

Silicon-Mediated Regulation of Sodium Distribution in Barley Plants

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Research Article

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Abstract

Salinity is one of the largest problems in the world today. Silicon (Si)-mediated increase in plant tolerance to saline environment has been well documented, while the underlying mechanisms remain unclear. Monosilicic acid, polysilicic acid, and sodium (Na) were analyzed in the apoplast and symplast of roots, stems and leaves of salt-stressed barley plants in dynamics. Sodium moved predominantly via apoplastic pathway. The dynamics of Na in apoplast represented a parabolic curve. Soluble Si in nutrient solution increased the total Na in the roots but restricted the Na root-to-shoot transport via apoplastic pathway and reduced Na accumulation in stems and leaves. Plant exposure to high concentration of Na resulted in increased polysilicic acids in the root symplast and stem apoplast and symplast. These increases are attributable to Si redistribution within plant with its accumulation in stressed tissue. Probably, Si moves in the form of polysilicic acid. Under optimum or low stress growth conditions, Si mainly accumulated in the roots and leaves. Under higher stress, this Si can be redistributed to a mostly stress-affected place.

Introduction

Salinization is a global problem which aggravates under current climatic changes. Today salinity is a major abiotic stress that adversely impacts crop productivity and quality. According to the United Nations Environment Program, 20% of agricultural land and 50% of cropland in the world are salt-stressed (Shrivastava and Kumar 2015). Reducing negative salt impact on plant growth is an important global challenge.

Over the last decade, numerous investigations have been reported that salt tolerance of cultivated plants could be markedly enhanced by the supplementation with plant-available Si (Coskun et al. 2016; Rizwan et al. 2015; Zhu et al. 2020). Silicon is the second most abundant element in the soil after oxygen, mostly present in the form of minerals. Though the Si content in plants ranges from 0.1 to 10%, its role in plant physiology has been poorly understood (Tripathi et al. 2020). Although not being listed among the essential elements for higher plants, Si was reported to benefit plant tolerance to numerous stresses (Epstein 1999; Gong et al. 2006). Several mechanisms underlying Si-induced plant defense have been suggested: 1) mechanical protection via accumulation in epidermal tissue and formation of thick epidermal layer that protects plant against fungi and insect attacks (Alhousari and Greger 2018); 2) physiological protection due to increasing plant viability through optimization of root development, improvement of photosynthesis and others (Frazão et al. 2020; Lavinsky et al. 2016); 3) chemical protection via chemical interaction between monosilicic acid and contaminants in plant tissue (Stevic et al. 2016); 4) reduction of the root-to-leaf transport of toxic elements (Imtiaz et al. 2016). These mechanisms are indirectly supported by high concentrations of mono- and polysilicic acids to be observed in the plant sap (Matichenkov et al. 2008). Soluble forms of Si also can play a role in additional catalytic synthesis of specific and non-specific stress hormones and antioxidants (Biel et al. 2008).

Wang and Hang (2007) hypothesized that Si alters the distribution of sodium (Na) in alfalfa plants to improve the tolerance in salt-stressed environment. Authors have concluded that Si alleviates salt stress by inhibiting Na uptake by roots and transport to shoots. Increased salinity tolerance of Si-supplied barley plants was reported to be due improving the photosynthetic activity and ultrastructure of leaf cell organelles as well as reducing electrolytic leakage of the leaves [Liang 1998; Liang et al. 1996). Silicon enhanced K:Na selectivity ratio, thus mitigating the Na toxicity (Rahimi et al. 2021). The stimulating impact of Si on the K uptake by plants under salt stress was suggested to rely on the activation of HC-ATPase, the enzyme responsible for selective uptake of mineral ions (Marschner and Part 1995). Silicon applied to salt-stressed barley enhanced the superoxide dismutase activity in leaves and the HC-ATPase activity in roots and reduced the Na accumulation in shoots and roots (Liang 1998, 1999). Improved plant Si nutrition was shown to alleviate the NaCl-induced oxidative damage in cucumbers by the regulation of hormone balance and increasing the activity of enzymes and biosynthesis of proline (Zhu et al. 2020).

