Ciência Rural, Santa Maria, v.46, n.3, p.506-512, mar, 2016 http://dx.doi.org/10.1590/0103-8478cr20150585
ISSN 0103-8478 BIOLOGY

Silicon reduces aluminum content in tissues and ameliorates its toxic effects on potato plant growth

Silício reduz o conteúdo de alumínio em tecidos e ameniza seus efeitos tóxicos sobre o crescimento de plantas de batata

Athos Odin Severo Dorneles[I] Aline Soares Pereira[I] Liana Verônica Rossato[II]
Gessieli Possebom[III] Victória Martini Sasso[III] Katieli Bernardy[I] Ruziele de Quadros Sandri[I]
Fernando Teixeira Nicoloso[I] Paulo Ademar Avelar Ferreira[IV] Luciane Almeri Tabaldi[I*]

ABSTRACT

*Aluminum (Al) is highly toxic to plants, causing stress and inhibiting growth and silicon (Si) is considered beneficial for plants. This chemical element has a high affinity with Al. The aim of this study was to investigate the potential of Si to mitigate the toxic effects of Al on potato (**Solanum tuberosum** L.) plants and assess whether this behavior is different among genotypes with differing degrees of sensitivity to Al. Potato plants of the genotypes SMIJ319-7 (Al-sensitive) and SMIF212-3 (Al-tolerant) were grown for fourteen days in nutrient solution (without P and pH 4.5±0.1) under exposure to combinations of Al (0 and 1.85mM) and Si (0, 0.5 and 1.0mM). After this period, shoot and roots of the two genotypes were collected to determine Al content in tissues and assess morphological parameters of root and shoot growth. Roots of both genotypes accumulated more Al than shoots and the Al-tolerant genotype accumulated more Al than the sensitive one, both in roots and in shoot. Furthermore, the presence of 0.5 and 1.0mM Si together with Al reduced the Al content in shoot in both genotypes and in roots of the Al-tolerant genotype, respectively. Si ameliorated the toxic effects of Al with regard to number of root branches and leaf number in both potato genotypes. Si has the potential to mitigate the toxic effects of Al in potato plants regardless of Al sensitivity.*

Key words: ***Solanum tuberosum***, *beneficial element, toxic element, interaction.*

RESUMO

*O alumínio (Al) é altamente tóxico para as plantas, causando estresse e inibindo o crescimento e o silício (Si) é considerado benéfico para as plantas. Este elemento químico tem uma alta afinidade com o Al. O objetivo deste estudo foi investigar o potencial do Si em amenizar os efeitos tóxicos do Al sobre plantas de batata (**Solanum tuberosum** L.) e avaliar se esse comportamento é diferente entre os genótipos com diferente sensibilidade ao Al. Plantas de batata dos genótipos SMIJ319-7 (sensível ao Al) e SMIF212-3 (tolerante ao Al) foram cultivadas por 14 dias em solução nutritiva (sem P e pH 4,5±0,1), sob exposição a combinações de Al (0 e 1,85mM) e Si (0; 0,5 e 1,0mM). Após esse período, parte aérea e raízes dos dois genótipos foram coletadas para determinar o conteúdo de Al nos tecidos e avaliar parâmetros morfológicos das raízes e parte aérea. Raízes de ambos os genótipos acumularam mais Al do que a parte aérea, e o genótipo tolerante ao Al acumulou mais Al do que o sensível, tanto nas raízes quanto na parte aérea. Além disso, a presença de 0,5 e 1,0mM de Si juntamente com Al reduziu o conteúdo de Al na parte aérea em ambos os genótipos e nas raízes do genótipo tolerante ao Al, respectivamente. O Si amenizou os efeitos tóxicos do Al para número de ramificações de raízes e de folhas em ambos os genótipos de batata. Si tem o potencial para amenizar os efeitos tóxicos do Al em plantas de batata, independente da sensibilidade ao Al.*

Palavras-chave: ***Solanum tuberosum***, *elemento benéfico, elemento tóxico, interação.*

INTRODUCTION

Potato (***Solanum tuberosum*** L.) is the third most important food crop in the world, after rice and wheat (BIRCH et al., 2012). Several variables affect the performance of potato plants. Among those which can be manipulated by man, nutritional management is one of the most important (WESTERMANN & DAVIS, 1992). Several studies showed that potato plants exposed to various toxic metals such as aluminum (Al) and cadmium through

---

[I] Programa de Pós-graduação em Agrobiologia, Universidade Federal de Santa Maria (UFSM), 97105-900, Santa Maria, RS, Brasil. E-mail: lutabaldi@yahoo.com.br. *Corresponding author.
[II] Programa de Pós-graduação em Agronomia, Universidade Federal de Santa Maria (UFSM), Santa Maria, RS, Brasil.
[III] Graduação em Engenharia Florestal, Universidade Federal de Santa Maria (UFSM), Santa Maria, RS, Brasil.
[IV] Departamento de Ciência do Solo, Universidade Federal de Santa Maria (UFSM), Santa Maria, RS, Brasil.

