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Influence of silicon on aluminium toxicity in common and durum wheats

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Abstract – In acid soils, aluminium toxicity is the primary stress factor limiting the growth of plants. Silicon may reduce the toxic effects of Al in hydroponic culture. The objective of this study was to examine the effects of Al and Si treatments on the growth and potassium uptake of roots and transport to the shoots of an Al-resistant common wheat (*Triticum aestivum* L.) and an Al-sensitive durum wheat (*T. durum* Desf.). Seedlings were grown hydroponically, at pH 4.1, with different levels of Al and Si. Increased levels of Al (0–100 µM) in the solution reduced root growth; however, shoot growth was not influenced, except in durum wheat in 7-d experiments. Si in the growth solution enabled plants to overcome Al toxicity symptoms. Seedlings of durum wheat proved to be more sensitive to Al and Si treatments. In short-term (6 h) uptake experiments, Si reduced the stimulatory effect of Al on K⁺(⁸⁶Rb) uptake of roots, which indicated a definite Al-Si interaction, principally in the roots. In long-term (4 d) Si pre-treatment experiments, no post-effect was detected.

aluminium / silicon / potassium uptake / root elongation / silicic acid / wheat

Résumé – Influence du silicium sur la toxicité de l'aluminium chez le blé tendre et le blé dur. Dans les sols acides, la toxicité de l'aluminium est la première contrainte qui limite la croissance des plantes. Le silicium pourrait réduire les effets toxiques de l'aluminium en culture hydroponique. L'objectif de cette étude a été d'examiner les effets des traitements à base d'aluminium et de silicium sur la croissance et l'absorption de potassium des racines et son transport vers les tiges d'un blé tendre résistant à la toxicité de l'Al (*Triticum aestivum* L.) et d'un blé dur sensible à l'Al (*Triticum durum* Desf.). Les semis ont été effectués en culture hydroponique à un pH de 4.1 avec différents niveaux d'Al et de Si. L'accroissement des niveaux d'Al (0 à 100 µM) dans la solution a réduit la croissance des racines, alors que la croissance des tiges n'était pas influencée excepté pour le blé dur dans les expériences de 7 jours. Le Si dans les solutions nutritives a permis aux plantes d'échapper aux symptômes de la toxicité de l'Al. Les semis de blé dur ont montré être plus sensibles au traitement à l'Al et Si. Dans les expériences d'absorption à court-terme (6 heures), le Si a réduit l'effet stimulant de l'Al sur le prélèvement de K⁺(⁸⁶Rb) par les racines qui indiquaient une interaction définie Al-Si principalement dans les racines. Dans les expériences de pré-traitement avec Si à long terme (4 jours) aucun effet remanant n'a été détecté.

aluminium / silicium / prélèvement de potassium / élongation des racines de blé

1. INTRODUCTION

Approximately 40% of the world's cultivated lands and up to 70% of the potentially arable lands are acidic [1]. Crop yield is reduced by soil acidity on ca. 30% [2]. Much of the damage to plant production is due to excess aluminium (Al), the most common metal in soil. Al in soils with pH > 5 mostly forms insoluble oxides and complex alumino-silicates. At lower pH values there is a release of bioactive forms of Al, particularly monomeric Al [3], which is toxic to plants. The toxic effect of Al on plants is well documented; however, the phys-

iological and biochemical reasons for inhibition of root elongation by Al are not completely understood. Recently, a number of authors have shown that silicon (Si) can decrease the toxic effects of Al in hydroponic culture in several species [4–10]. However, the literature is not very conclusive on the effects of Si on Al toxicity. Both an ameliorative effect, and little or no effect of Si on Al toxicity have been reported [8, 11]. Such inconsistency may be due to differences in nutrient solution, duration of treatments, initial Si status of plants, different plant age and development, and different plant species and cultivars [8].