Changes in the cell membrane properties induced by improved plant Si nutrition can also provide the protection against Na toxicity (He 2010).

Although Si-mediated control of Na⁺ uptake and translocation within plant under salt stress has been well documented (Bosnic et al. 2018; Flam-Shepherd et al. 2018; Gong et al. 2006; Wang et al. 2015), the most studies focus on the total content of Na, not analyzing its soluble forms and transport dynamics. The current investigation was designed to provide some insight into the mechanism of Si action. The main aim was to evaluate the transport of monosilicic acid, polysilicic acid and Na in the symplast and apoplast of barley plants depending on the concentrations of salt and plant-available Si.

Materials And Methods

The greenhouse test were conducted in 2019 in Institute of basic biological problems Russian academy of sciences with barley (*Hordeum vulgare* L. cv Preria PC1). This variety have high drought resistance and used for growing of the forage grain. Plants were grown in plastic pots filled with 1 kg of sieved air-dried soil each. The soil was classified as cultivated Luvic Greyzemic Phaeozems (WRB, 2014). The selected chemical soil properties were the following: pH_{H2O}=6.3 ± 0.1; Corg = 2.5 ± 0.2 %; CEC = 10.4 ± 0.4 mg eq/100 g; total Na = 1.7 ± 0.2 g kg⁻¹; total K = 4.5 ± 0.2 g kg⁻¹; P = 2.2 ± 0.1 g kg⁻¹; water-extractable Si = 6.7 ± 1.2 mg kg⁻¹; 0.1 M HCl-extractable Si = 215 ± 23 mg kg⁻¹, CaCl₂-extractable Si = 21.4 ± 1.5 mg kg⁻¹. Soil properties were analyzed using standard and elaborated methods (Matychenkov et al. 2016; Saihua et al. 2018; Sparks et al. 2020). The greenhouse growing conditions were: air temperature 26 ± 4°C during the day and 22 ± 2°C during the night; the light period was 12 h at intensity of 200 Imol photons m⁻² s⁻¹ by UV/Vis lighting, and the relative air humidity was 85 ± 5% during the day and 78 ± 5% during the night.

Barley plants were irrigated daily with 50 mL pot⁻¹ of tap water containing 6 ± 1 ppm of Si as monosilicic acid and 8 ± 3 ppm of Na and having pH 7.1. After growing for a month, plants were carefully taken off from pots, washed in distilled water (DW) and placed into vessels with DW (control), Si solution, Na solution or Na + Si solution. DW had no detectable levels of Si or Na. The Si solution contained 150 ± 3

ppm of Si as monosilicic acid, no detectable polysilicic acid, and 70 ± 4 ppm of Na. Sodium solution contained 12000 ± 10 ppm of Na and no detectable Si. The Na + Si solution contained 150 ± 3 ppm of Si as monosilicic acid, no detectable polysilicic acid, and 12000 ± 10 ppm of Na. Twenty-five plants with average fresh weight 2 ± 0.08 g plant⁻¹ were put into each vessel. The evaporation from the vessels was prevented by plastic cover. Plants were sampled in 0, 24, 48, and 96 h of staying in the solutions.

Total Si and Na in plant tissue

Total Si and Na were analyzed in roots, stems and leaves before and after 96 h staying in the solution. The collected roots, stems and leaves were dried at 75°C for 4 days and ground. Then plant tissues were digested in microwave (CEM MARS 6 MS5181) in a KOH-H₂O₂ matrix by the method of Saihua et al. (2018). Silicon and Na in solutions were analyzed using ICP OES Optima 5900 DV (Perkin Elmer, USA).

Monosilicic acid, polysilicic acid and Na in apoplast and symplast

Monosilicic acid, polysilicic acid, and Na were analyzed in the symplast and apoplast of roots, stems and leaves by the following methodology. To analyze apoplast, fresh plant tissues were cut into pieces of 2.0–2.5 cm in length and 0.25 g in weight, put into a flask containing 50 ml of DW and shaken for 24 h. During 24 h all apoplast was washed into solution (Matichenkov et al. 2008). Then the solutions were analyzed for monosilicic acid, polysilicic acid and Na.

