

## Silicon ameliorates the adverse effects of salt stress on sainfoin (*Onobrychis viciaefolia*) seedlings

GUO-QIANG WU<sup>1,\*</sup>, HAI-LONG LIU<sup>1</sup>, RUI-JUN FENG<sup>1</sup>, CHUN-MEI WANG<sup>2</sup>,  
YONG-YONG DU<sup>1</sup>

<sup>1</sup>*School of Life Science and Engineering, Lanzhou University of Technology, Lanzhou, Gansu, P.R. China*

<sup>2</sup>*Lanzhou Institute of Husbandry and Pharmaceutical Science, Chinese Academy of Agricultural Sciences, Lanzhou, Gansu, P.R. China*

\*Corresponding author: wugq08@126.com

### ABSTRACT

Wu G.-Q., Liu H.-L., Feng R.-J., Wang C.-M., Du Y.-Y.: (2017): Silicon ameliorates the adverse effects of salt stress on sainfoin (*Onobrychis viciaefolia*) seedlings. *Plant Soil Environ.*, 63: 545–551.

The objective of this study was to investigate whether the application of silicon (Si) ameliorates the detrimental effects of salinity stress on sainfoin (*Onobrychis viciaefolia*). Three-week-old seedlings were exposed to 0 and 100 mmol/L NaCl with or without 1 mmol/L Si for 7 days. The results showed that salinity stress significantly reduced plant growth, shoot chlorophyll content and root K<sup>+</sup> concentration, but increased shoot malondialdehyde (MDA) concentration, relative membrane permeability (RMP) and Na<sup>+</sup> concentrations of shoot and root in sainfoin compared to the control (no added Si and NaCl). However, the addition of Si significantly enhanced growth, chlorophyll content of shoot, K<sup>+</sup> and soluble sugars accumulation in root, while it reduced shoot MDA concentration, RMP and Na<sup>+</sup> accumulation of shoot and root in plants under salt stress. It is clear that silicon ameliorates the adverse effects of salt stress on sainfoin by limiting Na<sup>+</sup> uptake and enhancing selectivity for K<sup>+</sup>, and by adjusting the levels of organic solutes. The present study provides physiological insights into understanding the roles of silicon in salt tolerance in sainfoin.

**Keywords:** sodium toxicity; compatible solutes; cell permeability; photosynthetic pigments

Salinity is one of the abiotic factors that most limits the growth, development and productivity of crops, particularly in arid and semi-arid regions (Zhang and Shi 2013, Gupta and Huang 2014). It is estimated that approximately 7% of the land worldwide and one fifth of the world's cultivated land area are adversely affected by salinity (Munns and Tester 2008). Salinity stress leads to several physiological and biochemical modulations such as reduction of photosynthetic capacity, cell dehydration, ionic toxicity and nutritional imbalance in

plants (Zhang and Shi 2013, Rizwan et al. 2015). Additionally, higher accumulation of Na<sup>+</sup> and Cl<sup>-</sup> during salt conditions inhibits the uptake of K<sup>+</sup>, which is an essential macronutrient for plants growth and development (Kronzucker et al. 2013, Gupta and Huang 2014). Furthermore, salinity accelerates the over-production of harmful reactive oxygen species (ROS) that cause metabolism disturbance (Zushi et al. 2009) and membrane lipid peroxidation intensification (Gill and Tuteja 2010). Hence, an alternative strategy of silicon

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(Si) supplementation is the most practical and efficient approach of combating salinity stress in plants (Abbas et al. 2015, Rizwan et al. 2015, Soundararajan et al. 2017).

Silicon, the second most abundant element after oxygen in soil, is beneficial for the growth and development of plants (Ma et al. 2011) and its uptake has a positive effect on plants growth under salt stress (Guntzer et al. 2012). Previous studies have mostly addressed the promising effects of silicon on salt tolerance in tomato (*Lycopersicon esculentum*) (Al-aghaby et al. 2005), wheat (*Triticum aestivum*) (Tuna et al. 2008), sorghum (*Sorghum bicolor*) (Yin et al. 2013), okra (*Abelmoschus esculentus*) (Abbas et al. 2015), *Glycyrrhiza uralensis* (Li et al. 2016) and rose (*Rosa hybrida*) (Soundararajan et al. 2017). However, very little is known about beneficial effects of silicon on salinity stress in forage legumes.

Sainfoin (*Onobrychis viciaefolia*) is one of the major perennial forage legumes, it contains condensed tannins or proanthocyanidins (Mora-Ortiz et al. 2016), and it is the most important source for livestock feed due to its higher nutritive values (Carbonero et al. 2011). It also contributes to an increase of the levels of nitrogen in soil due to atmospheric nitrogen fixation in root nodules by rhizobia (Baimiev et al. 2007). Our previous studies found that under NaCl concentrations of 5–50 mmol/L, sainfoin could adapt to salt by maintaining homeostasis of K<sup>+</sup> and Na<sup>+</sup> (Wu et al. 2017a). However, when plants were exposed to high salinity stress (100 and 200 mmol/L), large amounts of Na<sup>+</sup> ions were accumulated in shoot of plants, leading to osmotic stress and growth inhibition (Wu et al. 2017a). As the growth of sainfoin was threatened by high salt, it is imperative to find approaches to enhance the vigorousness under salt stress.

