (Na^+, K^+, Ca^{2+}, and Mg^{2+}) uptake was calculated as follows:

$$\textit{Ion uptake} = \textit{Shoot ion content} + \textit{Root ion content}, \quad (1)$$

Ion translocation from roots to shoots is described by:

$$\textit{Ion translocation from roots to shoots} = \frac{\textit{Shoot ion content}}{\textit{Root ion content}}. \quad (2)$$

2.4 Determination of TCA intermediates

The TCA intermediates were determined by means of GC-MS. For GC-MS analysis, 200–300 mg of fresh mature rosette leaves (from 9th leaf to 14th leaf) were harvested and snap-frozen in liquid nitrogen. Approximately 500 mg pre-cooled beads were added to the samples in an Eppendorf tube and homogenized mechanically in a Retsch MM300 tissuelyzer (3 min, 30 Hz). Then, 1 mL of pre-cooled MeOH : chloroform : water (5 : 2 : 2) was added, vortexed, and homogenized mechanically in a Retsch MM300 tissuelyzer (6 min, 30 Hz). After centrifugation (30,000 *g*, 4°C, 5 min), 800 μL of the supernatant were transferred to a new tube and dried under nitrogen flow. Samples were reconstituted in 100 μL double-deionized water and derivatized with methyl chloroformate (MCF) according to the protocol described by *Smart* et al. (2010). For MCF derivatization, 37 μL NaOH (1 M), 25 μL pyridine, 75 μL methanol, and 10 μL MCF were added to an aliquot of 37 μL reconstituted sample and subsequently made a vortex for 30 s. Then, another 10 μL MCF were added and mixed vigorously for another 30 s. The derivatization reaction was stopped by adding 200 μL chloroform. D3-alanine was added as an internal standard (0.2 μmol per sample). All samples were analyzed in a randomized order. Analysis was performed using GC (7890B, Agilent) coupled with a quadrupole detector (59977B, Agilent). The system was controlled by ChemStation (Agilent). Chromatograms and mass spectra were processed by means of Chemstation (Agilent) and Matlab R2014b (Mathworks, Inc.) (*Johnsen* et al., 2017) to obtain analyzable chromatographic peak height and retention time. For the metabolite identification, the processed data were then matched with the mass spectral library NIST/EPA/NIH Mass spectral library (Version 2). The peaks of mass fragments were normalized against internal standard (d3-alanine) and sample fresh weight.

2.5 Sugar concentrations

For the determination of soluble sugars (*i.e.*, glucose, fructose, and sucrose), 200 mg of dried and ground shoot or root material were weighed in a 50-mL volumetric flask, then 30 mL hot double-deionized water were added. Samples were incubated at 60°C for 30 min, then filled up to 50 mL with double-deionized water after cooling down, finally filtered for the determination. The soluble sugars were measured enzymatically (R-Biopharm, Germany).

To measure the starch concentrations, 30 mg of the dried and ground shoot material were mixed with 1.8 mL 18% (w/v) HCl in a 2-mL reaction tube. Starch was extracted at 5°C for 60 min and centrifuged at 5,000 *g* for 20 min. Then, 300 μL of supernatant were mixed with 300 μL of Lugol's solution [0.5% (w/v) KI and 0.25% (w/v) I_2 in water] and determined at 530 nm and 605 nm. The starch concentration was calculated based on the method of *Appenroth* et al. (2010).

2.6 qRT-PCR

After 12 d of treatments with five iso-osmotic salts described above, 200–300 mg of fresh mature rosette leaves (from leaf number 9 to 14) were harvested to extract total RNA using RNeasy Plant Mini Kit (Qiagen). Then, total RNA was reversely transcribed by means of RevertAid First Strand cDNA Synthesis Kit (Thermo Scientific). qRT-PCR was performed in a StepOnePlus system (Applied Biosystems). The relative transcript level of genes was calculated by $2^{-\Delta\Delta Ct}$. ΔCt is the Ct value of tested target gene subtracted by the geometric mean of the Ct value of endogenous reference genes, SAND family protein (At2g28390) and TIP41-like protein (At4g34270) (*Czechowski* et al., 2005; *Dekkers* et al., 2012). $\Delta\Delta Ct$ is the difference between ΔCt under experimental conditions and ΔCt under control condition. Transcriptional FoldChange of a target gene was quantified as the quotient of its $2^{-\Delta\Delta Ct}$ value after salt treatments and that under control conditions. The value of $|\log_2 \text{FoldChange}| \geq 1$ was used as cutoff to evaluate significant differences in gene transcription. Primers used for qRT-PCR are listed in Tab. S2. The single target bands shown in supplementary Fig. S1 indicate high specificity of primers. The Ct values obtained from real-time PCR instrument are listed in Tab. S3.

2.7 Statistical analysis

Experiments in this study were conducted in four biological replicates, except for the qRT-PCR analysis and determination of TCA intermediates (three replicates). Data are presented as means ± standard errors (SE). Significant differences among treatments were statistically evaluated by one-way ANOVA and post-hoc analysis using Tukey's Honestly Significant Difference (HSD) method (SciStatCalc: http://scistatcalc.blogspot.com/2013/11/home.html) and are indicated by different letters ($P < 5\%$). Significant differences between two treatments are indicated by asterisks (*$P < 5\%$, **$P < 1\%$, ***$P < 0.1\%$, ****$P < 0.01\%$, *t*-test).

3 Results

3.1 Potassium salts induce more severe toxicity than sodium salts in Arabidopsis

Exposure to 105 mM NaCl caused no toxicity symptoms even after 12 d of treatment, while iso-osmotic KCl-treated plants showed chlorosis in young leaves after only 2 days of treat-

ment and the chlorosis progressed to old leaves with the extending treatment time (Fig. 1). After 2 d of treatment with 78.61 mM Na_2SO_4, plants showed no obvious toxicity symptoms. In contrast, iso-osmotic K_2SO_4 induced cell death in young leaves after 2 d of treatment, which was even more toxic than iso-osmotic KCl (Fig. 1a). When the treatment time was extended to 12 d, the Na_2SO_4-treated plants displayed small-scale necrosis at the leaf margins of old leaves and the K_2SO_4-treated plants showed necrosis in almost all the area of young leaves (Fig. 1b). Hence, plants treated with potassium salts (KCl and K_2SO_4) showed more severe toxicity symptoms compared to the corresponding iso-osmotic sodium salts (NaCl and Na_2SO_4). Plants treated with iso-osmotic $CaCl_2$ did not show toxicity symptoms even after 12 d of treatment (Fig. 1).