Samples of plant tissue obtained after filtering the remaining solution were homogenized in a mortar and mixed with a new portion of DW (40 mL). After that, the suspension was shaken for 60 min. The supernatant was centrifuged during 20 min at 5000 r/m for removing colloids and purified solution was analyzed for monosilicic acid, polysilicic acid, and Na. This data is related with the content of tested substances in the symplast (Matichenkov et al. 2008).

Monosilicic acid in all solutions was tested colorimetrically by the Mullen and Raily molybdate method (Mullin and Riley 1955) with spectrophotometer UNICO-2100 (USA). This method analyzes only monosilicic acid. Polysilicic acid was analyzed following its depolymerization. To depolymerize polysilicic acid, 20 mL of sample was added 0.3 mL of 50% NaOH and incubated in refrigerator at 4°C for 2 weeks. As a result, all polysilicic acid is transferred into monosilicic acid and then tested by the method described above. Sodium was analyzed using flame photometer BWB-XP Performance Plus (BWB Technologies, Great Britain).

Each treatment and analysis was conducted in 4 replications and standard deviations (S.D.) were calculated. Data was subjected to statistical analysis using the Student's t-test at 0.05 probability level by using EXCEL.

Results

Concentrations of Si (as monosilicic acid) and Na in the solutions before and after experiment are presented in Table 1.

Table 1
Concentrations of monosilicic acid and Na in solutions before and after staying barley plants, ppm.

Solution	Before experiment		After experiment	
	Si	Na	Si	Na
Control	0	0	8.1 ± 1.1	21.0 ± 2.0
Si	150 ± 3	65 ± 3	112.2 ± 1.3	55.3 ± 2.1
Na	0	12000 ± 10	6.5 ± 0.4	11903 ± 125
Na + Si	150 ± 3	12000 ± 10	101.3 ± 11.5	11925 ± 147

During 96 h the concentrations of Si and Na in control solution increased from 0 to 8.1 and 21.0 ppm, respectively, as a result of the release from plant tissue. In Si solution, the concentration of monosilicic acid declined from 150 to 112.2 ppm of Si. In Na + Si solution, the concentration of monosilicic acid was reduced up to 101.3 ppm of Si. The Na concentration in Na solution decreased from 12000 ppm to 11903 ppm, while in Na + Si solution a decrease was less, up to 11925 ppm. The amount of Na absorbed from Na solution was statistically larger as compared with that from Na + Si solution.

After 96 h-staying in the solutions, the total Si increased in all tested plant tissues in the Si, Na or Na + Si solutions (Table 2). Higher values of total Si were detected in the roots and stems in Na + Si solution. In the leaves, higher Si was detected in Si solution. Exposure to Na initiated the Si redistribution from leaves to stems and roots.

The total Na in the roots was maximum in Na + Si solution (1.28%), while in the stems and leaves the maximum total Na was detected in Na solution (1.99 and 1.04%, respectively). The maximum total Si in the roots (2.12%) and stems (0.93%) were determined in Na + Si solution. In the leaves, the maximum total Si (1.42%) was tested in Si solution, while the leaf Si was reduced to 0.82% in Na + Si solution.

The dynamics of monosilicic, polysilicic acids and Na in the apoplast and symplast of roots, stem and leaves is presented in Figs. 1–3.

Table 2
Total Si and Na in barley plants before and after staying in Si, Na and Na + Si solutions, %.

Solution	Before experiment		After experiment	
	Si	Na	Si	Na
Roots				
Control	0.82 ± 0.04	0.041 ± 0.004	0.87 ± 0.08 a	0.36 ± 0.06 a
Si			1.25 ± 0.08 b	0.34 ± 0.06 a
Na			1.53 ± 0.08 c	1.10 ± 0.07 b
Na + Si			2.12 ± 0.07 d	1.28 ± 0.07 c
Stems				
Control	0.45 ± 0.07	0.032 ± 0.004	0.42 ± 0.08 a	0.30 ± 0.06 a
Si			0.87 ± 0.08 c	0.33 ± 0.06 a
Na			0.61 ± 0.07 b	1.99 ± 0.05 c
Na + Si			0.93 ± 0.05 c	0.82 ± 0.04 b
Leaves				
Control	0.68 ± 0.07	0.052 ± 0.005	0.63 ± 0.08 a	0.54 ± 0.06 a
Si			1.42 ± 0.07 c	0.65 ± 0.05 a
Na			0.52 ± 0.06 a	1.04 ± 0.05 c
Na + Si			0.82 ± 0.06 b	0.81 ± 0.06 b