The objective of this work was to determine whether the application of silicon could alleviate the detrimental effects of salinity stress on sainfoin seedlings. For this purpose, plants were exposed to silicon treatment in the presence or absence of NaCl, and the analysis of several parameters related to the growth, inorganic ions and organic solutes was made.

## MATERIAL AND METHODS

**Plant materials, growth conditions and treatments.** Seeds of sainfoin (*O. viciaefolia* Scop. cv. Gansu) were kindly provided by Professor Yanzhong

Li at the Lanzhou University, China. Seeds were surface-sterilized for 2 min in 70% ethanol (v/v) and rinsed 4 times with distilled water, soaked in distilled water for 24 h and then germinated at 24°C in the dark. After 4 days of germination, morphologically uniform seedlings were transplanted into plastic containers (5 × 5 × 5 cm; three seedlings/container) filled with vermiculite and irrigated with modified half-strength Hoagland nutrient solution. The solution was renewed every 2 days. All of the seedlings were grown in a chamber (MGC-HP, Yiheng Instrument Co., Shanghai, China), where the light intensity was between 350 and 450 μmol/m<sup>2</sup>/s, the temperature was in a range of 22–24°C, and the relative humidity (RH) was approximately 50–55%.

Three-week-old plants were subjected to salt and Si treatment as follows: control (no added NaCl and Si, C); 1 mmol/L Si (Si); 100 mmol/L NaCl (NaCl) and 1 mmol/L Si plus 100 mmol/L NaCl (Si + NaCl). Silicon was introduced by adding Na<sub>2</sub>SiO<sub>3</sub>, and the treatment solution was adjusted to pH 6.8 with 100 mmol/L HCl. Na<sup>+</sup> introduced by the addition of Si was subtracted from the concentration of NaCl treatment. Each treatment was replicated 8 times and arranged in a randomized and complete block design. The plants were irrigated every 2 days with the above solutions for the corresponding treatment. After 7 days of salt and Si treatments, plants were collected to assay phenotypical and physiological parameters.

**Determination of fresh and dry weight, and calculation of tissue water content.** Fresh weights (FW) of plant shoot and root were immediately determined and dry weights (DW) were recorded being dried in an air drying oven (GZX-9030MBE, Boxun Instrument Co., Shanghai, China) at 80°C for 48 h. Tissue water contents (WC) were calculated with the following formula:

$$WC \text{ (g/g DW)} = (FW - DW)/DW.$$

**Assay of chlorophyll, malondialdehyde and relative membrane permeability.** Chlorophyll contents were tested according to the methods of Tuna et al. (2008). Malondialdehyde (MDA) concentration was determined using the thiobarbituric acid (TBA) protocol (Peever and Higgins 1989). Relative membrane permeability (RMP) was determined according to the method of Gibon et al. (1997) with a slight modification.

**Measurement of Na<sup>+</sup> and K<sup>+</sup> concentration, and calculation of Na<sup>+</sup>/K<sup>+</sup> ratios.** Na<sup>+</sup> and K<sup>+</sup> concentra-

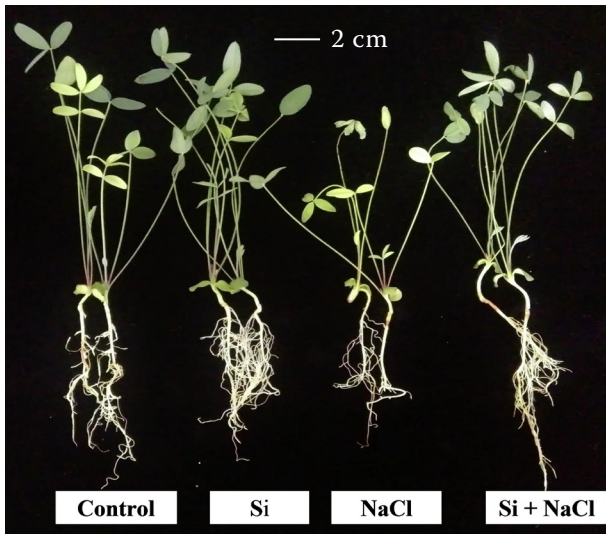


Figure 1. Effects of silicon (Si) on phenotypes in sainfoin under salt stress. Three-week-old seedlings were exposed to control; 1 mmol/L Si (Si); 100 mmol/L NaCl (NaCl), and 1 mmol/L Si plus 100 mmol/L NaCl (Si + NaCl) for 7 days

Hills, USA) according to the method as described by Wang et al. (2007) with a slight modification.  $\text{Na}^+/\text{K}^+$  ratios were calculated according to the method of Yue et al. (2012). The selective transport (ST) capacity for  $\text{K}^+$  over  $\text{Na}^+$  was calculated using the formula as described by Wang et al. (2005).