Shoot dry weight, root dry weight, and N-tester values were determined to examine plant growth under various salt stresses. Exposure to 105 mM NaCl for 12 d led to a reduction (35%) of shoot dry weight compared to control, while iso-osmotic KCl had a more severe inhibitory effect (52% reduction, not significant) on shoot dry weight (Fig. 2a). Similarly, shoot dry weight had a reduction of 28% or 64% in response to iso-osmotic Na_2SO_4 or K_2SO_4, being more severely suppressed by K_2SO_4 treatment (Fig. 2a). Root dry weight was not substantially altered after NaCl, KCl, and Na_2SO_4 treatments. However, it displayed a dramatic reduction after exposure to iso-osmotic K_2SO_4 and even increased in iso-osmotic $CaCl_2$-treated plants (Fig. 2b). Exposure to NaCl, Na_2SO_4, and $CaCl_2$ had no substantial effect on N-tester values, which reflect chlorophyll concentration. In contrast, the N-tester values decreased dramatically in KCl and K_2SO_4-treated plants (Fig. 2c).

3.2 Uptake and translocation of Na^+, K^+, Ca^{2+}, and Mg^{2+} under various salt stresses

The uptake of Na^+, translocation of Na^+ into shoots, and Na^+ concentration in shoots were always higher in plants treated with iso-osmotic Na_2SO_4 (157.22 mM Na^+ in hydroponic culture) than in plants treated with 105 mM NaCl (Fig. 3a–c), probably due to the higher external Na^+ in the Na_2SO_4 treatment. However, the uptake of K^+ by K_2SO_4-treated plants was lower than that by iso-osmotic KCl-treated ones (Fig. 3a). The translocation of K^+ into shoots was not altered by KCl treatment, but showed an increase under K_2SO_4 treatment compared to control (Fig. 3b). Surprisingly, exposure to K_2SO_4 (163.8 mM K^+ in hydroponic culture) led to lower K^+ concentration in shoots compared to iso-osmotic KCl treatment (107.38 mM K^+ in hydroponic culture), although the external K^+ concentration was even higher in the K_2SO_4 treatment (Fig. 3c).

Figure 1: Phenotypes of *Arabidopsis thaliana* under 105 mM NaCl, iso-osmotic KCl, iso-osmotic Na_2SO_4, iso-osmotic K_2SO_4, and iso-osmotic $CaCl_2$ treatments for 2 d (a) and 12 d (b). The 4-week-old seedlings were exposed to gradually increasing concentrations of NaCl (15.00 mM), KCl (15.34 mM), Na_2SO_4 (11.23 mM), K_2SO_4 (11.70 mM), and $CaCl_2$ (10.61 mM) every 24 h until reaching a final concentration of 105.00 mM, 107.38 mM, 78.61 mM, 81.90 mM, and 74.27 mM, respectively.

The uptake and translocation of dominant cations (Na^+ and K^+) under corresponding sodium and potassium salt treatments were compared. In the presence of Cl^-, KCl-treated plants showed higher levels of K^+ uptake and translocation compared to the Na^+ uptake and translocation in iso-osmotic NaCl-treated plants, resulting in the strong accumulation of K^+ after exposure to KCl (Fig. 3a–c). In contrast, exposure to K_2SO_4 led to lower K^+ uptake than Na^+ uptake induced by iso-osmotic Na_2SO_4 (Fig. 3a), but the translocation of K^+ or Na^+ under K_2SO_4 or Na_2SO_4 treatments was similar (Fig. 3b). Nevertheless, the K_2SO_4-treated plants still displayed higher K^+ concentration in shoots than Na^+ in response to iso-osmotic Na_2SO_4 (Fig. 3c).

The Ca^{2+} and Mg^{2+} uptake and translocation into shoots were significantly reduced in all salt treatments except the uptake of Ca^{2+} in plants treated with $CaCl_2$ (Fig. 3d–f). Exposure to 107.38 mM KCl induced a higher inhibitory effect on the uptake and translocation of Ca^{2+} and Mg^{2+} than exposure to 105 mM NaCl, thus resulting in lower Ca^{2+} and Mg^{2+} concentrations in the shoots of KCl-treated plants (Fig. 3d–f). Similarly, plants treated with 81.90 mM K_2SO_4 showed

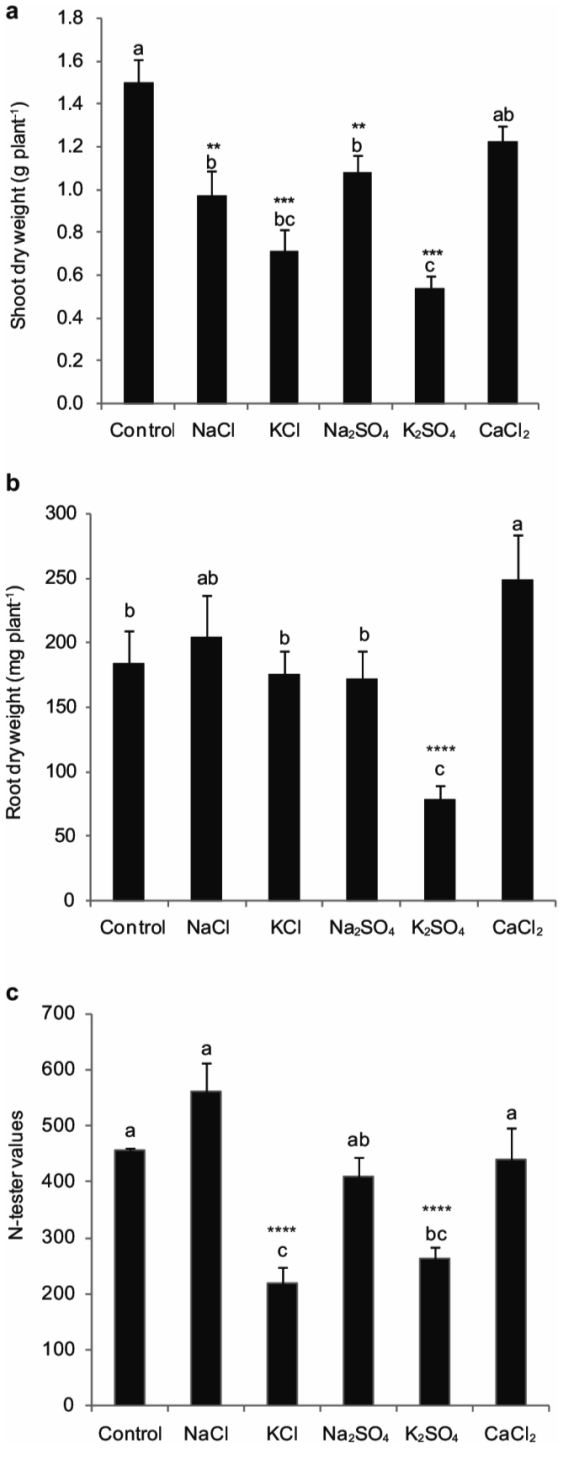

Figure 2: Growth responses of *Arabidopsis thaliana* to five iso-osmotic salt treatments. Four-week-old seedlings were treated with 105 mM NaCl, 107.38 mM KCl, 78.61 mM Na_2SO_4, 81.90 mM K_2SO_4, and 74.27 mM $CaCl_2$ for 12 d. Shoot dry weight (a), root dry weight (b), and N-tester values of rosette leaves (c) were determined. Data show means of four replicates. Error bars represent standard errors (SE). Significant differences are indicated by different letters ($P < 5\%$; one-way ANOVA and post-hoc analysis using Tukey's Honestly Significant Difference method) and by asterisks (*, **, ***, **** significant differences of fresh weight, dry weight, and N-tester values under five iso-osmotic salt treatments in comparison to the control with $P < 5\%$, 1%, 0.1%, 0.01% respectively; *t*-test).