Received 04.22.15 Approved 08.03.15 Returned by the author 11.18.15
CR-2015-0585.R1

the growth medium can absorb these metals and translocate them to leaves and tubers (TABALDI et al., 2007; GONÇALVES et al., 2009), whereby they can be introduced into the food chain.

Aluminum is the most abundant metal (GOODWIN & SUTTER, 2009) on earth. However, Al has no essentiality known to man (EXLEY, 2012) or to most vegetables (LIANG et al., 2005). Bioavailability and, in consequence, toxicity of Al is mainly restricted to acid environments (pH below 4.5) (POSCHENRIEDER et al., 2008), which leads to a high-risk health scenario for humans, animals, plants and micro-organisms (GHNAYA et al., 2013). Al interferes negatively in different cultures, reducing biomass production, interfering more directly in the growth of roots (GOODWIN & SUTTER, 2009); thus, affecting the uptake, transport and bioactivity of essential elements (Ca, Mg, P and K) and water by plants (MIMMO et al., 2009), as well as increased sensitivity to other stresses, especially drought stress (MA, 2005). The apoplastic-bound Al hinders, especially at pH 4.00 and 4.50, the phosphate uptake by plants (GESSA et al., 2005). Cell walls and intercellular spaces, the so-called apoplast, are the first compartments of the root that contact with the potentially toxic Al species present in the soil solution (POSCHENRIEDER et al., 2008). Scanning electron micrographs showed a collapse of the fibrillar structure of calcium-polygalacturonate network, as a consequence of Al^{3+} immobilization, and a loss of porosity (MIMMO et al., 2003). Thus, development of strategies that result in lower plant uptake of these toxic elements in the soil is important, because it optimize the use of natural resources and the production of safe food.

Among the alternatives sought to solve the problems with toxic metals in plant growth is the use of beneficial elements which can ameliorate the harmful effects of these elements when used in low concentrations. Accordingly, silicon (Si), although not essential to most plants, is considered a beneficial element for various crops (LI et al., 2011; CAMARGO et al., 2014), increasing the tolerance of plants to insect attacks, diseases, unfavorable weather conditions and presence of metals (DONCHEVA et al., 2009; LI et al., 2011; MEENA et al., 2014). Furthermore, Si improves the nutritional status of plants and the physical and chemical properties in soil, supporting the maintenance of nutrients in available forms for plants (MEENA et al., 2014). The supply of Si increased the edible yield and the quality level, reducing the nitrate concentration in edible tissues of corn salad (***Valerianella locusta*** (L.) Laterr) plants (GOTTARDI et al., 2012). Thus, the aim of this study was to investigate the potential of Si to mitigate the toxic effects of Al on potato genotypes differing in Al tolerance, SMIJ319-7 (Al-sensitive) and SMIF212-3 (Al-tolerant) and assess whether this behavior is related to different sensitivities to Al.

MATERIAL AND METHODS

Two potato genotypes, SMIJ319-7 (aluminum-sensitive) and SMIF212-3 (aluminum-tolerant), obtained from the Potato Improvement and Genetics Program, UFSM, Santa Maria, RS, were propagated *in vitro* during 25 days in MS medium (MURASHIGE & SKOOG, 1962) supplemented with 30g L^{-1} sucrose, 0.1g L^{-1} myo-inositol and 6g L^{-1} agar. After this period, plants were transferred to plastic trays with a 17-liter capacity containing complete nutrient solution for acclimatization. Plants were exposed to a complete nutrient solution for three days. The nutrient solution had the following composition (in µM): 6090.5 N; 974.3 Mg; 4986.76 Cl; 2679.2 K; 2436.2 Ca; 359.9 S; 243.592 P; 0.47 Cu; 2.00 Mn; 1.99 Zn; 0.17 Ni; 24.97 B; 0.52 Mo; and 47.99 Fe ($FeSO_4$/Na EDTA). After this period, plants were cultivated for fourteen days in a new nutrient solution (without P and pH 4.5±0.1) with exposure to combinations of two Al concentrations (0 and 1.85mM as $AlCl_3$) and three silicon (Si) concentrations (0, 0.5 and 1.0mM as Na_2SiO_3). A solution without P was used because P could be absorbed by Al already precipitated in the root free space or the P may be precipitated as insoluble Al phosphates (GESSA et al., 2005), which results in a smaller amount of free Al. A huge amount of precipitated Al can mask other fractions both in the apoplasm and symplasm (POSCHENRIEDER et al., 2008).