**Determination of soluble sugars and proline contents.** Sucrose, fructose and glucose contents were measured according to the methods of Liu et al. (2008). Proline was tested using the ninhydrin reagent according to the method described by Bates et al. (1973) with a slight modification.

**Statistical analysis.** Data were subjected to an analysis of variance (ANOVA) using the SPSS software (version 19.0, Chicago, USA) and significant differences were determined using the Duncan’s multiple range test at  $P < 0.05$ .

**RESULTS AND DISCUSSION**

**Effects of silicon on the growth of plants under salt stress.** Phenotypically, Si-treated plants grew better than untreated plants under salinity stress

tions were measured using a flame spectrophotometer (2655-00, Cole-Parmer Instrument Co., Vernon

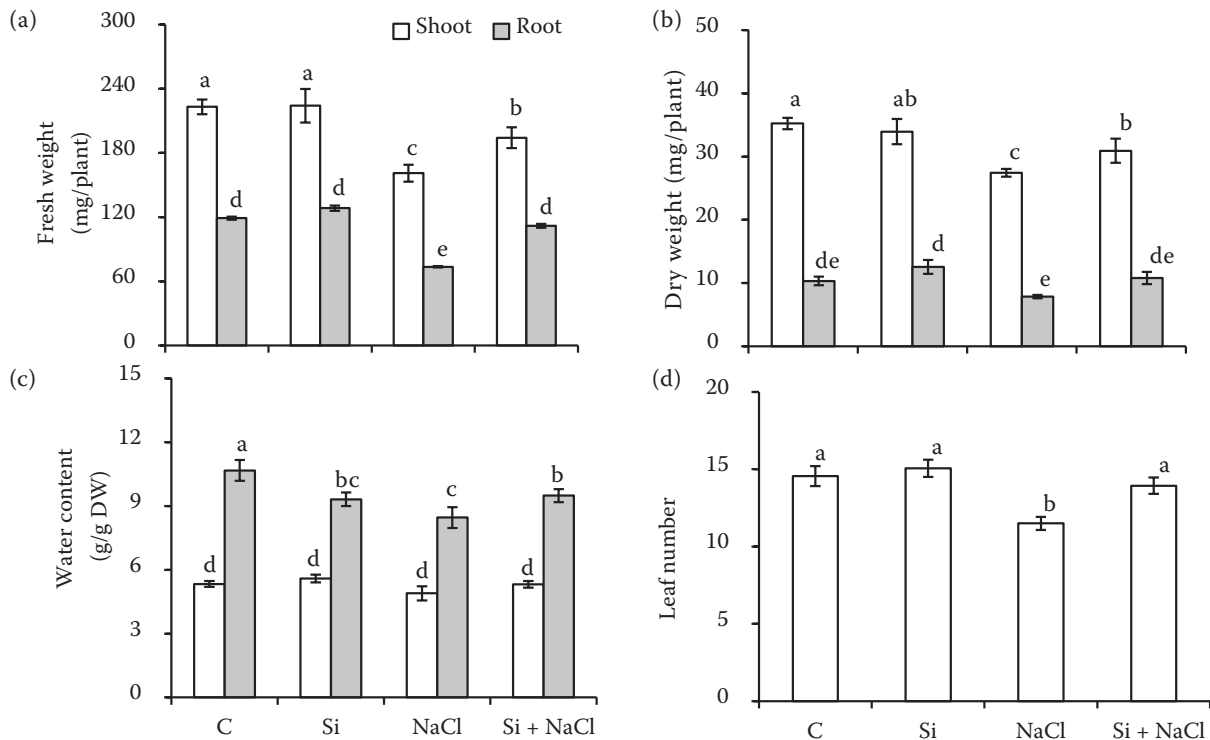


Figure 2. Effects of silicon (Si) on (a) fresh and (b) dry weight (DW), (c) water content and (d) leaf number in sainfoin under salt stress. Three-week-old seedlings were exposed to control (C); 1 mmol/L Si (Si); 100 mmol/L NaCl (NaCl), and 1 mmol/L Si plus 100 mmol/L NaCl (Si + NaCl) for 7 days. Three plants were pooled in each replicate ( $n = 8$ ). Values are mean  $\pm$  standard error (SE) and bars indicate SE. Columns with different letters indicate significant differences at  $P < 0.05$  (Duncan’s test)

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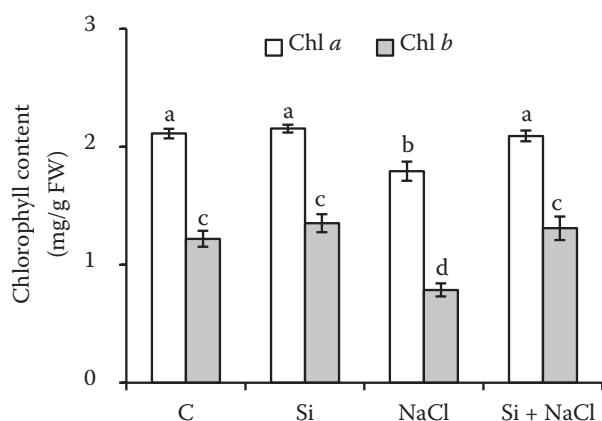