Data express the mean ± S.D. The different letters above the bar indicate significant differences between groups using the Duncan's multiple range test ($p < 0.05$).

In DW, the concentrations of monosilicic acid in the apoplast of root, stem and leaf gradually decreased, while its reduction in the symplast was observed only in roots. The monosilicic acid in the symplast of stem and leaf increased.

Exposure to Na initiated reducing monosilicic acid only in the root and leaf apoplast. In the stem apoplast and symplast, monosilicic acid significantly increased. Supplementation with monosilicic acid increased the monosilicic acid content in all organs, except the leaf apoplast. Higher increase was observed in the root apoplast in Na-Si solution.

The dynamics of polysilicic acid in the apoplast and symplast of stem was similar in all solutions: it increased for 96 hours, with smaller changes in DW and larger ones in Na + Si solution. In the root

apoplast, considerable continuous increase in polysilicic acid was only in Na + Si solution. In DW, polysilicic acid was reduced in the root and leaf apoplast, whereas it remained stable in the root and leaf symplast. The polysilicic acid concentration increased in the stem and leaf apoplast in Si solution, but did not increase in the root apoplast. However, polysilicic acid increased in the symplast of all organs and in all solutions, except the leaf symplast in DW.

In DW, the Na concentrations decreased during 96 hours from 200 to 135 ppm and from 245 to 119 ppm in the root and stem apoplast, respectively, while the leaf apoplast Na slightly increased (from 50 to 68 ppm). In DW, the Na in the symplast of root, stem and leaf was reduced, but differently. Higher Na reduction was observed in the root (by 47%) and lesser in the leaf (by 6.6%). In Si solution, the root apoplast and symplast Na increased markedly from 200 to 523 and from 480 to 604 ppm, respectively, for 96 h, whereas the leaf symplast Na was reduced from 1500 to 1270 ppm. The fact of increasing Na in the apoplast and symplast of roots may be attributable to the Na plant uptake from Si solution because it contained about 70 ppm of Na.

The dynamics of Na in the apoplast and symplast of all organs of salt-exposed plants represented a parabolic curve. The Na reached equilibrium in the root apoplast within the first 24 h, while in the stem apoplast the equilibrium was observed in 48 h and in the leaf apoplast in 96 h. It is important to emphasize that under salt exposure the penetration of Na into the root and stem symplast was much lower than that into the corresponding apoplast, whereas the dynamics of Na was similar in the leaf apoplast and symplast.

After 96 hours, the Na in the apoplast of root, stem, and leaf decreased from 9320 to 6520 mg kg⁻¹, from 23600 to 3350 mg kg⁻¹ and from 30120 to 2945 mg kg⁻¹, respectively. In symplast, the Na was reduced only in stem (from 2670 to 3450 mg kg⁻¹), whereas it increased from 557 to 682 mg kg⁻¹ in root and from 6510 to 10240 mg kg⁻¹ in leaf.

Discussion

As well known, plants adsorb Si as monosilicic acid (Ma and Takahashi 2002). The Si transport from soil to roots and inside plant tissue is mediated by different transporters (Kaur and Greger 2019). Our results have shown that the concentrations of monosilicic acid in the apoplast and symplast of barley plants were higher than those in external solutions (Table 1). This data suggests that the uptake of monosilicic acid by roots occurred against a concentration gradient. In the presence of Si in the solution with or without Na, the concentrations of monosilicic acid were significantly increased in the symplast of all tissues, while an increase in the apoplast was observed only in the roots. Probably, the apoplast of stems and leaves mostly provides the Si transport, but not its accumulation.