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The critical question in this area was raised by Hodson and Evans [8] who did not find a clear effect of Si on the activity of Al in solution. On the other hand, Barcelo et al. [5] demonstrated that Si could ameliorate the toxic effects of Al in teosinte and also reported a significant decrease in concentration of monomeric Al species in the nutrient solutions in the presence of Si. Ma et al. [10], working on corn roots, suggested that amelioration of Al toxicity was due to the formation of Al and Si complexes in solution rather than any physiological effect of Si on the plant. They found that the concentration of toxic Al^{3+} was reduced in the presence of Si and the decrease in toxic Al^{3+} was paralleled by an increase in root elongation.

Some recent studies have indicated that Si ameliorates Al toxicity not only by decreasing the activity of free Al^{3+} in solution, but also reducing the internal toxicity of Al in the plant [4–6, 9]. These results indicate Al-Si interaction (probably hydroxy-alumino-silicate, HAS formation) occurs in plants, though complexes of Al and Si in solution *ex planta* may also be formed to a limited extent.

It is known that a high proportion of Al taken up into plant roots remains in the apoplast, and this comprises as much as 85–90% of the total in some species [12]. That is, one of the possible mechanisms for the detoxification of Al by Si in plants is co-precipitation of the two elements in roots [8].

Si is the second most abundant element in the soil, but its speciation is simpler than that of Al [11]. The “soil solution” contains Si mainly as silicic acid at 0.1–0.6 mM concentration [13, 14]. Below pH 9, Si exists as neutral silicic acid, which is the form available for plant uptake [15].

Our aim in the present work was to investigate the effect of Si and Al, separately and in combination, on the growth of two wheat species at low pH. In order to corroborate the evidence from analysis of seedling growth, examination of K^+ uptake of roots and the transport towards the shoots was also carried out.

2. MATERIALS AND METHODS

2.1. Plant materials

Common wheat (*Triticum aestivum* L. cv. Jubilejnaja 50) and durum wheat (*T. durum* Desf. cv. GK Betadur) were the experimental material in this study. Earlier tests in acid soil [16, 17] showed that Jubilejnaja 50 is a moderately tolerant cultivar and GK Betadur is a moderately sensitive one.

We chose to carry out our experiments in very simple nutrient media (0.5 mM CaSO_4), and thus avoid complications from Al interactions with nutrient elements (particularly phosphorus) and also to maintain the cell membrane integrity. These experiments have to be of short duration in order to avoid nutrient deficiencies.

Seeds were washed and germinated in Petri dishes in darkness at 25 °C. The seedlings were placed on stainless steel screens over glass beakers. Each beaker contained 300 ml growth solution and 8 seedlings. Seedlings were grown hydroponically in 0.5 mM CaSO_4 solution at pH 4.1 with different levels of Al and Si in a Conviron growth chamber, and the conditions were: the light intensity at plant level, 60 $\text{W}\cdot\text{m}^{-2}$; the relative humidity, 65%; light/dark periods, 16/8 h;

and day/night temperatures, 25/20 °C. Treatments were 0 (control), 10, 50 and 100 μM AlCl_3 and 0 (control), 500, 1000 and 1500 μM $\text{Na}_2\text{SiO}_3\cdot 5\text{H}_2\text{O}$. The initial pH values were adjusted with 0.1 M HCl or 0.1 M NaOH if needed, and checked every day. All growth solutions were renewed daily.

2.2. Experiments

^{86}Rb was used to monitor the K^+ transport in plants [18]. In the K^+ (^{86}Rb) uptake experiments, plants were pre-cultured in 0.5 mM CaSO_4 solution for 4 or 6 days. After the 4th or 6th day, plants were transferred to different uptake solutions containing 1 mM $\text{K}(^{86}\text{Rb})\text{Cl}$ + 0.5 mM CaCl_2 + AlCl_3 and Na_2SiO_3 as indicated in the figure legends. The concentration of ^{86}Rb in the uptake solution was 185 $\text{kBq}\cdot\text{l}^{-1}$. The pH of the absorption solution was initially adjusted to the appropriate value with HCl or NaOH, and checked again at the end of the absorption period.