Treatments were arranged in a completely randomized design with three replicates per treatment and fifteen plants per replicate for each genotype. With the exception of Al and Si, concentrations of other mineral elements in the nutrient solution were the same for all treatments. The nutrient solution was replaced every seven days and the pH was adjusted daily.

At the end of the experiment (fourteen day of exposure to Al and/or Si), samples (roots and shoot) were separated and washed with deionized water twice and dried at 60°C until reaching constant weight. Dried tissues were weighed and ground into a fine powder before nitric-percloric digestion. Al concentrations were determined by atomic absorption spectrometry. A standard calibration curve was prepared for the 0–200mg L^{-1} Al concentration range.

Leaves and roots of two potato genotypes were collected to determine number of leaves and stolons, leaf area (with the aid of an Epson 11000 XL scanner and WinRhizo Pro Software), dry biomass of shoot and roots (roots and shoot were placed in paper bags and taken to the oven at 65°C until constant weight), and morphological parameters of the root system: total length, surface area, total volume, root diameter, and number of branches and tips. The roots of the two potato genotypes were digitalized with the aid of an Epson 11000 XL scanner and analyzed using WinRhizo Pro Software. Data were analyzed as a two-factor experiment (genotype x treatment) using analysis of variance and Scott Knott test for treatments at 5% error probability, using the Sisvar application (FERREIRA, 2008).

RESULTS AND DISCUSSION

In this study, calculations with 'Visual MINTEQ' software showed that about 67% of the nominal aluminum (Al) concentration (based on the initial ion concentration) are in the monomeric form, both in the presence and absence of silicon (Si), while over 92% of the Si concentrations are in the form that is absorbed by plants (H_4SiO_4), both in the presence or absence of Al.

In general, potato plant roots accumulated more Al in both genotypes, whereas small amounts of Al were transported to the shoot (Table 1). This accumulation of Al in the roots can cause root growth inhibition, directly or indirectly affecting the growth, metabolism and productivity of the entire plant. The presence of 0.5 and 1.0mM Si in the growth medium together with Al reduced the Al content in shoot of both genotypes and in roots of the Al-tolerant genotype, respectively (Table 1), which results in there being a smaller amount of Al free to cause damage in these tissues. This reduction in Al content is attributed to the formation of biologically inactive hydroxyaluminosilicate complexes in the growth medium (MA et al., 1997). However, in acidic solutions (pH 4.5), such as that used in this study, this is not the main factor because only low concentrations of Al hydroxide are formed in solutions with a low pH (KIDD et al., 2001) (in this study, only 7.5%, according to Visual MINTEQ software). Therefore, we consider an effect *in planta* as the main factor contributing to the reduction in the content of Al by Si. BARCELÓ et al. (1993) suggested that the formation of alumino silicate compounds in the walls of root cortex cells inhibits the uptake of A1 into the protoplast. Thus, it is suggested that part of Al is complexed with Si in the plant; thus, reducing translocation to the shoot. Furthermore, Si deposition on the plant may have reduced binding sites for Al, resulting in lower metal translocation from roots to shoot.

In the presence of Al, there was a significant reduction in root length, in number of root tips and in root surface area (Table 1) for both genotypes. Aluminum binds strongly to negatively charged carboxylic groups in the cell wall of cortical and epidermal cells in the roots (DELHAIZE et al., 1993), altering the binding and distribution of ions in the apoplast (KINRAIDE, 1993), which directly influences the growth of the organ. MIMMO et al. (2009) showed that the pectin matrix is the main target of Al accumulation, thereby affecting extensibility and porosity of the cell wall (HORST et al., 1999). Besides, MIMMO et al. (2003) suggest that Al interaction with the fibrillar structure of calcium–polygalacturonate hinder the transport of metal ions (nutrients) across the soil–root interface and thus the nutrient uptake by plants.

Silicon failed to alleviate the toxic effects of Al on these parameters, even though Al accumulation was lower in the Al-tolerant genotype exposed to the higher Si concentration. Nevertheless, the growth parameters exposed in table 1 related a tendency for Si to reduce the damage caused by Al. So, exposure time of plants to the different treatments was not sufficient for Si to ameliorate the toxic effects of Al.

For root diameter (Table 1), there was no significant difference among treatments in both potato genotypes. Thus, under the experimental conditions used in this research, Al decreased the elongation of roots, but did not affect the diameter of these roots (Table 1).