The plant Si uptake increased under a stress as compared to non-stressed conditions. It should be noted that besides salt stress, hypoxia stress was simulated additionally as a result of transferring barley plants from soil to solution. Salt together with hypoxia initiated higher increases in the root and stem total Si

than hypoxia alone. The redistribution of Si inside stressed plant occurred into the symplast as monosilicic acid and into both the symplast and apoplast as polysilicic acid. As a result, the total Si in leaves of stressed plants was reduced.

The role of additional Si nutrition in decreasing the leaf Na has been observed in some plants (Gong et al. 2006; Zuccarini 2008). The net root-to-shoot transport rate of Na (expressed per unit of root mass) was decreased in rice seedlings by added silicate (Gong et al. 2006, 2008). Authors have suggested that the Si deposition in exodermis and endodermis reduced the Na uptake through a reduction in apoplastic transport across the root. The Si treatment significantly decreased the Na content in the roots of alfalfa plants (Wang and Hang 2007). Tuna with co-authors (Tuna et al. 2007) observed the reduction in the Na translocation into roots and shoots of wheat by Si supplied to the nutrient solution at salt stress. Silicon-induced decrease in the permeability of plasma membranes for Na was recognized as major mechanism of mitigating salt toxicity by Si.

As evident from our results, in the salt-stressed barley plants Na mainly accumulated in the leaf symplast, in spite of higher Na concentrations observed in the apoplast, because a volume of apoplast is relatively small (Polevoi 1989).

In Na + Si solution, the Na movement into and within barley plants was suppressed compared with that in Na solution. Silicon increased the total Na accumulation in roots, but decreased in stems and leaves as well as had a direct effect on the Na transport through the apoplast. Reductions in the Na concentration in the root, stem, and leaf apoplastic solutions were 31; 88.1; and 92%, accordingly. In a 96-h period, the Na concentration in the leaf apoplast became 11.2-fold lower in Na + Si solution than that in Na solution, amounting to 3450 ppm and 38663 ppm, respectively. A delay in the Na penetration into the leaf symplast was observed as well.

We assume that Si blocks the Na transport at sites of apoplastic leakage. This mechanism may be related to the formation of monosilicic-Na or polysilicic-Na complexes. To verify these mechanisms, more research is required.

At high Na in external solution, Na penetrated into the root and stem apoplast, but did not penetrate into the root and stem symplast. Probably, another protective mechanism against salt toxicity exists in symplast of root and stem. In the presence of Si and low Na in the solution, a sharp increase in the root symplast Na was observed. At the same time in the presence of Si and high Na in the solution, this Na remained low. These results imply that the Na translocation into the root symplast is controlled by plant signaling system to be able to recognize the Na concentration in the apoplast.

The additional penetration of Na into the symplast of roots and stems observed at low Na in the external solution could be related with the fact that Na is considered as a beneficial nutrient for some of the C₄ photosynthetic plants, necessary for importing pyruvate into mesophyll chloroplasts by a Na⁺/pyruvate cotransporter (Ohnishi et al. 1990). Probably, Si promotes improving Na nutrition if the plant signals a lack of Na.

Conclusions

Silicon significantly decreased the Na root-to-leaf transport in barley plants exposed to salt stress. A reduction in the Na root-to-leaf transport was mainly in the apoplastic pathway. The root and stem symplast is capable of regulating the Na penetration from the apoplast depending on the Na concentration.

The Si transport within plant probably occurs in the form of polysilicic acid being primary formed in the root zone. At optimum or low stressed conditions, Si mainly accumulated in the roots and leaves. Under stress, this Si was redistributed to a mostly stress-affected place.

The data obtained indicates a significant role of Si compounds in plants exposed to salt stress. Additional investigations are necessary to verify the basic mechanisms responsible for mitigating salt toxicity by Si.

Declarations

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Conflicts of Interest: The authors declare no conflict of interest.

Availability of data and material: All data generated or analysed during this study are included in this published article

Code availability: The special software was not used in this research.