lower levels of Ca^{2+} uptake and concentration in shoots as well as Mg^{2+} than those treated with 78.61 mM Na_2SO_4 (Fig. 3d, f). Considering the translocation of Ca^{2+} and Mg^{2+}, K_2SO_4-treated plants also displayed lower levels of Ca^{2+} translocation than Na_2SO_4-treated ones, but the translocation of Mg^{2+} showed similar reductions after exposure to Na_2SO_4 and K_2SO_4 (Fig. 3e).

3.3 Effects of chloride and sulfate salts on the accumulation of TCA intermediates

The Cl^- concentration in shoots showed significant increases after exposure to NaCl, KCl, and $CaCl_2$ (Fig. 4a, b). The plants treated with KCl showed the strongest accumulation of Cl^- in shoots followed by the $CaCl_2$- and NaCl-treated plants (Fig. 4a). The shoot concentration of SO_4^{2-} presented higher levels in K_2SO_4-treated plants than in Na_2SO_4-treated ones (Fig. 4b). Moreover, the Cl^- concentration under chloride salt treatments was extremely higher than the concentration of SO_4^{2-} under iso-osmotic sulfate salt treatments (Fig. 4).

The TCA cycle is a series of chemical reactions that contribute to the production of chemical energy in the form of NADH + H^+ and ATP. The concentration of tested TCA intermediates (sum of concentrations of fumarate, succinate, α-ketoglutarate, isocitrate, cis-aconitate, and citrate) had no substantial differences after exposure to 105 mM NaCl and iso-osmotic KCl for 12 d, while exposure to Na_2SO_4 and K_2SO_4 increased the total amount of TCA intermediates, twice as much as that in control (Tab. 1). These increases were mainly due to fumarate and succinate. The fumarate concentration in Na_2SO_4- and K_2SO_4-treated plants showed 2.4- and 2.7-fold increases compared to control, respectively (Tab. 1). Considering succinate, exposure to K_2SO_4 induced the highest accumulation of succinate in shoots (7.4-fold higher compared to control) followed by exposure to Na_2SO_4 which led to 3.9-fold increases (Tab. 1).

3.4 Effects of sodium and potassium salts on sugar concentrations

The total concentration of tested soluble sugars (*i.e.*, glucose, fructose, and sucrose) increased after salt treatments both in shoots and roots (Fig. 5a, b). Among these, sucrose was the major soluble sugar in salt-treated *Arabidopsis* plants. In shoots, plants accumulated sucrose under all five iso-osmotic salt treatments, displaying the strongest accumulation in plants treated with potassium salts (KCl and K_2SO_4) (Fig. 5a). Different from sucrose, the concentration of glucose and fructose remained unaffected by NaCl, KCl, and Na_2SO_4 treatments, but increased after exposure to K_2SO_4 and $CaCl_2$ (Fig. 5a). In roots, the concentration of total tested soluble sugars also increased after salt treatments, but was significantly lower than that in shoots (Fig. 5b). The starch concentration was not substantially altered in shoots after exposure to NaCl, KCl, and Na_2SO_4. However, KCl and K_2SO_4-treated plants showed a reduction (38% or 23%) of starch concentration compared to control (Fig. 5c).