Figure 3. Effects of silicon (Si) on chlorophyll content in sainfoin under salt stress. Three-week-old seedlings were exposed to control (C); 1 mmol/L Si (Si); 100 mmol/L NaCl (NaCl), and 1 mmol/L Si plus 100 mmol/L NaCl (Si + NaCl) for 7 days. Three plants were pooled in each replicate ( $n = 8$ ). Values are mean  $\pm$  standard error (SE) and bars indicate SE. Columns with different letters indicate significant differences at  $P < 0.05$  (Duncan's test). FW – fresh weight

(Figure 1). In control conditions, applied silicon did not have significant effects on plant growth ( $P > 0.05$ ). Compared with the control, salinity stress remarkably reduced fresh weights of shoot and root, dry weights of shoot, water contents of root and leaf number ( $P < 0.05$ ). However, addition of Si alleviated the growth reduction caused by salinity ( $P < 0.05$ ) (Figures 1 and 2a–d), in agreement with previous reports regarding the beneficial effects of silicon on growth in plants, such as halophytic grass *Spartina densiflora* (Mateos-Naranjo et al. 2013), okra (Abbas et al. 2015) and rose (Soundararajan et al. 2017).

**Effects of silicon on chlorophyll, MDA contents and RMP in sainfoin under salt stress.** There is evidence that plant growth relies on photosynthesis capacity (Abbas et al. 2015). Photosynthetic pigments were shown to play critical roles in maintaining the photosynthetic capacity of plants (Lu et al. 2017). Chlorophyll is one of the major photosynthetic pigments of higher plants (Al-aghabary

et al. 2005). In the present study, chlorophyll *a* and *b* contents in salt-stressed plants were significantly lower than those in control plants ( $P < 0.05$ ). However, under salinity stress, chlorophyll contents were significantly enhanced when silicon was added ( $P < 0.05$ ) (Figure 3). Likewise, Abbas et al. (2015) also found that the addition of silicon increased chlorophyll contents of leaf in okra plants grown under salinity stress. Additionally, it was documented that application of Si improved plant defence systems for detoxifying ROS induced by salinity, and in turn, which helped to increase chlorophyll contents (Mateos-Naranjo et al. 2013).

It was well documented that silicon plays important roles in cell membrane stability and maintaining cell permeability when plants were exposed to salinity stress (Li et al. 2016). In the present study, addition of silicon did not change MDA concentrations in both shoot and root ( $P > 0.05$ ), but significantly decreased shoot RMP in non-stress

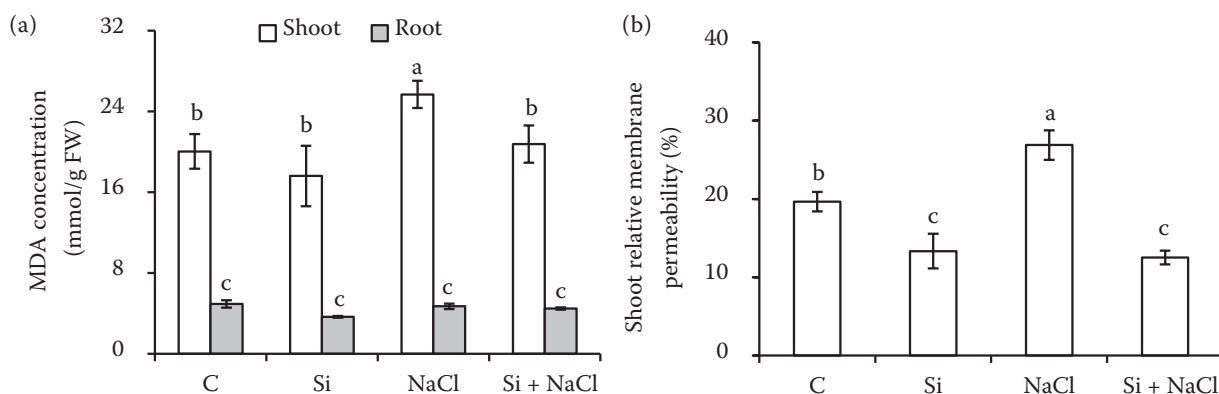


Figure 4. Effects of silicon (Si) on (a) MDA (malondialdehyde) concentration (b) and shoot relative membrane permeability in sainfoin under salt stress. Three-week-old seedlings were exposed to control (C); 1 mmol/L Si (Si); 100 mmol/L NaCl (NaCl), and 1 mmol/L Si plus 100 mmol/L NaCl (Si + NaCl) for 7 days. Three plants were pooled in each replicate ( $n = 8$ ). Values are mean  $\pm$  standard error (SE) and bars indicate SE. Columns with different letters indicate significant differences at  $P < 0.05$  (Duncan's test). FW – fresh weight

conditions ( $P < 0.05$ ). Salinity stress significantly increased MDA concentration and RMP in shoot, while they were decreased when silicon was applied ( $P < 0.05$ ) (Figure 4a,b). These are in agreement with the results of Al-aghabary et al. (2005), who found that the addition of silicon decreased the permeability of plasma membrane of leaf cells in tomato plants subjected with salinity stress. Therefore, these results implied that silicon ameliorates the adverse effects of salinity stress on sainfoin plants by enhancing the cell membrane stability.