The presence of 1.0mM Si in the growth medium promoted an increase in the volume of roots (Table 1) in the SMIF212-3 genotype (Al-tolerant) when compared to the control. This allows a greater area for water and nutrient uptake. Furthermore, for some root growth parameters, plants of SMIF212-3 genotype receiving 0.5mM Si without Al inferred considerable lower growth than those receiving 1.0mM Si without Al. In this genotype, there was inhibition and activation of ascorbate peroxidase activity (an enzyme of antioxidant system) at 0.5 and 1.0mM Si, respectively (DORNELES, 2015), possibly influencing the root growth in this genotype. Besides, calculations with Visual MINTEQ software

Table 1 - Effect of silicon (0, 0.5 and 1.0mM) on Al content in the shoot and roots, root branch number, root tips, root surface area, root length, root diameter, root volume and stolon number in two potato genotypes, SMIJ319-7 (Al-sensitive) and SMIF212-3 (Al-tolerant) cultured in the presence (+Al; 1.85mM) or absence of Al (-Al).

Treatments	---------Al content in shoot (ppm)-------		-----------Al content in root (ppm)--------		---------------Root branch number------------	
	SMIJ319-7	SMIF212-3	SMIJ319-7	SMIF212-3	SMIJ319-7	SMIF212-3
Control	155.5±3.8 Ab	99.7±27.5 Ad	264.2±17.7 Ad	166.7±8.6 Bf	8962 ± 3947 Ba	23653 ± 16643 Aa
0.5 Si	82.6±3.6 Ac	67.1±12.4 Ad	270.1±33.8 Ad	259.6±6.9 Ad	9926 ± 2131 Aa	9745 ± 3125 Ab
1.0 Si	77.9±7.9 Ac	73.9±9.7 Ad	270.5±0.94 Ad	222.5±15.7 Be	13026 ± 1747 Ba	24616 ± 5733 Aa
Al	353.8±11.7 Ba	434.9±25.2 Aa	2032.5±2.7 Bc	7033.1±0.76 Ab	456 ±67 Ac	576 ± 19 Ad
0.5 Si + Al	214.4±27.3 Ab	193.6±4.6 Ab	5827.8±1.1 Ba	7056.8±1.2 Aa	1158 ±12 Ab	1291 ± 94 Ac
1.0 Si + Al	350.7±112.8 Ba	412.6±2.5 Aa	5970.1±1.3 Ab	5831.5±1.04 Ac	1346 ± 35 Ab	455 ± 87 Ad
Treatments	-------------------Root tips-----------------		-----------Root Surface Area (cm^2)--------		-----------------Root length (cm)--------------	
	SMIJ319-7	SMIF212-3	SMIJ319-7	SMIF212-3	SMIJ319-7	SMIF212-3
Control	2931±506 Ba	7088±3874 Aa	506.1±89.7 Ba	687.7±924.6 Aa	4719±1094 Ba	12320±2409 Aa
0.5 Si	3324±1278 Aa	3358±954 Ab	553.4±36.2 Aa	565.7±136.3 Ab	4852±1509 Aa	5642±482 Ab
1.0 Si	3298±956 Ba	7700±1477 Aa	513.1±95.8 Ba	1147.2±273.5 Aa	4816±1165 Ba	11493±1950 Aa
Al	324±72 Ab	348±5.5 Ac	58.5±13.7 Ab	46.3±1.7 Ac	385±120 Ab	402±34 Ac
0.5 Si + Al	675±95 Ab	629±82 Ac	81.3±14.3 Ab	81.7±10.4 Ac	824±136 Ab	808±77 Ac
1.0 Si + Al	602±106 Ab	392±172 Ac	100.3±17.3 Ab	45.5±25.8 Ac	701±151 Ab	526±247 Ac
Treatments	-------------Root diameter (mm)----------		--------------Root volume (cm^3)-----------		-------------------Stolon number---------------	
	SMIJ319-7	SMIF212-3	SMIJ319-7	SMIF212-3	SMIJ319-7	SMIF212-3
Control	0.343 ± 0.032 Aa	0.326 ± 0.01 Aa	4.51 ± 1.84 Aa	6.06 ± 0.52 Ab	5.1±0.7 Bb	5.1±0.7 Bb
0.5 Si	0.340 ± 0.016 Aa	0.320 ± 0.02 Aa	4.31 ± 0.99 Aa	3.89 ± 1.16 Ac	4.5±0.2 Bb	4.5±0.2 Bb
1.0 Si	0.340 ± 0.036 Aa	0.333 ± 0.03 Aa	4.56 ± 1.96 Ba	11.6 ± 1.33 Aa	3.6±0.6 Bb	3.6±0.6 Bb
Al	0.370 ± 0.001 Aa	0.366 ± 0.01 Aa	0.41 ± 0.12 Ab	0.42 ± 0.005 Ad	4.5±1.1 Ab	4.5±1.1 Ab
0.5 Si + Al	0.360 ± 0.017 Aa	0.336 ± 0.01 Aa	0.88 ± 0.11 Ab	0.72 ± 0.11 Ad	5.1±0.6 Bb	5.1±0.6 Bb
1.0 Si + Al	0.363 ± 0.005Aa	0.353 ± 0.01 Aa	0.74 ± 0.15 Ab	0.58 ± 0.16 Ad	7.3±0.3 Aa	7.3±0.3 Aa