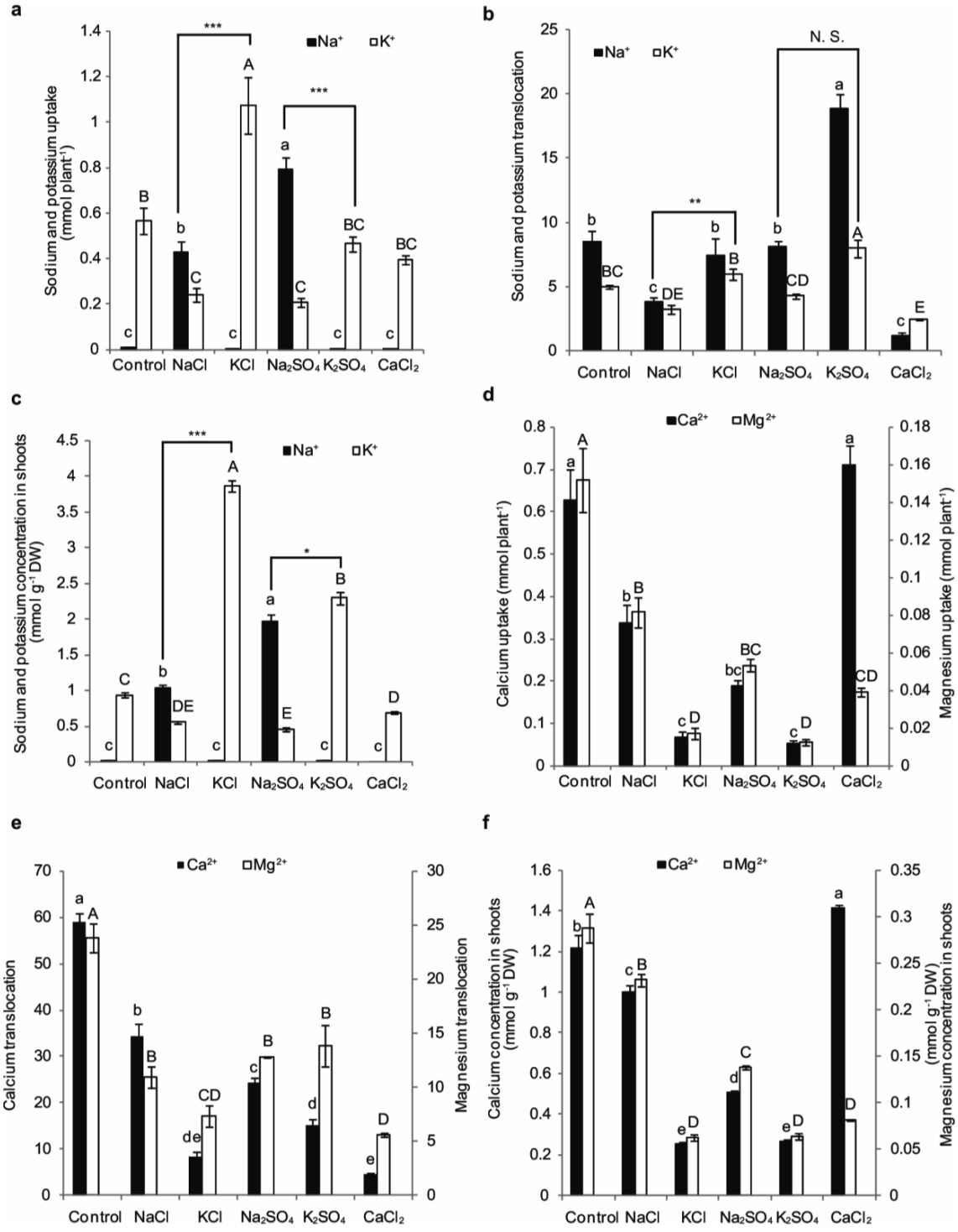

Figure 3: Effect of sodium and potassium salts on the uptake, translocation, and concentration of cations (Na^+, K^+, Ca^{2+}, and Mg^{2+}). Four-week-old seedlings were treated with 105 mM NaCl, 107.38 mM KCl, 78.61 mM Na_2SO_4, 81.90 mM K_2SO_4, and 74.27 mM $CaCl_2$. After 12 d, Na^+ and K^+ uptake (a), translocation into shoots (b), and concentrations in shoots (c) were calculated. In parallel, the Ca^{2+} and Mg^{2+} uptake (d), translocation (e), and shoot concentrations (f) were determined. DW indicates dry weight, and N.S. indicates no significant difference. Data represent the means of four replicates (± SE). Significant differences of cation uptake, translocation, and shoot concentration among treatments are indicated by different letters ($P < 5\%$; one-way ANOVA and post-hoc analysis using Tukey's Honestly Significant Difference method). The lower-case letters indicate statistical differences among treatments in regard to sodium and calcium; the capital letters indicate statistical differences among treatments in regard to potassium and magnesium. The significant differences of K^+ uptake, translocation, and concentration under KCl or K_2SO_4 treatments in comparison to Na^+ uptake, translocation, and concentration under NaCl or Na_2SO_4 treatments are indicated by asterisks (*$P < 5\%$, **$P < 1\%$, ***$P < 0.1\%$, ****$P < 0.01\%$, *t*-test).

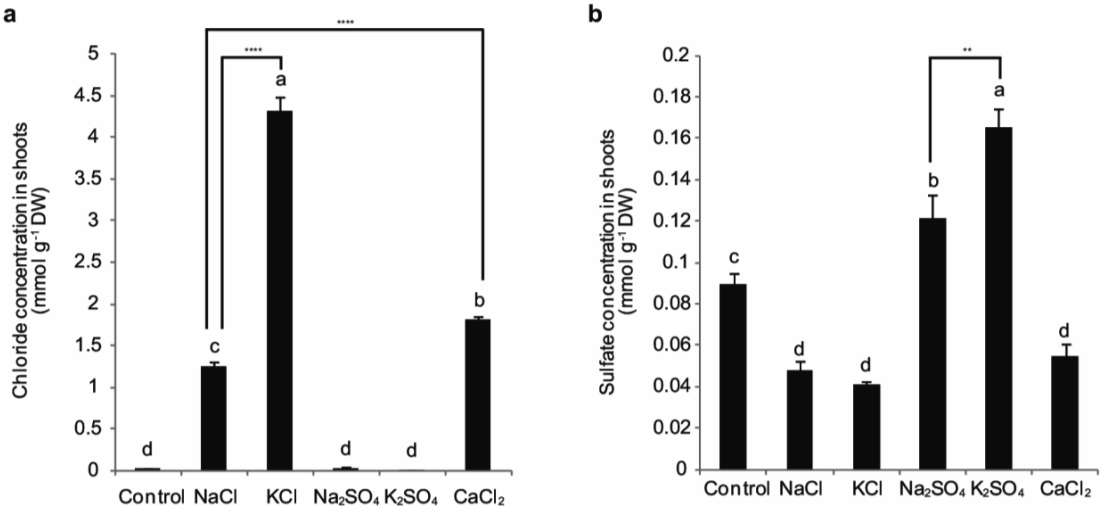

Figure 4: Effect of chloride and sulfate salts on Cl^- and SO_4^{2-} accumulation in shoots. Four-week-old seedlings were exposed to 105 mM NaCl, 107.38 mM KCl, 78.61 mM Na_2SO_4, 81.90 mM K_2SO_4, and 74.27 mM $CaCl_2$. After 12 d, the concentrations of Cl^- (a) and SO_4^{2-} (b) in shoots were calculated. DW indicates dry weight. Data represent the means of four replicates (± SE). Significant differences of Cl^- and SO_4^{2-} shoot concentrations among treatments are indicated by different letters (P < 5%; one-way ANOVA and post-hoc analysis using Tukey's Honestly Significant Difference method). The significant differences of Cl^- concentration under KCl and $CaCl_2$ treatments in comparison to that under NaCl treatment are indicated by asterisks (*P < 5%, **P < 1%, ***P < 0.1%, ****P < 0.01%, t-test). The significant differences of SO_4^{2-} concentration in Na_2SO_4-treated plants in comparison to those treated with K_2SO_4 are indicated by asterisks (*P < 5%, **P < 1%, ***P < 0.1%, ****P < 0.01%, t-test).

Table 1: Effect of five iso-osmotic salt treatments on tested TCA intermediates (μmol mg^{-1} DW). Four-week-old seedlings were exposed to 105 mM NaCl, 107.38 mM KCl, 78.61 mM Na_2SO_4, 81.90 mM K_2SO_4, and 74.27 mM $CaCl_2$. After 12 d of salt treatment, the concentrations of TCA intermediates in rosette leaves were determined by means of GC-MS analysis. Data represent the means of three replicates (± SE). DW indicates dry weight.

TCA	Treatment					
	Control	NaCl	KCl	Na_2SO_4	K_2SO_4	$CaCl_2$
Fumarate	176.80 ± 9.44	263.10 ± 20.49	234.18 ± 18.06	428.66 ± 34.75	479.58 ± 3.62	120.13 ± 5.04
Succinate	8.60 ± 1.69	5.92 ± 0.85	10.17 ± 0.68	33.34 ± 0.95	63.67 ± 5.71	3.89 ± 0.13
α-Ketoglutarate	0.89 ± 0.07	1.66 ± 0.32	15.00 ± 0.95	18.19 ± 2.25	14.37 ± 1.25	3.03 ± 0.24
Isocitrate	0.07 ± 0.01	0.07 ± 0.01	0.47 ± 0.06	1.36 ± 0.19	0.14 ± 0.02	0.11 ± 0.01
cis-Aconitate	4.28 ± 0.24	1.74 ± 0.26	3.13 ± 0.36	7.93 ± 0.95	2.51 ± 0.33	0.74 ± 0.11
Citrate	184.18 ± 7.07	64.99 ± 5.85	110.19 ± 14.02	286.84 ± 11.81	190.26 ± 4.97	43.66 ± 1.76
Total TCA intermediates	374.80 ± 3.65	337.49 ± 17.33	373.14 ± 6.39	776.33 ± 33.91	750.52 ± 9.11	171.57 ± 6.73