Author Contributions: Wei Xiao developed the conceptuality of the investigation and data processing; Zhang Pengbo analyzed the data; Bocharnikova Elena made analyses and organized the greenhouse tests; Matichenkov Vladimir designed experiment and wrote the article.

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Figures

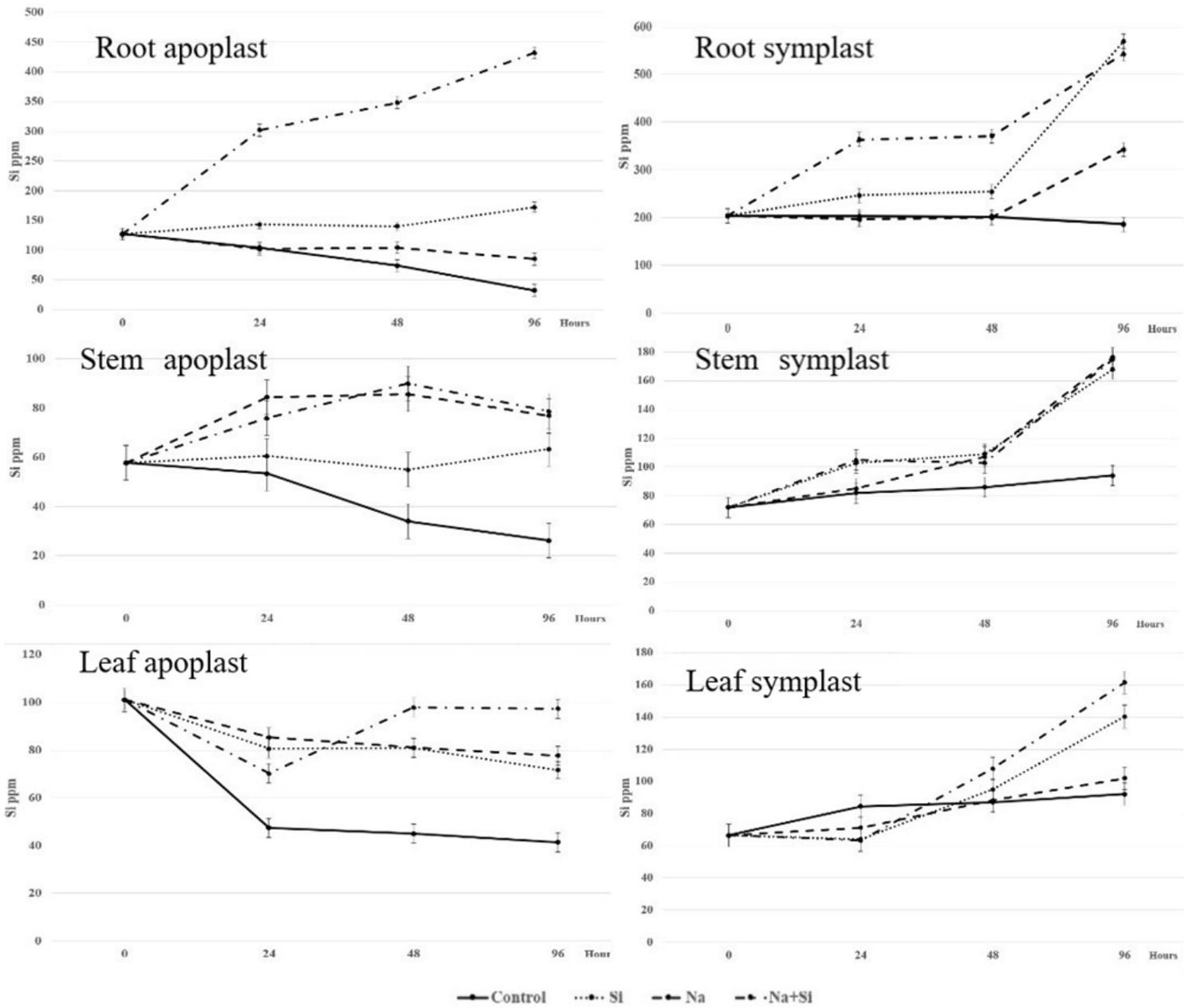


Figure 1

Dynamics of monosilicic acid in apoplast and symplast of roots, stems and leaves of barley.