**Effects of silicon on  $\text{Na}^+$  and  $\text{K}^+$  accumulation in sainfoin under salt stress.** Compared to the control, salinity dramatically increased  $\text{Na}^+$  concentrations in both shoots and roots, but reduced the accumulation of  $\text{K}^+$  in roots ( $P < 0.05$ ) (Figure 5a,b). Similar results were observed in other crops species exposed to salinity stress (Ashraf et al. 2010, Guo et al. 2013). It was shown that one of the primary plant responses to salinity was the reduction of  $\text{K}^+$  accumulation in plant tissues and thus the substitution of  $\text{K}^+$  by  $\text{Na}^+$  in salinity stress resulted in high  $\text{Na}^+/\text{K}^+$  ratio which damaged the plant metabolism and ultimately plant growth was severely inhibited (Ashraf et al. 2010). Under salin-

ity stress, addition of silicon significantly reduced the levels of  $\text{Na}^+$  in both shoot and root, while it increased  $\text{K}^+$  concentration in root ( $P < 0.05$ ) (Figure 5a,b). These results are consistent with those observed in salt-stressed tomato (Li et al. 2015) and white clover (Guo et al. 2013). The increases of  $\text{K}^+$  levels by addition of silicon under salinity stress could improve the stability of cell membrane and enhance salt tolerance of sainfoin. It was documented that the application of silicon could inhibit uptake and transport of  $\text{Na}^+$  by being precipitated as amorphous silica ( $\text{SiO}_2 \cdot n\text{H}_2\text{O}$ ) in cell walls and lumens (Gong et al. 2006). Furthermore,  $\text{Na}^+/\text{K}^+$  ratios in shoot and root were remarkably increased by salinity stress compared to the control ( $P < 0.05$ ) (Figure 5c). However, addition of silicon significantly reduced  $\text{Na}^+/\text{K}^+$  ratios in the presence of NaCl (Figure 5c). These results are consistent with a study of white clover (Guo et al. 2013). The capacity to a lower cytosolic  $\text{Na}^+/\text{K}^+$  ratio is an important indicator of plant tolerance (Guo et al. 2013); therefore, controlling of  $\text{K}^+$  and  $\text{Na}^+$  uptake is critical for plants adapting to salinity stress (Munns and Tester 2008). Moreover, added silicon remarkably increased the selective transport