In order to understand the largely accumulated sucrose after potassium salt treatments, the transcription of genes related to sucrose synthesis, sucrose degradation, and sucrose transport was determined *via* qRT-PCR. The absolute value of $\log_2$ FoldChange ≥ 1 was used as cutoff to evaluate significant differences in gene transcription. Sucrose is synthesized from UDP-glucose and fructose-6-phosphate *via* sucrose phosphate synthase (SPS), a key enzyme for sucrose synthesis. Four SPS genes (*i.e., SPS1, SPS2, SPS3*, and *SPS4*) have been characterized in *Arabidopsis thaliana* (*Ruan*, 2014). After exposure to five iso-osmotic salts, the transcription of *SPS1* and *SPS3* was not modified, while *SPS2* was induced and *SPS4* was repressed (Fig. 6a). The transcription of *SPS2* showed a similar level in plants treated with NaCl or KCl, as well as in plants treated with K_2SO_4 or Na_2SO_4. The transcription of *SPS4* was more strongly suppressed by potassium salts (KCl and K_2SO_4) compared to corresponding sodium salts (NaCl and Na_2SO_4) (Fig. 6a).

Two sucrose-cleaving enzymes contribute to sucrose degradation: invertase and sucrose synthase (SUS). Invertase hydrolyzes sucrose irreversibly into glucose and fructose, while SUS cleaves sucrose reversibly into fructose and UDP-glucose (or ADP-glucose) (*Stein* and *Granot*, 2019). SUS not

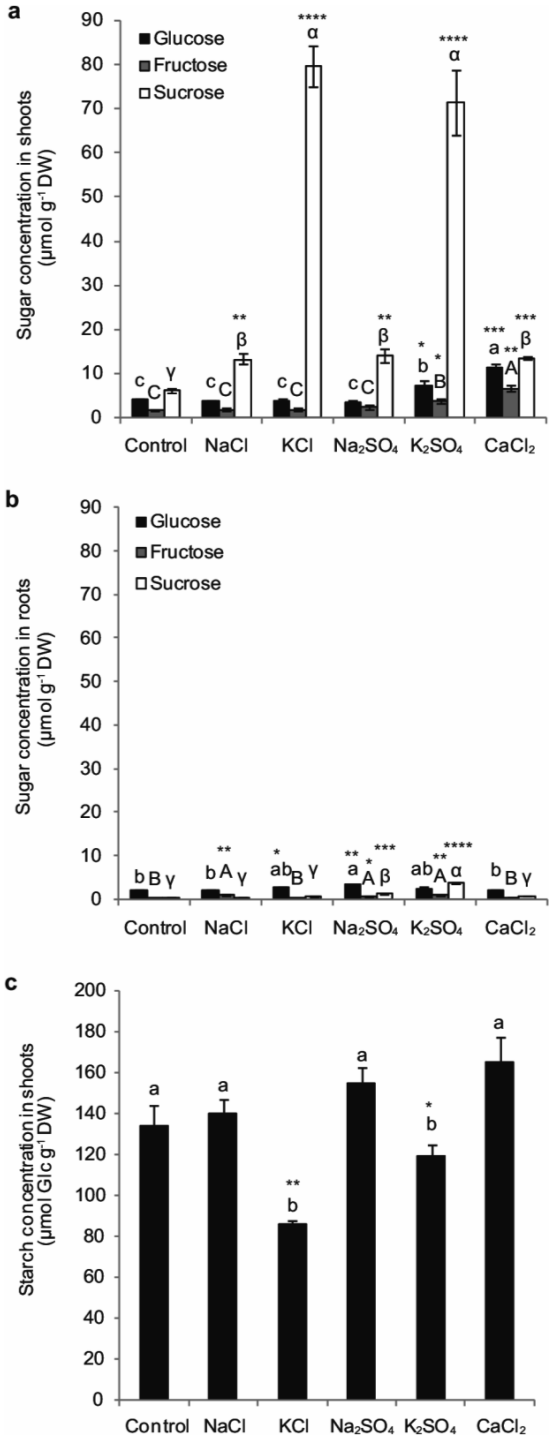

Figure 5: Effect of sodium and potassium salts on sugar concentrations. Four-week-old seedlings were treated with 105 mM NaCl, 107.38 mM KCl, 78.61 mM Na_2SO_4, 81.90 mM K_2SO_4, and 74.27 mM $CaCl_2$ for 12 d. The concentrations of glucose, fructose, and sucrose in shoots (a) and roots (b), as well as the starch concentration in shoots (c) were determined. DW indicates dry weight. Data represent the means of four replicates (± SE). Significant differences in sugar concentrations among treatments are indicated by different letters ($P < 5\%$; one-way ANOVA and post-hoc analysis using Tukey's Honestly Significant Difference method). The significant differences of sugar concentrations after salt treatments in comparison to those under control conditions are indicated by asterisks (*$P < 5\%$, **$P < 1\%$, ***$P < 0.1\%$, ****$P < 0.01\%$, *t*-test).

only involves sucrose cleavage but also mediates sucrose re-synthesis (*Noël* and *Pontis*, 2000; *Stein* and *Granot*, 2019). Fifteen isoforms of invertase have been identified in *Arabidopsis* (*Ruan*, 2014). Among these, two cytosolic invertase genes (*CINV1* and *CINV2*) are characterized for their important roles in plant growth and development (*Vargas* and *Salerno*, 2010). In this study, both *CINV1* and *CINV2* showed decreased transcription after five iso-osmotic salt treatments, *CINV2* being more highly suppressed and displayed a lower transcript level in plants treated with KCl or K_2SO_4 compared to those treated with NaCl or Na_2SO_4 (Fig. 6b).

In *Arabidopsis*, six isoforms of SUS genes (*i.e., SUS1, SUS2, SUS3, SUS4, SUS5*, and *SUS6*) have been characterized (*Stein* and *Granot*, 2019) and they were all determined in this study. After five iso-osmotic salt treatments, the transcripts of *SUS1, SUS2, SUS3, SUS4*, and *SUS6* presented a higher level compared to control (Fig. 6b). In contrast, *SUS5* had no substantial changes at the transcriptional level (Fig. 6b). The *SUS1* and *SUS3* genes were more transcribed in KCl or K_2SO_4-treated plants compared to those in NaCl or Na_2SO_4-treated ones.