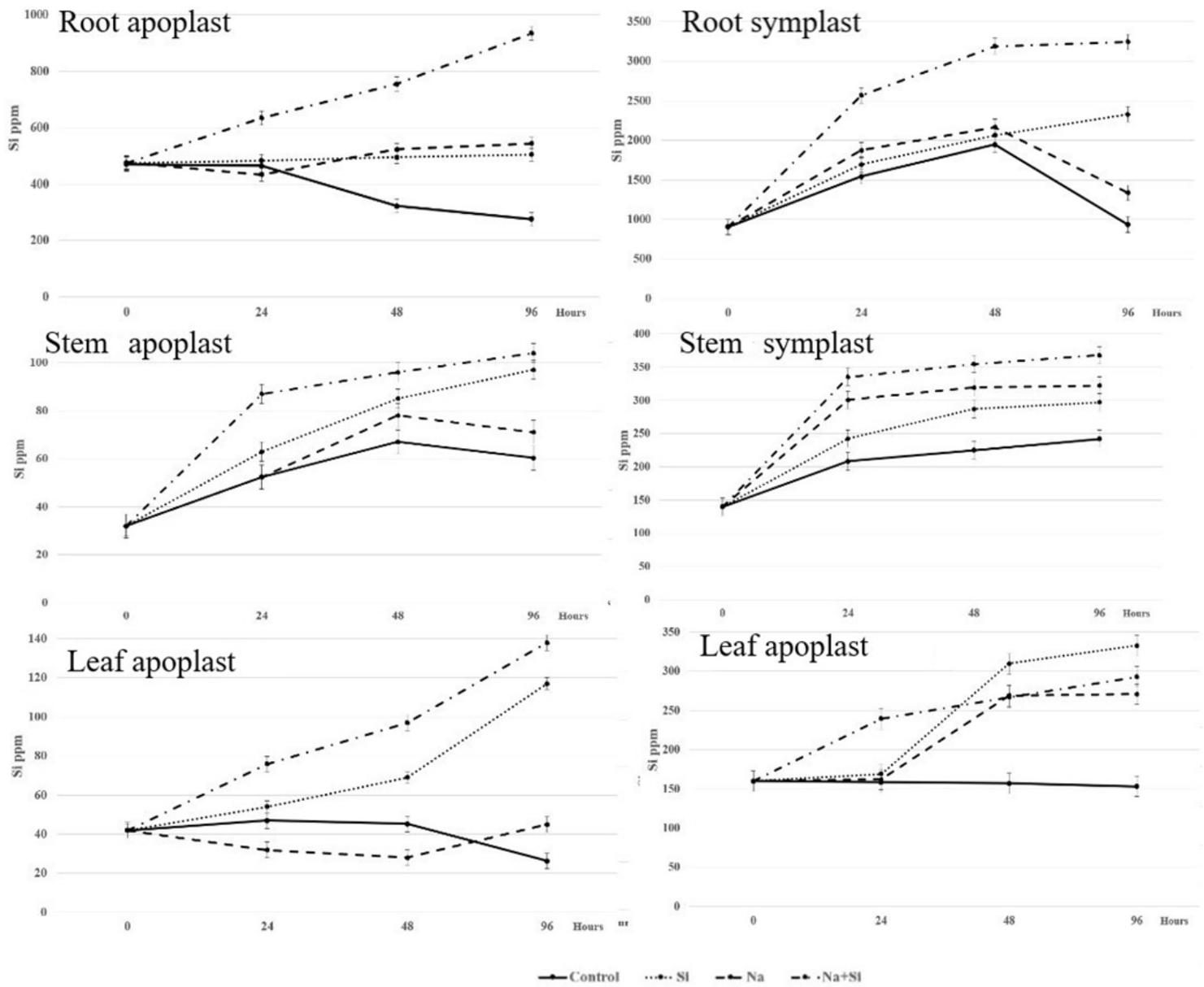


Figure 2

Dynamics of polysilicic acids in apoplast and symplast of roots, stems and leaves of barley.