The K^+ (^{86}Rb) uptake experiments lasted for 6 hours. After the uptake time, the roots of the intact plants were rinsed three times in 400 ml distilled water for 1 minute. Because of the importance of this washing step, washing solutions of different compositions (0.5 mM CaCl_2 , 1 and 5 mM KCl, distilled water), pH and time were also tested (data not shown). Since no significant differences were found, distilled water was used for washing in the subsequent experiments. Roots and shoots were then separated and the radioactivity of ^{86}Rb in the plant material was measured by a liquid scintillation counter (Canberra Packard Prias PL, Tri-Carb).

The dry weights of the roots and shoots of all plants were determined upon harvesting. Shoots and roots were harvested separately and subsequently dried at 70 °C until they reached constant weight. All experiments were performed in triplicate with whole plants; the data given below are averages with standard deviation (SD) ($n = 8$). A typical series of three independent experiments is presented in the figures below. The statistical analysis of data was done by two-way analysis of variance (ANOVA) or co-variance (ANCOVA).

3. RESULTS

In the 7-day experiments, Si treatments from 500 to 2000 μM inhibited the growth (DW) of GK Betadur roots. In shoots, however, the opposite phenomenon occurred: the DW increased as the Si concentration increased in the medium. Under the same experimental conditions, Jubilejnaja 50 did not show any effect of Si treatments (data not shown).

In Figure 1 growth data are presented, showing that increasing Al concentrations caused a clear and significant decrease in root dry matter yield, especially in Al-sensitive GK Betadur seedlings. The presence of Si in the growth solution reduced (with low significance) the Al toxicity, particularly in Al-tolerant Jubilejnaja 50. In GK Betadur durum wheat, however, the ameliorative effect of Si was not so unambiguous, in comparison with the untreated control plants and Jubilejnaja 50, respectively.

The effects of Si pre-treatments on dry weight of Jubilejnaja 50 and GK Betadur seedlings are shown in Figure 2.