[*] Different capital letters indicate significant differences between genotypes within the same treatment. Different lowercase letters indicate significant differences among treatments within the same genotype.

showed that at 0.5mM Si, Si activity was higher (50.15μmol L^{-1} Si) than at 1.0mM Si (29.30μmol L^{-1} Si), suggesting that this higher activity of Si caused inhibition in these growth parameters. Conversely, the Al presence in the growth medium resulted in a reduction in root volume and in number of root branches in both potato genotypes when compared with the control (Table 1). The presence of Si (0.5 and 1.0mM in the Al-sensitive and 0.5mM in the Al-tolerant genotype) significantly ameliorated the toxic effects of Al to number of root branches, when compared with treatment with only Al.

In general, Si was beneficial for both genotypes in regard to leaf number, leaf area (Table 2), and stolon number (Table 1). This increase in leaf number and leaf area promoted by Si resulted in greater interception of solar radiation, and consequently higher accumulation of biomass in these plants. In addition, leaf number (Table 2) was significantly reduced in Al treatments in both genotypes. Al transported from roots to shoot (Table 1) may have negatively influenced the formation and growth of these organs, which could trigger a reduced photosynthetic rate and lower production of biomass in these plants.

For SMIJ319-7, there was a significant increase in leaf number in the Si (1.0mM) + Al treatment, when compared to treatment containing only Al. In this case, Si significantly alleviated the toxic effects of Al on this parameter (Table 2). KORNDÖRFER & LEPSCH (2011) reported that Si has beneficial effects on growth of different cultures due to deposition of Si in the cuticle of leaves, giving protection to plants and mitigating the effects of biotic and abiotic stresses. The number of stolons (Table 1) was higher in SMIF212-3 when compared with SMIJ319-7 genotype. In the Al-sensitive genotype, 1.0mM Si + Al treatment induced an increase in stolon number, when compared to control plants and plants exposed only to Al.

In both genotypes an increase was observed in shoot dry weight when the potato plants were exposed to 1.0mM Si (Table 2). The same response was observed in the roots of the Al-tolerant genotype (SMIF212-3) (Table 2). The beneficial effect of Si can

Table 2 - Silicon (0, 0.5 and 1.0mM) on the leaves number, leaf area, shoot dry biomass and root dry biomass in two potato genotypes, SMIJ319-7 (Al-sensitive) and SMIF212-3 (Al-tolerant) cultured in the presence (+Al, 1.85mM) or absence of Al (-Al).

Treatments	---------------------------Leaves Number-------------------------		----------------------------Leaf Area (cm²)---------------------------	
	SMIJ319-7	SMIF212-3	SMIJ319-7	SMIF212-3
Control	9.4±0.9 Bb	15.1±1.9 Aa	38.9±5.7 Bb	59.4±4.2 Ab
0.5 Si	9.9±1.3 Ab	12.4±1.2 Ab	41.3±0.6 Bb	61.5±1.1 Ab
1.0 Si	14.3±3.3 Aa	15.4±1.1 Aa	60.8±9.4 Ba	100.9±10.6 Aa
Al	4.8±0.4 Bd	9.6±0.1 Ac	8.1±2.1 Bd	13.5±0.4 Ac
0.5 Si + Al	5.2±0.4 Bd	10.3±2.1 Ac	13.2±0.9 Bd	22.7±4.6 Ac
1.0 Si + Al	7.6±1.2 Ac	9.2±0.2 Ac	18.2±0.7 Ac	20.1±2.7 Ac
Treatments	--------------------Shoot dry biomass (g plant^{-1})----------------		---------------------Root dry biomass (g plant^{-1})--------------------	
	SMIJ319-7	SMIF212-3	SMIJ319-7	SMIF212-3
Control	0.9±0.11 Bb	2.1±0.99 Ab	0.033±0.006 Ba	0.048±0.015 Ab
0.5 Si	1.1±0.05 Bb	1.9±0.14 Ab	0.036±0.001 Ba	0.057±0.009 Ab
1.0 Si	1.7±0.39 Ba	3.7±0.75 Aa	0.034±0.008 Ba	0.073±0.011 Aa
Al	0.4±0.06 Ab	0.5±0.01 Ac	0.005±0.0004 Ab	0.007±0.001 Ac
0.5 Si + Al	0.6±0.03 Ab	0.8±0.05 Ac	0.004±0.001 Ab	0.006±0.0004 Ac
1.0 Si + Al	0.8±0.08 Ab	0.4±0.18 Ac	0.007±0.001 Ab	0.005±0.002 Ac

Different capital letters indicate significant differences between genotypes within the same treatment. Different lowercase letters indicate significant differences among treatments within the same genotype.

be attributed, at least in part, to anatomical variations produced by the deposition of silica on the walls of epidermal cells, which keep the leaves upright and improve light interception, stimulating photosynthesis and thereby promoting higher accumulation of biomass (MA & TAKAHASHI, 2002; SÁVIO et al., 2011). In addition, Si improves mineral absorption of plants, increasing the availability of some nutrients (PAVLOVIC et al., 2013) as nitrate and iron (GOTTARDI et al., 2012), causing an increase in biomass production (LEE et al., 2010).