In *Arabidopsis* plants, sucrose-proton symporters (SUC) and SWEET sucrose transporters are involved in sucrose transport from source to sink. Nine isoforms of *SUC* genes and seven isoforms of *SWEET* transporters were tested in *Arabidopsis* plants in the study of *Durand* et al. (2018). They found that only *SUC1, SUC2, SUC3, SUC4, SWEET11, SWEET12, SWEET13*, and *SWEET15* were expressed in *Arabidopsis* rosette leaves. Thus, these eight sucrose transporters were used for the determination of sucrose transport at the transcriptional level in this study. The transcription of *SUC1, SWEET11, SWEET12*, and *SWEET13* was repressed after five iso-osmotic salt treatments, while the transcription pattern of *SUC2, SUC3*, and *SUC4* remained unaffected and *SWEET15* was enhanced (Fig. 6c). The transcription of *SWEET11* and *SWEET12* was more strongly suppressed by KCl and K_2SO_4 than by NaCl and Na_2SO_4.

4 Discussion

4.1 Potassium salts are more toxic than sodium salts in *Arabidopsis thaliana* (ecotype: Col–0)

According to the three-phase model (*Munns*, 1993; *Schubert*, 2011), plants show wilting symptoms during Phase 0 because of a transient decrease in turgor. Growth rate is limited during Phase 1 due to osmotic stress, but without water deficit in shoots. Plants develop chlorosis or even necrosis during Phase 2 resulting from ion toxicity. The aim of this study was to investigate which ion is responsible for the toxicity symptoms in *Arabidopsis* plants under the experimental conditions in this study. To avoid the differences caused by Phase 1 (osmotic stress), five different salts (NaCl, KCl, Na_2SO_4, K_2SO_4, and $CaCl_2$) were applied iso-osmotically. According to Figs. 1 and 2, plants treated with NaCl, Na_2SO_4, and $CaCl_2$ displayed no obvious toxicity symptoms except the Na_2SO_4-treated ones (promoting small-scale necrosis at leaf margins) and showed similar reductions in shoot dry weight after

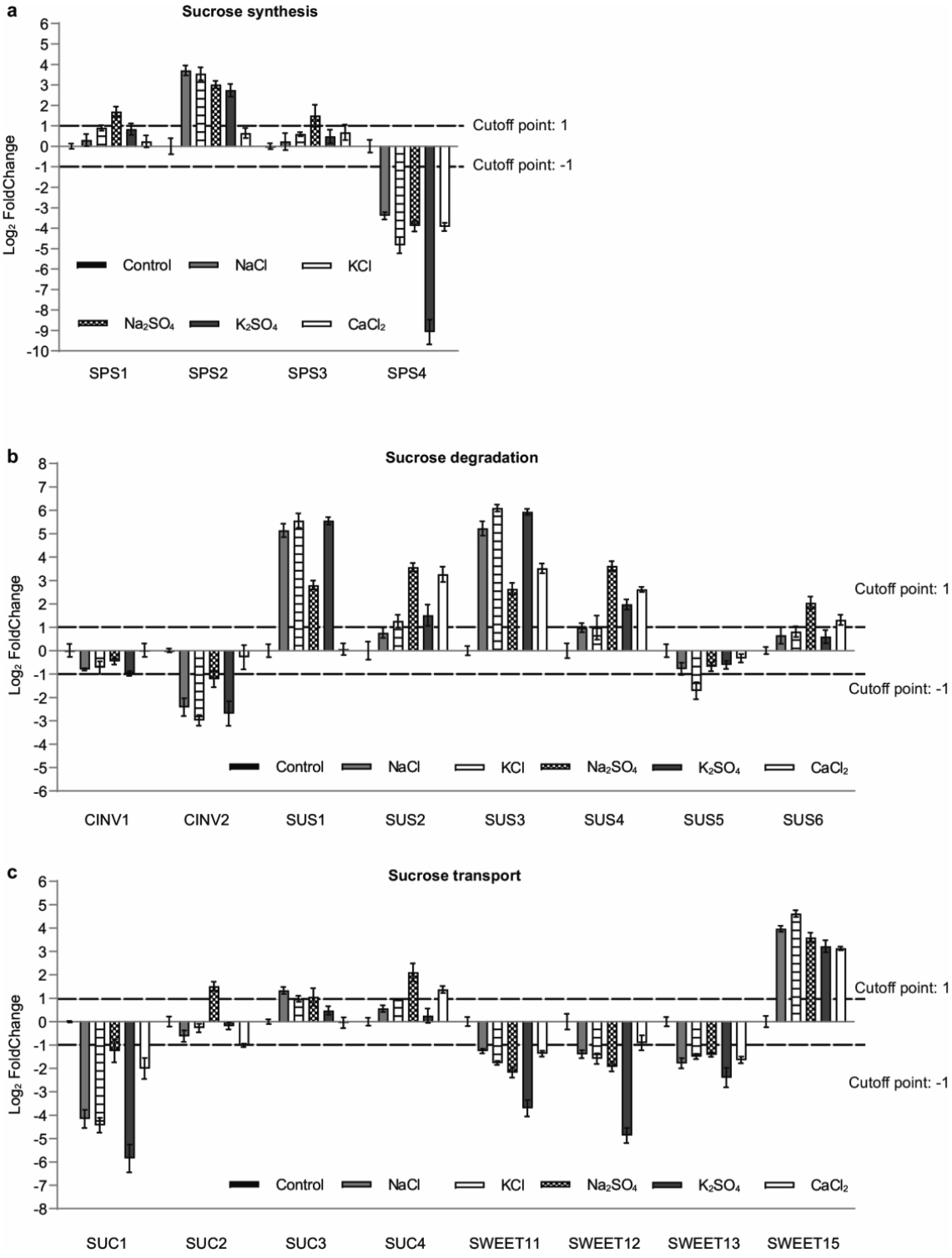

Figure 6: Effect of sodium and potassium salts on the transcription of genes related to sucrose synthesis, degradation, and transport. Four-week-old seedlings were treated with 105 mM NaCl, 107.38 mM KCl, 78.61 mM Na_2SO_4, 81.90 mM K_2SO_4, and 74.27 mM $CaCl_2$ for 12 d. The transcription of genes related to sucrose synthesis (a), sucrose degradation (b), and sucrose transport (c) was measured *via* qRT-PCR. SPS indicates sucrose phosphate synthase; CINV indicates cytosolic invertase; SUS indicates sucrose synthase; SUC indicates sucrose transporter. Data represent the means of three replicates (± SE). $|\log_2 \text{FoldChange}| \geq 1$ was used as cutoff to evaluate differentially transcribed genes. The dotted black lines indicate cutoff points.

12 days of treatment, indicating that these reductions mainly resulted from osmotic stress rather than ion toxicity. In contrast, exposure to KCl and K_2SO_4 led to severe toxicity (Fig. 1) and induced higher reductions in shoot dry weight than exposure to the other three salts (Fig. 2a), suggesting that these severe damages were not only due to osmotic stress but can also be attributed to additional ion toxicity which is presumably due to strong accumulation of K^+ (Fig. 3).

4.2 A high preference for K^+ over Na^+ in *Arabidopsis*

In this study, potassium salts (KCl and K_2SO_4) induced more severe toxicity than sodium salts (NaCl and Na_2SO_4) (considering toxicity symptoms and biomass) in *Arabidopsis* (Figs. 1 and 2). There are two explanations for the differences detected among these five iso-osmotic salt treatments.