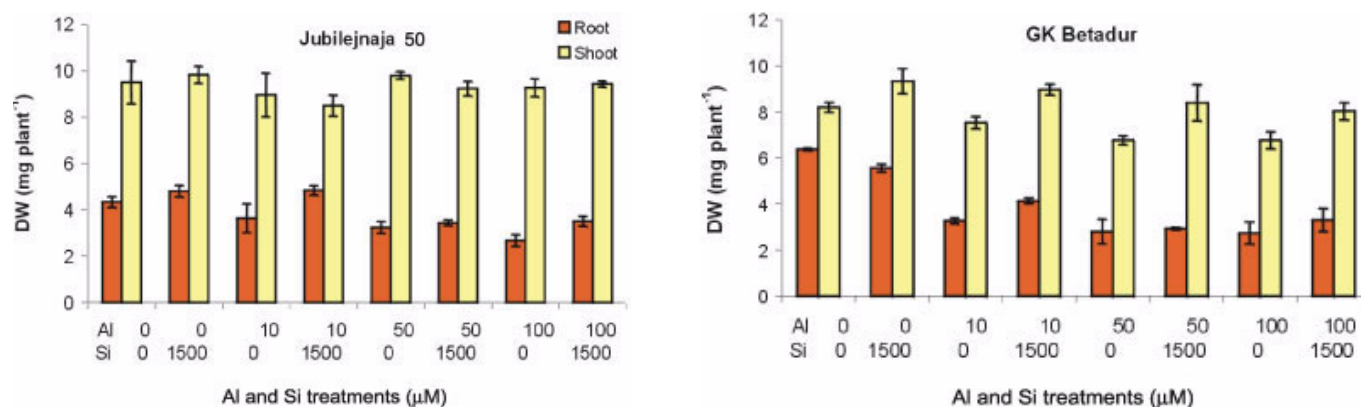


Figure 1. Effects of Al and Si treatments on the growth of Al-resistant Jubilejnaja 50 (common wheat) and Al-sensitive GK Betadur (durum wheat) seedlings. Plants were grown for 7 days on 0, 10, 50 and 100 μM AlCl₃ and Na₂SiO₃ (1500 μM) combinations in 0.5 mM CaSO₄ solution as indicated on the graph, pH was 4.1. All data show the means ± SD (Shoot: *Jubilejnaja 50*: Al: 0.1185 n.s., Si: 0.6300 n.s., Al+Si: 0.5735 n.s.; *GK Betadur*: Al: 1.016×10^{-3} **, Si: 7.081×10^{-6} ***, Al+Si: 0.8493 n.s.; root: *Jubilejnaja 50*: Al: 6.161×10^{-6} ***, Si: 3.794×10^{-4} ***, Al+Si: 0.1417 n.s.; *GK Betadur*: Al: 7.942×10^{-10} ***, Si: 0.2504 n.s., Al+Si: 0.01143 *) [Significance codes: 0 **** 0.001 *** 0.01 ** 0.1 * n.s. 1].

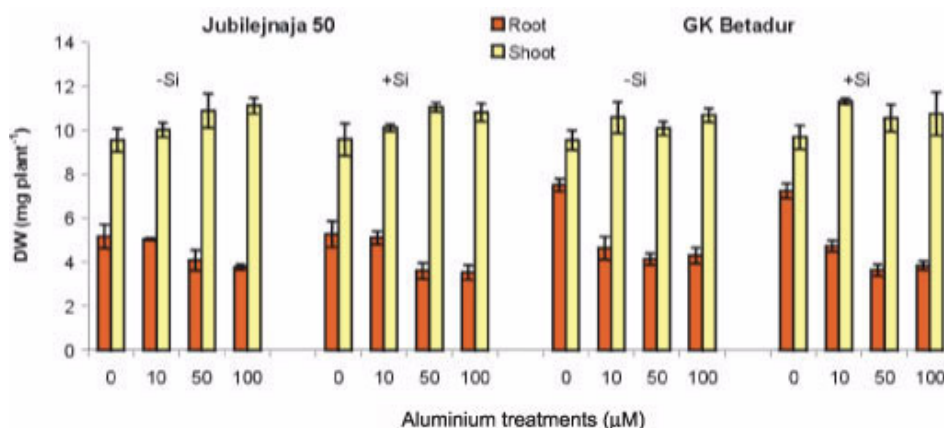


Figure 2. Effects of Si pre-treatments on DW of Al-resistant Jubilejnaja 50 and Al-sensitive GK Betadur seedlings. Plants were grown in 0.5 mM CaSO₄ solution at pH 4.1 for 4 days in the presence (+Si) or absence (-Si) of 1500 μM Na₂SiO₃ as indicated on the graph. After the Si pre-treatment, the seedlings were tested for 3 days in 0.5 mM CaSO₄ solution with 0, 10, 50 and 100 μM AlCl₃, at pH 4.1. All data show the means ± SD (Shoot: *Jubilejnaja 50*: Al: 1.562×10^{-3} **, Si: 1.000 n.s., Al+Si: 0.9066 n.s.; *GK Betadur*: Al: 2.163×10^{-2} *, Si: 0.2339 n.s., Al+Si: 0.8252 n.s.; root: *Jubilejnaja 50*: Al: 2.567×10^{-5} ***, Si: 0.5020 n.s., Al+Si: 0.7031 n.s.; *GK Betadur*: Al: 1.579×10^{-10} ***, Si: 0.1007 n.s., Al+Si: 0.5559 n.s.) [Significance codes: 0 **** 0.001 *** 0.01 ** 0.1 * n.s. 1].

From the data it is evident that according to the Al-sensitivity of the species, with increasing Al levels the DW of roots – with or without Si pre-treatments – showed a very significant decreasing trend at pH 4.1. In the case of the shoot DW, this tendency was the opposite. The DW of roots clearly indicated that a 4-day Si pre-treatment did not significantly affect the Al toxicity of the plants used in our experiments.