Exposure to Al caused a reduction in shoot and root dry weight in both genotypes, when compared with the control (Table 2), and the addition of Si did not ameliorate the toxic effects of Al on these parameters. The reduction in shoot and root dry weight may possibly be related to a limited absorption of nutrients, such as Ca and Mg, caused by Al (MERIÑO-GERGICHEVICH et al., 2010). Biomass data corroborate the data for the morphological parameters of the root system (Table 1) and shoot growth (Table 2), where the presence of Al produced a significant reduction of these parameters in both potato genotypes.

CONCLUSION

Si reduced Al accumulation in shoot in both genotypes (0.5mM) and in roots of Al-tolerant genotype (1.0mM) and ameliorated the toxic effects of Al in regard to number of root branches and leaves in both potato genotypes. Therefore, Si has the potential to mitigate the toxic effects of Al in potato plants regardless of the Al sensitivity. In addition, this research contributes to the development of strategies that result in lower plant uptake of toxic elements, optimizing the use of natural resources and the production of safe food.

ACKNOWLEDGEMENTS

The authors thank Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Coordenação e Aperfeiçoamento de Pessoal de Nível Superior (CAPES) and Fundação de Amparo à Pesquisa de Estado do Rio Grande do Sul (FAPERGS) for support to this research.

REFERENCES

BARCELO, J. et al. Silicon amelioration of aluminium toxicity in teosinte (***Zea mays*** L. ssp. ***mexicana***). **Plant and Soil**, v.154, p.249-255, 1993. Available from: <http://link.springer.com/article/10.1007%2FBF00012530>. Accessed: Jun. 25, 2015. doi: 10.1007/BF00012530.

BIRCH, P.R.J. et al. Crops that feed the world 8: Potato: are the trends of increased global production sustainable? **Food Security Journal**, v.30, n.4, p.477-508, 2012. Available from: <http://link.springer.com/article/10.1007%2Fs12571-012-0220-1>. Accessed: Nov. 25, 2014.

CAMARGO, M.S. et al. Silicate fertilization of sugarcane cultivated in tropical soils. **Field Crops Research**, v.89, n.167, p.64-75, 2014. Available from: <http://www.scielo.br/scielo.

php?pid=S0100-06832013000500016&script=sci_arttext>. Accessed: Nov. 25, 2014.

DELHAIZE, E. et al. Aluminum tolerance in wheat (***Triticum aestivum*** L.). I. Uptake and distribution of aluminum in root apices. **Plant Physiology**, v.103, p.685-693, 1993. Available from: <http://www.ncbi.nlm.nih.gov/pmc/articles/PMC159037/>. Accessed: Nov. 25, 2014.

DONCHEVA, S.N. et al. Silicon amelioration of manganese toxicity in Mn-sensitive and Mn-tolerant maize varieties. **Environmental and Experimental Botany**, v.65, p.189-197, 2009. Available from: <http://www.researchgate.net/publication/248214885_Silicon_amelioration_of_manganese_toxicity_in_Mn-sensitive_and_Mn-tolerant_maize_varieties>. Accessed: Jun. 25, 2015. doi: 10.1016/j.envexpbot.2008.11.006.

DORNELES, A.O.S. **Interação entre silício e alumínio em genótipos de batata (*Solanum tuberosum* L.)**. 2015. 110f. Dissertação (Mestrado em Agrobiologia) - Programa de Pós-Graduação em Agrobiologia, Universidade Federal de Santa Maria, RS.

EXLEY, C. The coordination chemistry of aluminium in neurodegenerative disease. **Coordination Chemistry Reviews**, v.256, n.77, p.2142-2146, 2012. Available from: <http://www.sciencedirect.com/science/article/pii/S0010854512000392>. Accessed: Nov. 25, 2014. doi: 10.1016/j.ccr.2012.02.020.

FERREIRA, D.F. SISVAR: a program for statistical analysis and teaching. **Revista Symposium**, v.6, n.2, p.36-41, 2008. Available from: <http://www.scielo.br/pdf/cagro/v35n6/a01v35n6.pdf>. Accessed: Nov. 25, 2014.