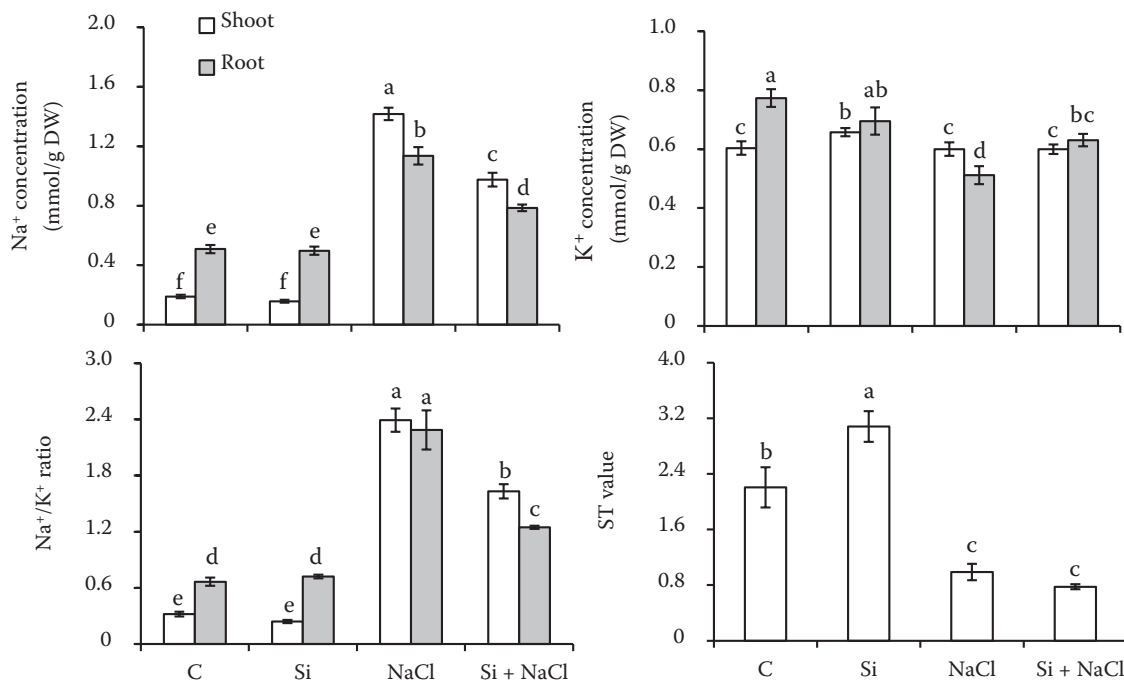


Figure 5. Effects of silicon (Si) on (a)  $\text{Na}^+$  and (b)  $\text{K}^+$  concentrations, (c)  $\text{Na}^+/\text{K}^+$  ratios and (d) ST (selective transport capacity for  $\text{K}^+$  over  $\text{Na}^+$ ) value in sainfoin under salt stress. Three-week-old seedlings were exposed to control (C); 1 mmol/L Si (Si); 100 mmol/L NaCl (NaCl), and 1 mmol/L Si plus 100 mmol/L NaCl (Si + NaCl) for 7 days. Three plants were pooled in each replicate ( $n = 8$ ). Values are mean  $\pm$  standard error (SE) and bars indicate SE. Columns with different letters indicate significant differences at  $P < 0.05$  (Duncan's test). DW – dry weight



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Table 1. Effects of silicon (Si) on sucrose, fructose and glucose contents (mg/g DW) and proline contents ( $\mu\text{g/g}$  DW) in sainfoin under salt stress

Treatment	Shoot				Root			
	sucrose	fructose	glucose	proline	sucrose	fructose	glucose	proline
C	31.29 $\pm$ 3.38 <sup>a</sup>	39.81 $\pm$ 2.59 <sup>a</sup>	17.69 $\pm$ 0.94 <sup>a</sup>	94.96 $\pm$ 28.60 <sup>b</sup>	31.58 $\pm$ 2.89 <sup>c</sup>	34.76 $\pm$ 3.57 <sup>b</sup>	13.79 $\pm$ 1.45 <sup>ab</sup>	122.34 $\pm$ 17.78 <sup>b</sup>
Si	28.53 $\pm$ 2.18 <sup>a</sup>	34.53 $\pm$ 3.50 <sup>ab</sup>	15.47 $\pm$ 1.49 <sup>a</sup>	136.37 $\pm$ 17.43 <sup>ab</sup>	27.50 $\pm$ 3.05 <sup>c</sup>	35.86 $\pm$ 2.80 <sup>b</sup>	14.59 $\pm$ 2.00 <sup>ab</sup>	274.47 $\pm$ 49.53 <sup>a</sup>
NaCl	22.08 $\pm$ 1.59 <sup>b</sup>	30.27 $\pm$ 2.52 <sup>ab</sup>	11.31 $\pm$ 0.29 <sup>b</sup>	146.96 $\pm$ 25.39 <sup>ab</sup>	46.68 $\pm$ 2.45 <sup>b</sup>	34.15 $\pm$ 5.23 <sup>b</sup>	11.39 $\pm$ 1.10 <sup>b</sup>	225.73 $\pm$ 34.94 <sup>a</sup>
Si + NaCl	22.95 $\pm$ 4.60 <sup>b</sup>	25.25 $\pm$ 2.33 <sup>b</sup>	10.81 $\pm$ 0.34 <sup>b</sup>	223.32 $\pm$ 29.41 <sup>a</sup>	58.46 $\pm$ 3.19 <sup>a</sup>	48.28 $\pm$ 4.05 <sup>a</sup>	16.33 $\pm$ 0.82 <sup>a</sup>	291.09 $\pm$ 29.68 <sup>a</sup>

Three-week-old seedlings were exposed to control (C); 1 mmol/L Si (Si); 100 mmol/L NaCl (NaCl), and 1 mmol/L Si plus 100 mmol/L NaCl (Si + NaCl) for 7 days. Three plants were pooled in each replicate ( $n = 8$ ). Values are mean  $\pm$  standard error (SE) and bars indicate SE. Columns with different letters indicate significant differences at  $P < 0.05$  (Duncan's test). DW – dry weight

(ST) capacity for  $\text{K}^+$  over  $\text{Na}^+$  in the absence of salt ( $P < 0.05$ ), while did not affect it in the presence of salt ( $P > 0.05$ ) (Figure 5d). These results indicated that silicon could regulate  $\text{Na}^+/\text{K}^+$  ratio by limiting  $\text{Na}^+$  uptake and enhancing selectivity for  $\text{K}^+$ .

**Effects of silicon on soluble sugars and proline accumulation in sainfoin under salt stress.** Under salinity stress, compatible solutes increased in plants mainly including soluble sugars and proline (Wu et al. 2015, 2017b). These compatible solutes may improve plant tolerance to salinity stress (Wu et al. 2015). In the present study, compared to the control, addition of silicon did not alter the contents of sucrose, fructose and glucose in both shoot and root ( $P > 0.05$ ) (Table 1). However, salt stress significantly increased sucrose levels in shoot and reduced glucose contents in shoot and root ( $P < 0.05$ ) (Table 1). It was observed that sucrose, fructose and glucose contents of root in Si-treated plants were significantly higher than those in untreated plants under salinity stress ( $P < 0.05$ ) (Table 1). Addition of silicon significantly increased proline accumulation in root compared to the control ( $P < 0.05$ ), while it remained unchanged under salt stress ( $P > 0.05$ ) (Table 1). Yin et al. (2013) reported that the application of silicon increased the contents of sucrose and fructose while it reduced the levels of proline in sorghum under salinity stress. These results suggested that the addition of silicon might enhance the plant tolerance to salinity stress by adjusting the levels of organic solutes.