The effects of Al and Si treatments on root elongation of Jubilejnaja 50 and GK Betadur seedlings at pH 4.1 are presented in Figure 3. The data exhibit obvious Al-Si interaction in root elongation of Jubilejnaja 50, while little if any ameliorative effect of Si could be demonstrated for root elongation of GK Betadur seedlings. It is remarkable that the ameliorative effects of Si on Al toxicity were most marked at low Al treat-

ments, and a definite Si-induced growth stimulation even appeared in Jubilejnaja 50 at 10 μM Al.

Figure 4 shows the effect of short-term (6 h) Al and Si exposure on K⁺(⁸⁶Rb) uptake of the roots and the transport towards the shoots in Jubilejnaja 50 and GK Betadur seedlings at pH 4.1. The addition of Si to the solution weakened the stimulatory effect of Al on K⁺(⁸⁶Rb) uptake of the roots, which is obvious at 100 μM aluminium in the absence of Si.

In long-term (3 d) Al and Si pre-treatment experiments, however, it was not possible to detect significant post-effects in K⁺(⁸⁶Rb) uptake by the roots of Al+Si treated plants (Fig. 5). It is remarkable that Si treatments alone, in contrast to Al, did not influence considerably the K⁺(⁸⁶Rb) uptake of the roots and the transport to the shoots.

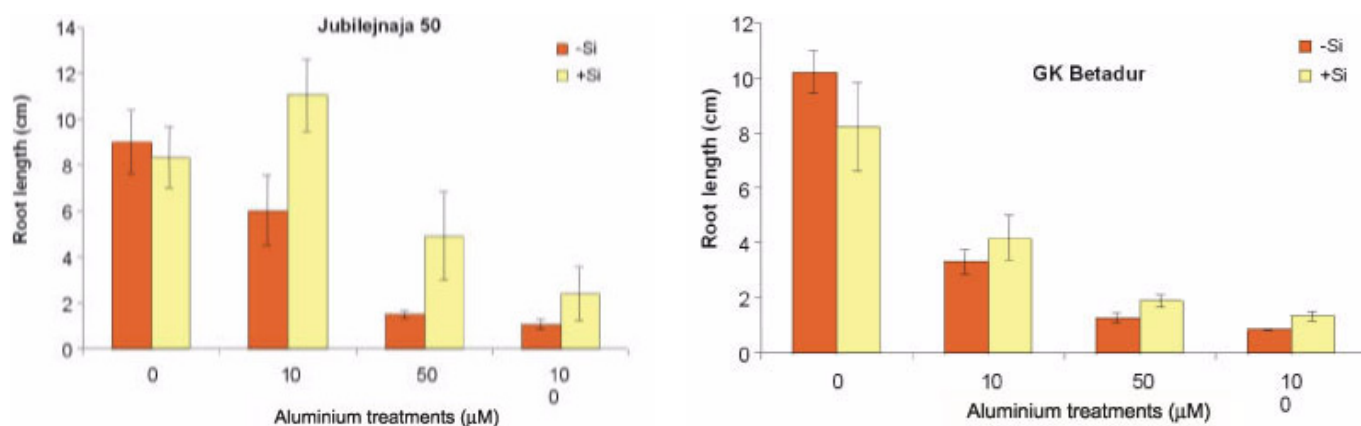


Figure 3. Effects of Al and Si treatments on the root elongation of Al-resistant Jubilejnaja 50 and Al-sensitive GK Betadur seedlings. Plants were grown for 7 days on varied AlCl_3 concentrations (0, 10, 50 and 100 μM) in 0.5 mM CaSO_4 solution in the presence (+Si) or absence (-Si) of 1500 μM Na_2SiO_3 as indicated on the graph, pH was 4.1. All data show the means \pm SD (Roots: *Jubilejnaja 50*: Al: 6.126×10^{-7} ***, Si: 3.053×10^{-3} **, Al+Si: 0.0347 *; *GK Betadur*: Al: 2.081×10^{-5} ***, Si: 0.8243 n.s., Al+Si: 0.4276 n.s.) [Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.1 'n.s.' 1].