One explanation could be that *Arabidopsis* plants accumulate more K^+ than Na^+ in shoots under iso-osmotic concentrations of potassium or sodium salt treatments, as shown in Fig. 3c. First, K^+ is more easily taken up than Na^+ by *Arabidopsis*. As shown in Fig. 3a, the uptake of K^+ under KCl treatment was higher than the uptake of Na^+ under iso-osmotic NaCl treatment. This is in line with the observation of *Lazof* and *Cheeseman* (1988) that also revealed that K^+ accumulation in roots was faster and higher than Na^+ in *Lactuca sativa*. The higher preference for K^+ in plants can be explained from an evolutionary standpoint. As potassium has important functions in enzyme activation, charge balance, and osmoregulation, cytosolic K^+ concentration is tightly regulated around 100–200 mM (*Leigh* and *Wyn Jones*, 1984; *Walker* et al., 1996; *Maathuis*, 2009). Therefore, plants need to create strategies for efficient K^+ uptake to meet the high demand of K^+ in cytosol. In contrast, excessive Na^+ in cytosol is toxic. Plants usually cannot tolerate cytosolic Na^+ concentrations greater than 20 mM (*Walker* et al., 1996; *Munns* and *Tester*, 2008). Moreover, previous studies have demonstrated that the non-selective cation channels (NSCCs), which are the main pathway for ion uptake at high ion external concentrations, have a higher permeability for K^+ than Na^+ in plants (*Zhang* et al., 2010; *Kronzucker* and *Britto*, 2011). For example, the voltage-insensitive NSCCs permeability of K^+ is 1.49-fold of Na^+ in *Arabidopsis* plants (*Demidchik* and *Tester*, 2002). The lower permeability of Na^+ may be attributed to its larger hydration shell relative to K^+, thus, hindering the transport of Na^+ through cation channels in plasma membrane (*Schubert*, 2015). Although the uptake of K^+ in K_2SO_4-treated plants was lower than the Na^+ uptake after exposure to iso-osmotic Na_2SO_4, the K^+ concentration in shoots was still higher than Na^+ after corresponding K_2SO_4 and Na_2SO_4 treatments. This may have resulted from the severely reduced biomass under K_2SO_4 treatment; thus, the K^+ was concentrated in K_2SO_4-treated plants. Second, the translocation of K^+ from roots to shoots was higher than Na^+ at iso-osmotic concentrations as shown in Fig. 3b. Previous studies demonstrated that some Na^+ transporters (*e.g.*, Nax1, Nax2, Kna1, and Skc1), which mediate Na^+ translocation, have higher translocation rates of K^+ (*Gorham* et al., 1990; *Ren* et al., 2005; *James* et al., 2006).

Another explanation is that excessive K^+ inhibits the uptake and/or translocation of calcium and magnesium. In this study, potassium salts (KCl and K_2SO_4) had a higher inhibitory effect on the uptake and translocation of Ca^{2+} and Mg^{2+} than iso-osmotic sodium salts (NaCl and Na_2SO_4) (Fig. 3d, e). Calcium is an important macronutrient, functioning in signal transduction, cell-wall structure, membrane permeability, and enzyme activation (*Hepler*, 2005; *Dodd* et al., 2010). The salt stress-induced reduction of Ca^{2+} concentration in *Arabidopsis* (Fig. 3f) is in line with the observations in sugar beet, maize, and sorghum (*Bernstein* et al., 1993; *Fortmeier* and *Schubert*, 1995; *Wakeel* et al., 2011). Magnesium is an essential constituent of chlorophyll and is thus crucial for photosynthesis (*Gerendás* and *Führs*, 2013). The reduced level of Ca^{2+} and Mg^{2+} under salt stress can be explained from physiological and chemical views. First, the translocation of Ca^{2+} and Mg^{2+} mainly occurs in xylem which is mainly driven by transpiration. Salt stress reduces the absolute transpiration rate in maize (*Schubert*, 2011). In this study, the absolute transpiration rates under potassium salt treatments (KCl and K_2SO_4) were lower than those under sodium salt treatments (NaCl and Na_2SO_4) (Fig. S2), which may explain the lower Ca^{2+} and Mg^{2+} translocation observed in plants treated with KCl and K_2SO_4 (Fig. 3e). Second, Ca^{2+} and Mg^{2+} enter roots through NSCCs which are permeable to various cations such as Na^+, K^+, Ca^{2+}, and Mg^{2+}. *Davenport* and *Tester* (2000) demonstrated competition among these cations during the uptake *via* NSCCs. In *Arabidopsis*, NSCCs have a higher affinity to K^+ than Na^+ (*Demidchik* and *Tester*, 2002). Hence, K^+ has a stronger competition with Ca^{2+} and Mg^{2+} than iso-osmotic Na^+, which may explain the higher inhibitory effect on the uptake of Ca^{2+} and Mg^{2+} observed in KCl^- and K_2SO_4-treated plants (Fig. 3d).

The first hypothesis that *Arabidopsis* plants are more sensitive to sodium salts than potassium salts has to be rejected. In *Arabidopsis*, exposure to Na_2SO_4 and K_2SO_4 (1) induced much more severe toxicity symptoms, (2) led to dramatic reductions in shoot biomass and chlorophyll concentration, and (d) strongly inhibited the uptake of nutrients Ca^{2+} and Mg^{2+} relative to the exposure to iso-osmotic NaCl and KCl. According to the study of *Reich* et al. (2017), high concentrations of NaCl and KCl both reduced plant biomass in *Brassica rapa* plants, but plants treated with NaCl showed more reductions. It seems that Brassica is more sensitive to sodium salts, which is different from the observation in *Arabidopsis* plants in this study. *Arabidopsis* and *Brassica* belong to the same family, Brassicaceae. The difference between *Brassica* and *Arabidopsis* might be attributed to two reasons. First, the salt sensitivity differs between *Brassica rapa* and *Arabidopsis thaliana*. According to the salt-reduced shoot dry matter, *Arabidopsis thaliana* is much more sensitive to salinity than most crops including rice, barley, and maize (*Munns* and *Tester*, 2008). After exposure to similar concentrations of KCl, the K^+ concentrations in *Brassica* and *Arabidopsis* plants are similar. *Brassica* can endure such high levels of K^+ in shoots. In contrast, *Arabidopsis* plants cannot. Second, *Arabidopsis* plants might lack the capacity of K^+ exclusion. In *Arabidopsis*, the K^+ concentration was more than three times that of Na^+ after exposure to similar concentrations of NaCl and KCl. This indicates that *Arabidopsis* plants can exclude excessive Na^+

to avoid severe damages, but apparently have a problem in K^+ exclusion. Similarly, another crop plant, wheat, is also more sensitive to NaCl than KCl (*Adiloglu* et al., 2007). Compared to crop plants, *Arabidopsis thaliana*, a wild plant, might lack the ability to regulate the K^+ transporters related to K^+ uptake and translocation under high K^+ circumstances, thus resulting in strong accumulation of K^+ in shoots.