GESSA, C. et al. Effect of aluminium and pH on the mobility of phosphate through a soil–root interface model. **Plant and Soil**, v.272, p.301-311, 2005. Available from: <http://link.springer.com/article/10.1007%2Fs11104-004-5693-z>. Accessed: Jun. 26, 2015. doi: 10.1007/s11104-004-5693-z.

GHNAYA, T. et al. Implication of organic acids in the long-distance transport and the accumulation of lead in ***Sesuvium portulacastrum*** and ***Brassica juncea***. **Chemosphere**, v.90, n.23, p.1449-1454, 2013. Available from: <http://www.sciencedirect.com/science/article/pii/S0045653512011290>. Accessed: Nov. 25, 2014. doi: 10.1016/j.chemosphere.2012.08.061.

GONÇALVES, J.F. et al. Cadmium-induced oxidative stress in two potato cultivars. **Biometals**, v.22, p.779-792, 2009. Available from: <http://link.springer.com/article/10.1007%2Fs10534-009-9225-4>. Accessed: Nov. 25, 2014.

GOODWIN, S.B.; SUTTER, T.R. Microarray analysis of ***Arabidopsis*** genome response to aluminum stress. **Biologia Plantarum**, v.53, n.39, p.85-99, 2009. Available: <http://link.springer.com/article/10.1007%2Fs10535-009-0012-4>. Accessed: Nov. 25, 2014.

GOTTARDI, S. et al. Beneficial effects of silicon on hydroponically grown corn salad (***Valerianella locusta*** (L.) Laterr) plant. **Plant Physiology and Biochemistry**, v.56, p.14-23, 2012. Available from: <http://www.researchgate.net/publication/224949193_Beneficial_effects_of_silicon_on_hydroponically_grown_corn_salad_%28Valerianella_locusta_%28L.%29_Laterr%29_plants>. Accessed: Jun. 26, 2015. doi: 10.1016/j.plaphy.2012.04.002.

HORST, W.J. et al. Does aluminium affect root growth of maize through interaction with cell wall–plasma membrane–cytoskeleton continuum? **Plant and Soil**, v.215, p.163-174, 1999. Available from: <http://link.springer.com/article/10.1023%2FA%3A1004439725283#page-1>. Accessed: Jun. 26, 2015. doi: 10.1023/A:1004439725283.

KIDD, P.S. et al. The role of root exudates in aluminium resistance and silicon-induced amelioration of aluminium toxicity in three varieties of maize (***Zea mays*** L.). **Journal of Experimental Botany**, v.52, n.359, p.1339-1352, 2001. Available from: <http://jxb.oxfordjournals.org/content/52/359/1339.full.pdf+html>. Accessed: Nov. 25, 2014.

KINRAIDE, T.B. Aluminum enhancement of plant growth in acid rooting media: a case of reciprocal alleviation of toxicity by two toxic cations. **Physiologia Plantarum**, v.88, p.619-625, 1993. Available from: <http://onlinelibrary.wiley.com/doi/10.1111/j.1399-3054.1993.tb01380.x/abstract>. Accessed: Nov. 25, 2014. doi: 10.1111/j.1399-3054.1993.tb01380.x.

KORNDÖRFER, G.H.; LEPSCH, I. Effect of silicon on plant growth and yield. In: DATNOFF, L.E. et al. (Eds.). **Silicon in agriculture**, Amsterdam: Elsevier, 2001. p.133-147. Available from: <http://www.sciencedirect.com/science/article/pii/S0928342001800112>. Accessed: Nov. 25, 2014. doi: 10.1016/S0928-3420(01)80011-2.

LEE, S.K. et al. Effect of silicon on growth and salinity stress of soybean plant grown under hydroponic system. **Agroforest Systems**, v.80, p.333-340, 2010. Available from: <http://link.springer.com/article/10.1007%2Fs10457-010-9299-6>. Accessed: Nov. 25, 2014. doi: 10.1007/s10457-010-9299-6.

LI, S. et al. Demonstrating a link between nutrient use and water management to improve crop yields and nutrient use efficiency in arid Northwest China. **Better Crops with Plant Food**, v.95, n.50, p.20-22, 2011. Available from: <http://www.ipni.net/publication/bettercrops.nsf/0/AE1A454F52D70E258525797C007907A7/$FILE/Better%20Crops%202011-3%20p20-22.pdf>. Accessed: Nov. 25, 2014.

LIANG, Y.C. et al. Silicon-mediated enhancement of cadmium tolerance in maize (***Zea mays*** L.) grown in cadmium contaminated soil. **Chemosphere**, v.45, n.58, p.475-483, 2005. Available from: <http://www.sciencedirect.com/science/article/pii/S0045653504008148>. Accessed: Nov. 23, 2014. doi: 10.1016/j.chemosphere.2004.09.034.