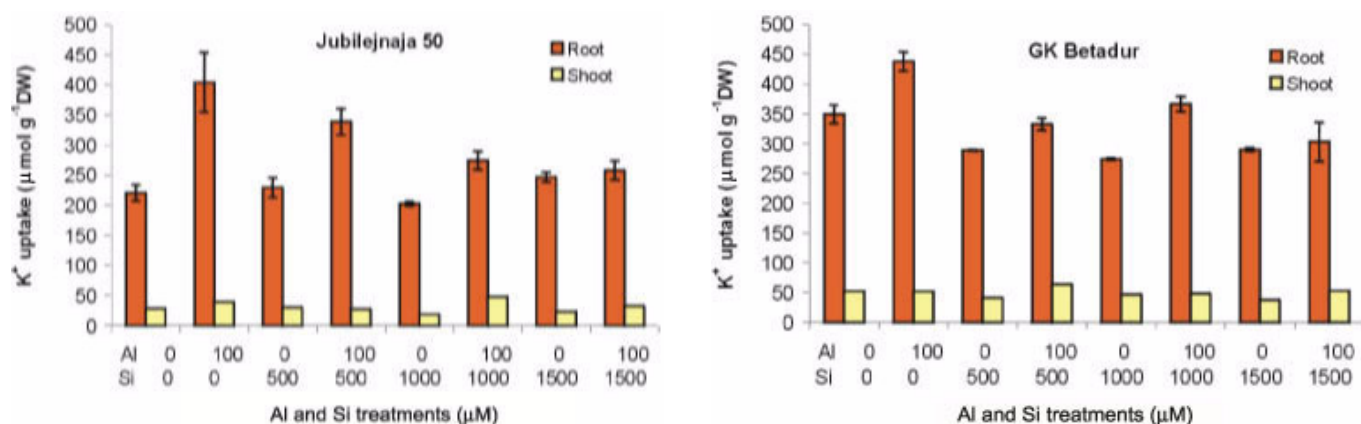


Figure 4. Effects of Al and Si treatments on the K^+ (^{86}Rb) uptake of the roots and the translocation to the shoots of Al-resistant Jubilejnaja 50 and Al-sensitive GK Betadur seedlings. Plants were grown for 7 days in 0.5 mM CaSO_4 solution at pH 6.5. After the 7th day the seedlings were treated for 6 h with 1 mM K^+ (^{86}Rb)Cl + 0.5 mM CaCl_2 + AlCl_3 and Na_2SiO_3 solution as indicated on the graph, pH value was 4.1. All data show the means \pm SD (Roots: *Jubilejnaja 50*: Al: 1.831×10^{-4} ***, Si: 0.0373 *, Al+Si: 0.0224 *; *GK Betadur*: Al: 6.657×10^{-4} ***, Si: 1.181×10^{-3} **, Al+Si: 0.1027 n.s.) [Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.1 'n.s.' 1].

Figure 6 shows the post-effects of Si pre-treatments on K^+ (^{86}Rb) uptake of roots and transport to the shoots of Jubilejnaja 50 and GK Betadur seedlings in the presence of various concentrations of Al at pH 4.1. Our results demonstrate that plants pre-treated with 1500 μM Si for 3 days and subsequently exposed to Al (up to 100 μM) for 6 h showed significantly lower K^+ (^{86}Rb) uptake than plants which were not pre-treated with Si.

4. DISCUSSION

Analysis of the effects of Si in the absence of Al revealed that external Si at 500 to 2000 μM resulted in an increase in shoot DW of Al-sensitive GK Betadur seedlings (data not

shown). The increase in weight of shoots by Si treatments was not due to an elevated Si uptake as shown by ashing tests, since Si content was only 10–24% of the difference. It seems likely that the favourable effect of Si on shoot growth (DW) in GK Betadur was a secondary effect, resulting from physiological alterations in the root.

Comparing the DW production of Al-resistant Jubilejnaja 50 and Al-sensitive GK Betadur in an identical growth medium, we found a species-specific positive Al-Si interaction at low Al concentration in root growth (DW) of Jubilejnaja 50, while no significant effect was demonstrated in growth (DW) of GK Betadur seedlings (Fig. 1). It was remarkable that the DW production of Al-Si treated plants were not always in accordance with the root length of treated plants (Fig. 3).