4.3 Sulfate salts are more toxic than chloride salts

Although the KCl-treated plants showed a higher concentration of K^+ in shoots than those treated with K_2SO_4 (Fig. 3c), exposure to K_2SO_4 induced more severe toxicity symptoms in *Arabidopsis* (Fig. 1). Thus, SO_4^{2-} may also contribute to the toxicity symptoms induced by K_2SO_4. It has been previously demonstrated that sulfate salts inhibit plant growth more strongly than chloride salts, even when SO_4^{2-} level is much lower than Cl^- (*Leonova* et al., 2009; *Llanes* et al., 2013; *Reginato* et al., 2014; *Reich* et al., 2017). Similar results were observed in this study: plants treated with sulfate salts (Na_2SO_4 and K_2SO_4) showed more severe damages than plants treated with chloride salts (NaCl and KCl) (Figs. 1 and 2), and *Arabidopsis* plants preferred to accumulate Cl^- over SO_4^{2-} in shoots (Fig. 4). Exposure to sulfate salts (Na_2SO_4 and K_2SO_4) induced stronger accumulation of TCA intermediates (especially fumarate and succinate) than exposure to chloride salts (NaCl and KCl) (Tab. 1). Succinate and fumarate are intermediates of the TCA cycle, and they are interchangeable *via* SDH (succinate dehydrogenase) (*Dröse*, 2013; *Tretter* et al., 2016). SDH is a component of the respiratory Complex II in the mitochondrial electron transport chain, passing electrons *via* ubiquinone to Complex III (*Cecchini*, 2003; *Dröse*, 2013). It has been demonstrated that the accumulation of succinate can stimulate reverse electron transport and generate reactive oxygen species (ROS) to induce secondary oxidative stress in plants (*Muller* et al., 2008; *Starkov*, 2008; *Dröse*, 2013).

The results presented above support the second hypothesis that sulfate salts have a higher inhibitory effect on the growth of *Arabidopsis* plants than those treated with chloride salts, because exposure to sulfate salts induced the overproduction of organic acids especially fumarate and succinate, which might induce oxidative stress.

4.4 Potassium salts suppress or even block sucrose degradation

As growth was inhibited after salt treatments and sugar is an important source for plant growth and development, the concentrations of glucose, fructose, sucrose, and starch were determined. Plants treated with KCl and K_2SO_4 presented the strongest accumulation of sucrose in shoots, twelvefold as much as in control ones (Fig. 5a), the contrary was found for the starch level, which showed the lowest concentration (Fig. 5c). The massive accumulation of sucrose observed above can be explained in three aspects: (1) sucrose synthesis, (2) sucrose degradation, and (3) sucrose partitioning from source to sink. First, the decreased concentration of chlorophyll observed in KCl and K_2SO_4-treated plants (Fig. 2c) may reflect suppressed photosynthetic activity, implying a reduction in the primary income of sucrose from photosynthesis. However, the strongly accumulated sucrose in plants treated with KCl and K_2SO_4 shows that plants had sufficient photosynthates and that sucrose might have repressed the photosynthesis *via* a feedback inhibition. Hence, the increased sucrose concentration in response to KCl and K_2SO_4 was not due to enhanced photosynthesis but due to decreased sucrose consumption. The SPS genes, encoding key enzymes for sucrose synthesis, did not show notable differences in transcription pattern between potassium and sodium salt treatments (Fig. 6a). Second, the suppressed transcription of tested invertase genes *CINV1* and *CINV2*, especially *CINV2* being more severely repressed under potassium salt treatments (Fig. 6b), indicates a reduction of irreversible sucrose degradation mediated by *CINV1* and *CINV2*. In contrast, the transcription of *SUS* genes (*i.e., SUS1, SUS2, SUS3*, and *SUS4*) was enhanced. SUS catalyzes sucrose degradation reversibly, facilitating sucrose degradation as well as sucrose re-synthesis (*Noël* and *Pontis*, 2000; *Stein* and *Granot*, 2019). The sucrose cleavage facilitated by SUS may be suppressed or even blocked in plants treated with potassium salts (KCl and K_2SO_4). This hypothesis can be supported by the lower concentration of starch observed in KCl and K_2SO_4-treated plants (Fig. 5c), because the production of SUS-mediated sucrose degradation, UDP-glucose or ADP-glucose, determines the rate of sucrose-starch conversion (*Baroja-Fernández* et al., 2001; *Stein* and *Granot*, 2019). Third, sucrose is generated in source tissues such as mature leaves, and then transported *via* phloem to different sink organs (*Ruan*, 2014). In this study, root is a major sink in the developing stage of *Arabidopsis* plants. The genes related to sucrose transport, especially SWEET sucrose transporters (*i.e., SWEET11, SWEET12*, and *SWEET13*), were mostly suppressed after various salt treatments (Fig. 6c), suggesting inhibited sucrose translocation, which may explain the lower level of sucrose presented in roots compared to that in shoots (Fig. 5b).

In conclusion, when *Arabidopsis* plants were treated with KCl or K_2SO_4, the SUS mediated-sucrose degradation was suppressed or even blocked, subsequently resulting in an accumulation in shoots in contrast to starch. In addition, the irreversible sucrose cleavage promoted by invertase *CINV1* and *CINV2* and the sucrose transport mediated by *SUC1, SWEET11, SWEET12*, and *SWEET13* were also suppressed according to the transcription pattern.

5 Conclusions

The results demonstrate, for the first time, that potassium salts can also induce toxicity symptoms and that they are even more toxic than iso-osmotic sodium salts in *Arabidopsis thaliana*. We propose three possible explanations: (1) the uptake and translocation of K^+ were much higher than of Na^+ under iso-osmotic concentrations of potassium or sodium salt treatments, thus resulting in higher accumulation of K^+ in plants treated with potassium salts; (2) potassium salts had a higher inhibitory effect on the uptake and translocation of Ca^{2+} and Mg^{2+} than iso-osmotic sodium salts; (3) massive accumulation of K^+ suppressed or even blocked the SUS

mediated-sucrose degradation, thus leading to strong accumulation of sucrose, subsequently inhibiting photosynthesis *via* feedback inhibition. Hence, an excessive supply of K^+ needs to be avoided in physiological experiments with *Arabidopsis* in the future. Most salinity experiments are based on NaCl stress. However, the contribution of K^+-based stress should not be neglected. Moreover, the potassium salt-induced damages in *Arabidopsis* differ from the observations in wheat and rapeseed. Although high concentrations of sodium and potassium salts can inhibit the growth of wheat and rapeseed plants, wheat and rapeseed seem to be more sensitive to sodium salts. The effects of potassium salt on other crop plants need to be further investigated.

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