MA, J.F. Physiological mechanisms of Al resistance in higher plants. **Soil Science & Plant Nutrition**, v.61, p.609-612, 2005. Available from: <http://www.tandfonline.com/doi/pdf/10.1111/j.1747-0765.2005.tb00074.x>. Accessed: Jul. 10, 2015. doi: 10.1111/j.1747-0765.2005.tb00074.x.

MA, J.F. et al. Detoxifying aluminium with buckwheat. **Nature**, v.81, n.390, p.569-570, 1997. Available from: <http://www.nature.com/nature/journal/v390/n6660/abs/390569c0.html>. Accessed: Sept. 19, 2014. doi: 10.1038/37518.

MA, J.F.; TAKAHASHI, E. **Soil, Fertilizer, and Plant Silicon Research in Japan**. Amsterdam: Elsevier Science, 2002. Cap.6, p.73-106.

MEENA, V.D. et al. A case for silicon fertilization to improve crop yields in tropical soils. **Proceedings of the National Academy of Sciences, India Section B: Biological Sciences**, v.84, n.3, p.505-518, 2014. Available from: <http://link.springer.com/article/10.1007%2Fs40011-013-0270-y>. Accessed: Feb. 19, 2015. doi: 10.1007/s40011-013-0270-y.

MERIÑO-GERGICHEVICH, C. et al. Al^{3+}-Ca^{2+} interaction in plants growing in acid soils: Al-phytotoxicity response to calcareous amendments. **Journal of Soil Science and Plant Nutrition**, v.10, p.217-243, 2010. Available from: <http://www.scielo.cl/pdf/jsspn/v10n3/art03.pdf>. Accessed: Jul. 28, 2014.

MIMMO, T. et al. Effects of aluminium sorption on a Ca-polygalacturonate network used as a soil–root interface model. **Biopolymers**, v.70, p.655-666, 2003. Available from: <http://www.researchgate.net/publication/5927716_Effects_of_aluminum_sorption_on_calcium-polygalacturonate_network_used_as_soil-root_interface_model>. Accessed: Jun. 26, 2015. doi: 10.1002/bip.10545.

MIMMO, Tet al. Does the degree of pectin esterification influence aluminium sorption by the root apoplast? **Plant and Soil**, v.314, p.159-168, 2009. Available from: <http://link.springer.com/article/10.1007%2Fs11104-008-9715-0>. Accessed: Jun. 26, 2015. doi: 10.1007/s11104-008-9715-0.

MURASHIGE, T.; SKOOG, F. A revised medium for rapid growth and bioassays with tobacco tissue culture. **Plant Physiology**, v.6, n.15, p.473-497, 1962. Available from: <http://www.uel.br/revistas/uel/index.php/semagrarias/article/view/3946>. Accessed: Jun. 15, 2013.

PAVLOVIC, J. et al. Silicon alleviates iron deficiency in cucumber by promoting mobilization of iron in the root apoplast. **New Phytology**, v.198, n.4, p.1096-1107, 2013. Available from: <http://www.uel.br/revistas/uel/index.php/semagrarias/article/view/3946>. Accessed: Sept. 19, 2014. doi: 10.1111/nph.12213.

POSCHENRIEDER, C. et al. A glance into aluminum toxicity and resistance in plants. **Science of the Total Environment**, v.400, p.356-368, 2008. Available from: <http://www.researchgate.net/publication/51430369_A_glance_into_aluminum_toxicity_and_resistance_in_plants>. Accessed: Jun. 26, 2015. doi: 10.1016/j.scitotenv.2008.06.003.

SÁVIO, F.L. et al. Produção de biomassa e conteúdo de silício em gramíneas forrageiras sob diferentes fontes de silicato. **Semina: Ciências Agrárias**, v.32, n.1, p.103-110, 2011. Available from: <http://www.uel.br/revistas/uel/index.php/semagrarias/article/view/3946>. Accessed: Jun. 14, 2014. doi: 10.5433/1679-0359.2011v32n1p103.

TABALDI, L.A. et al. Physiological and oxidative stress responses of four potato clones to aluminum in nutrient solution. **Brazilian Journal of Plant Physiology**, v.19, n.3, p.211-222, 2007. Available from: <http://www.scielo.br/scielo.php?pid=S167704202007000300005&script=sci_arttext>. Accessed: Feb. 15, 2013. doi: 10.1590/S1677-04202007000300005.

WESTERMANN, D.T.; DAVIS, J.R. Potato nutritional management changes and challenges into the next century. **American Potato Journal**, v.69, n.23, p.753-767, 1992. Available from: <http://link.springer.com/article/10.1007/BF02853817>. Accessed: Apr. 2013.