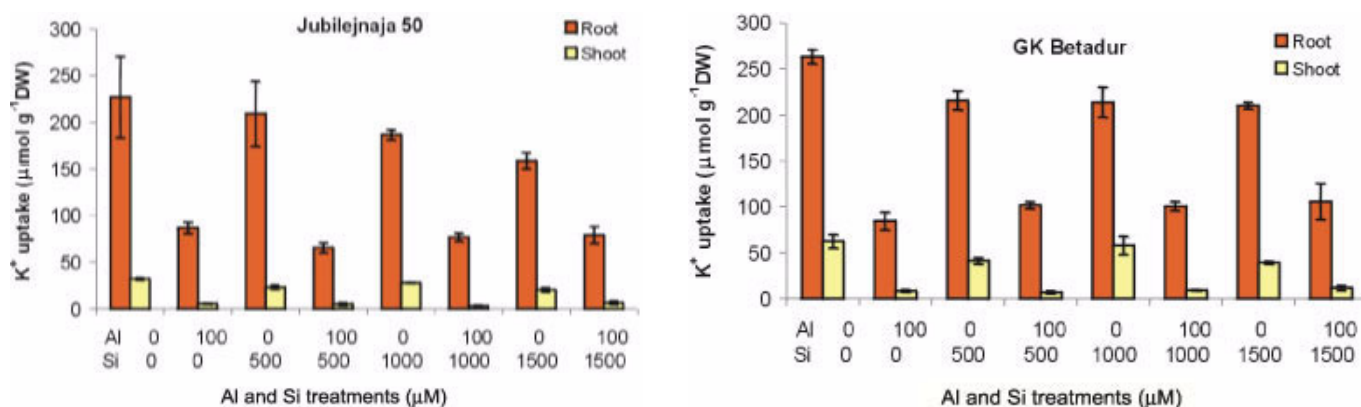


Figure 5. Effects of Al and Si pre-treatments on the K⁺(⁸⁶Rb) uptake of the roots and the translocation to the shoots of Al-resistant Jubilejnaja 50 and Al-sensitive GK Betadur seedlings. Plants were grown for 4 days in 0.5 mM CaSO₄ solution at pH 6.5 and subsequently treated for 3 days with 0.5 mM CaSO₄ + 100 μM AlCl₃ and 500, 1000 and 1500 μM Na₂SiO₃ solution as indicated on the graph, pH value was 4.1. Post-effect experiments were carried out for 6 h in 1 mM K(⁸⁶Rb)Cl + 0.5 mM CaCl₂ at pH value 4.1. All data show the means ± SD (Roots: *Jubilejnaja 50*: Al: 3.383×10^{-12} ***, Si: 0.0126 *, Al+Si: 0.0294 *; *GK Betadur*: Al: 9.669×10^{-15} ***, Si: 0.3619 n.s., Al+Si: 0.0014 **) [Significance codes: 0 **** 0.001 *** 0.01 * 0.1 'n.s.' 1].