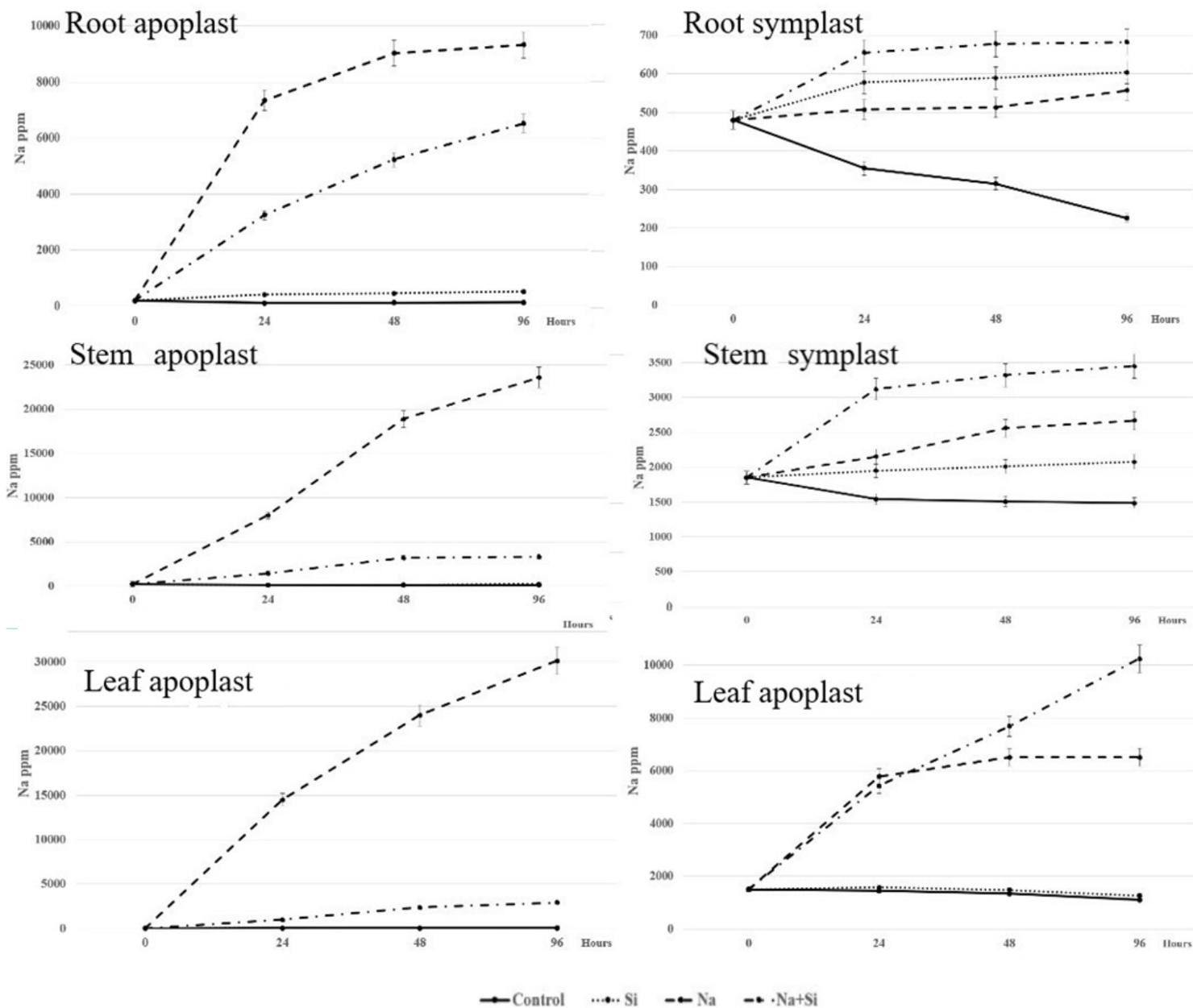


Figure 3

Dynamics of Na in apoplast and symplast of roots, stems and leaves of barley.