In conclusion, our results indicated that the addition of silicon remarkably increased fresh and

dry weights of both shoot and root, leaf numbers, chlorophyll contents of shoot,  $\text{K}^+$  and soluble sugar concentrations of root, while it reduced MDA concentrations and RMP of shoot, and  $\text{Na}^+$  accumulation and  $\text{Na}^+/\text{K}^+$  ratios of both shoot and root in plants under salinity stress. It was proposed that silicon could alleviate the detrimental effects of salinity stress on sainfoin by limiting  $\text{Na}^+$  uptake and enhancing selectivity for  $\text{K}^+$ , and by adjusting the levels of organic solutes.

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## REFERENCES

- Abbas T., Balal R.M., Shahid M.A., Pervez M.A., Ayyub C.M., Aqueel M.A., Javaid M.M. (2015): Silicon-induced alleviation of NaCl toxicity in okra (*Abelmoschus esculentus*) is associated with enhanced photosynthesis, osmoprotectants and antioxidant metabolism. *Acta Physiologiae Plantarum*, 37: 6.
- Al-aghaby K., Zhu Z.J., Shi Q.H. (2005): Influence of silicon supply on chlorophyll content, chlorophyll fluorescence, and antioxidative enzyme activities in tomato plants under salt stress. *Journal of Plant Nutrition*, 27: 2101–2115.
- Ashraf M., Rahmatullah, Afzal M., Ahmed R., Mujeeb F., Sarwar A., Ali L. (2010): Alleviation of detrimental effects of NaCl by silicon nutrition in salt-sensitive and salt-tolerant genotypes of sugarcane (*Saccharum officinarum* L.). *Plant and Soil*, 326: 381–391.
- Baimiev A.K., Baimiev A.K., Gubaidullin I.I., Kulikova O.L., Chemeris A.V. (2007): Bacteria closely related to *Phyllobacte-*