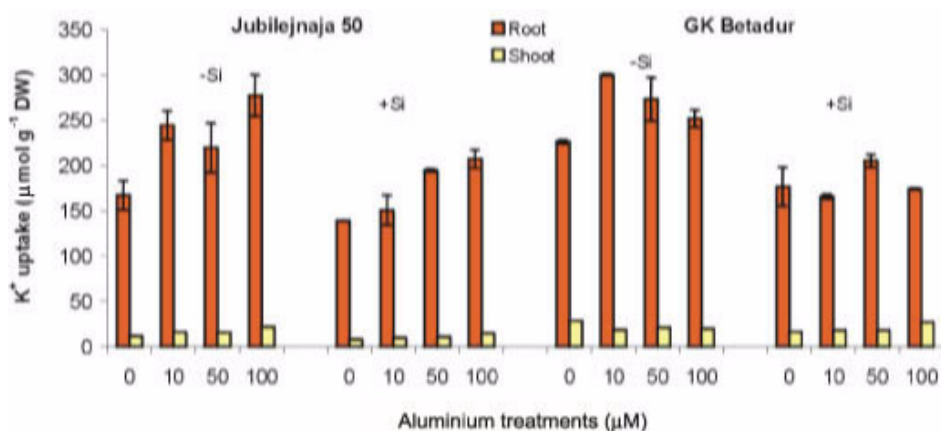


Figure 6. Effects of Si pre-treatments on the K⁺(⁸⁶Rb) uptake of Al-resistant Jubilejnaja 50 and Al-sensitive GK Betadur seedlings. Plants were grown in 0.5 mM CaSO₄ solution at pH 6.5. After the 4th day one group of seedlings (+Si) was pre-treated for 3 days with 0.5 mM CaSO₄ + 1500 μM Na₂SiO₃ solution as indicated on the graph, pH value was 4.1. After the Si pre-treatments, the seedlings were tested for 6 h with 1 mM K(⁸⁶Rb)Cl + 0.5 mM CaCl₂ + 0, 10, 50 and 100 μM AlCl₃ as indicated on the graph, pH value was 4.1. All data show the means ± SD (Roots: *Jubilejnaja 50*: Al: 3.622×10^{-3} **, Si: 1.497×10^{-3} **, Al+Si: 0.1820 n.s.; *GK Betadur*: Al: 0.0582 *, Si: 1.209×10^{-3} ***, Al+Si: 0.0483 *) [Significance codes: 0 **** 0.001 *** 0.01 * 0.1 'n.s.' 1].

We also demonstrated that DW production of plants pre-treated with Si for 4 days and then exposed to Al toxicity for 3 days was similar to that of the control plants, which had no Si pre-treatment (Fig. 2). We can conclude from these results that 4-day pre-treatment with Si had no significant influence (post-effect) on Al toxicity of plants.

That is, for significant ameliorative effects of Si on Al toxicity, at least in the case of DW production, Si has to be simultaneously present with Al in the external growing medium. These data are in accordance with the findings of Ma et al. [10] concerning the ameliorative effect of Si on Al toxicity in plants. On the other hand, it was also observed that in long-term experiments, Si pre-treatments for 3 days decreased the K⁺(⁸⁶Rb) uptake of roots in the presence of Al, suggesting a definite post-effect of Si treatments at plant level (Fig. 6).

Earlier we found a rapid specific stimulation of K⁺(⁸⁶Rb) uptake in wheat roots treated with 20, 50 and 100 μM Al [19]. This Al-stimulated K⁺(⁸⁶Rb) uptake was highly metabolism-dependent, and it was eliminated in the presence of 10 μM 2,4-DNP (2,4-dinitrophenol) in 6-h treatments [19]. From the present data it seems that Si treatments eliminate this formerly experienced “stimulatory” effect of Al on K⁺(⁸⁶Rb) uptake (Figs. 4 and 6), probably through the co-deposition of Al and Si in root cell walls [11].

These data suggest that Si can detoxify Al within the root and could reduce both the transport of Al into the symplast and further toxic effects on growth and K⁺ transport of plants. The ameliorative effect of Si treatments on Al toxicity, however, is significantly influenced by the Al sensitivity of the plant species too (Figs. 1 and 3).

In summary, our data indicated that the beneficial effect of Si is not only due to its influence on Al speciation in the external solution, but also to Al-Si interactions principally in the roots. It is possible that formation of alumino-silicate (AS) compounds in the cell walls of the cortex [8] can influence the uptake of K^+ (^{86}Rb) in roots (Fig. 6).

In conclusion, durum wheat (GK Betadur) proved to be more sensitive to Al and Si treatments than the common wheat (Jubilejnaja 50). The results confirmed that in an acidic environment, Si added to the growth medium not only ameliorated Al toxicity in plants, but stimulated significant growth (root elongation) at low Al concentration. A genotypic difference was found in the response of wheat species to Si applications.

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