- rium trifolii* according to their 16S rRNA gene are discovered in the nodules of Hungarian sainfoin. *Russian Journal of Genetics*, 43: 587–590.
- Bates L.S., Waldren R.P., Teare I.D. (1973): Rapid determination of free proline for water-stress studies. *Plant and Soil*, 39: 205–207.
- Carbonero C.H., Mueller-Harvey I., Brown T.A., Smith L. (2011): Sainfoin (*Onobrychis viciifolia*): A beneficial forage legume. *Plant Genetic Resources*, 9: 70–85.
- Gibon Y., Bessieres M.A., Larher F. (1997): Is glycine betaine a non-compatible solute in higher plants that do not accumulate it? *Plant, Cell and Environment*, 20: 329–340.
- Gill S.S., Tuteja N. (2010): Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. *Plant Physiology and Biochemistry*, 48: 909–930.
- Gupta B., Huang B.R. (2014): Mechanism of salinity tolerance in plants: Physiological, biochemical, and molecular characterization. *International Journal of Genomics*, 2014: 1–18.
- Guntzer F., Keller C., Meunier J.-D. (2012): Benefits of plant silicon for crops: A review. *Agronomy for Sustainable Development*, 32: 201–213.
- Guo Q., Meng L., Mao P., Tian X. (2013): Role of silicon in alleviating salt-induced toxicity in white clover. *Bulletin of Environmental Contamination and Toxicology*, 91: 213–216.
- Gong H.J., Randall D.P., Flowers T.J. (2006): Silicon deposition in the root reduces sodium uptake in rice (*Oryza sativa* L.) seedlings by reducing bypass flow. *Plant, Cell and Environment*, 29: 1970–1979.
- Kronzucker H.J., Coskun D., Schulze L.M., Wong J.R., Britto D.T. (2013): Sodium as nutrient and toxicant. *Plant and Soil*, 369: 1–23.
- Li H.L., Zhu Y.X., Hu Y.H., Han W.H., Gong H.J. (2015): Beneficial effects of silicon in alleviating salinity stress of tomato seedlings grown under sand culture. *Acta Physiologiae Plantarum*, 37: 71.
- Li Y.-T., Zhang W.-J., Cui J.-J., Lang D.-Y., Li M., Zhao Q.-P., Zhang X.-H. (2016): Silicon nutrition alleviates the lipid peroxidation and ion imbalance of *Glycyrrhiza uralensis* seedlings under salt stress. *Acta Physiologiae Plantarum*, 38: 96.
- Liu H.L., Wang Q.Q., Yu M.M., Zhang Y.Y., Wu Y.B., Zhang H.X. (2008): Transgenic salt-tolerant sugar beet (*Beta vulgaris* L.) constitutively expressing an *Arabidopsis thaliana* vacuolar Na<sup>+</sup>/H<sup>+</sup> antiporter gene, *AtNHX3*, accumulates more soluble sugar but less salt in storage roots. *Plant, Cell and Environment*, 31: 1325–1334.
- Lu Y., Lei J.-Q., Zeng F.-J., Zhang B., Liu G.-J., Liu B., Li X.-Y. (2017): Effect of NaCl-induced changes in growth, photosynthetic characteristics, water status and enzymatic antioxidant system of *Calligonum caput-medusae* seedlings. *Photosynthetica*, 55: 96–106.
- Ma J.F., Yamaji N., Mitani-Ueno N. (2011): Transport of silicon from roots to panicles in plants. *Proceedings of the Japan Academy. Series B, Physical and Biological Sciences*, 87: 377–385.
- Mateos-Naranjo E., Andrades-Moreno L., Davy A.J. (2013): Silicon alleviates deleterious effects of high salinity on the halophytic grass *Spartina densiflora*. *Plant Physiology and Biochemistry*, 63: 115–121.
- Munns R., Tester M. (2008): Mechanisms of salinity tolerance. *Annual Review of Plant Biology*, 59: 651–681.
- Mora-Ortiz M., Swain M.T., Vickers M.J., Hegarty M.J., Kelly R., Smith L.M.J., Skot L. (2016): *De-novo* transcriptome assembly for gene identification, analysis, annotation, and molecular marker discovery in *Onobrychis viciifolia*. *BMC Genomics*, 17: 756.
- Peever T.L., Higgins V.J. (1989): Electrolyte leakage, lipoxygenase, and lipid peroxidation induced in tomato leaf tissue by specific and nonspecific elicitors from *Cladosporium fulvum*. *Plant Physiology*, 90: 867–875.
- Rizwan M., Ali S., Ibrahim M., Farid M., Adrees M., Bharwana S.A., Zia-Ur-Rehman M., Qayyum M.F., Abbas F. (2015): Mechanisms of silicon-mediated alleviation of drought and salt stress in plants: A review. *Environmental Science and Pollution Research*, 22: 15416–15431.
- Soundararajan P., Manivannan A., Ko C.H., Muneer S., Jeong B.R. (2017): Leaf physiological and proteomic analysis to elucidate silicon induced adaptive response under salt stress in *Rosa hybrida* 'Rock Fire'. *International Journal of Molecular Sciences*, 18: 1768.
- Tuna A.L., Kaya C., Higgs D., Murillo-Amador B., Aydemir S., Girgin A.R. (2008): Silicon improves salinity tolerance in wheat plants. *Environmental and Experimental Botany*, 62: 10–16.
- Wang S.M., Zhao G.Q., Gao Y.S., Tang Z.C., Zhang C.L. (2005): *Puccinellia tenuiflora* exhibits stronger selectivity for K<sup>+</sup> over Na<sup>+</sup> than wheat. *Journal of Plant Nutrition*, 27: 1841–1857.
- Wang S.-M., Zhang J.-L., Flowers T.J. (2007): Low-affinity Na<sup>+</sup> uptake in the halophyte *Suaeda maritima*. *Plant Physiology*, 145: 559–571.
- Wu G.-Q., Feng R.-J., Liang N., Yuan H.-J., Sun W.-B. (2015): Sodium chloride stimulates growth and alleviates sorbitol-induced osmotic stress in sugar beet seedlings. *Plant Growth Regulation*, 75: 307–316.
- Wu G.-Q., Jia S., Liu H.-L., Wang C.-M., Li S.-J. (2017a): Effect of salt stress on growth, ion accumulation, and distribution in sainfoins (*Onobrychis viciaefolia*) seedlings. *Pratacultural Science*, 34: 1661–1668. (In Chinese)
- Wu G.-Q., Feng R.-J., Li S.-J., Du Y.-Y. (2017b): Exogenous application of proline alleviates salt-induced toxicity in sainfoin seedlings. *Journal of Animal and Plant Sciences*, 27: 246–251.
- Yin L.N., Wang S.W., Li J.N., Tanaka K., Oka M. (2013): Application of silicon improves salt tolerance through ameliorating osmotic and ionic stresses in the seedling of *Sorghum bicolor*. *Acta Physiologiae Plantarum*, 35: 3099–3107.
- Yue L.J., Li S.X., Ma Q., Zhou X.R., Wu G.Q., Bao A.K., Zhang J.L., Wang S.M. (2012): NaCl stimulates growth and alleviates water stress in the xerophyte *Zygophyllum xanthoxylum*. *Journal of Arid Environments*, 87: 153–160.
- Zhang J.L., Shi H. (2013): Physiological and molecular mechanisms of plant salt tolerance. *Photosynthesis Research*, 115: 1–22.
- Zushi K., Matsuzoe N., Kitano M. (2009): Developmental and tissue-specific changes in oxidative parameters and antioxidant systems in tomato fruits grown under salt stress. *Scientia Horticulturae*, 122: 362–368.

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