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BASIC AREAS - Article

Aluminum stress tolerance in potato genotypes grown with silicon

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ABSTRACT: Potato cultivation is widespread around the world, being exposed to several abiotic stresses, including soils with high aluminum (Al) availability. Silicon (Si) is recognized for alleviating the stress caused by Al in various plant species. Thus, the aim of this study was to investigate the potential of Si to mitigate the oxidative stress caused by Al in potato genotypes, exhibiting differential sensitivity toward this element. Plants of the Al-sensitive genotype (SMIJ319-7) and Al-tolerant genotype (SMIF212-3) were grown for two weeks in a hydroponic system with the nutrient solution containing combinations of Al (0 and 1.85 mM) and Si (0, 0.5 and 1.0 mM). At the end of the experiment, photosynthetic parameters, pigment content, root and shoot growth, superoxide dismutase and guaiacol peroxidase activity and lipid peroxidation were evaluated. In both potato genotypes Al inhibited root and shoot growth and decreased all photosynthetic parameters and superoxide dismutase activity. Silicon was able to partially alleviate the damage caused by Al in parameters of root growth in the Al-tolerant genotype while increasing the activity of antioxidant enzymes and mitigating the Al-induced damage to membrane lipids in roots and shoot in both genotypes. The Al-tolerant genotype showed greater water use efficiency and transpiration rate in control conditions as compared to the Al-sensitive genotype. These data indicate that Si application can improve the defense ability of the tested potato genotypes against Al toxicity and that the Al-tolerant genotype is more responsive to Si.

Key words: *Solanum tuberosum,* beneficial elements, enzyme activity, oxidative stress, toxic elements.

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INTRODUCTION

Potatoes (*Solanum tuberosum* L.) are among the most widely cultivated crops in the world. They are considered an inexpensive source of high-quality proteins, minerals, and antioxidants (Valiñas et al. 2015). Therefore, the conditions where potato plants are grown are of great importance. The cultivated potato is very sensitive to abiotic stresses such as drought, cold, salinity and high irradiation. In addition, some genotypes of this species are sensitive to aluminum (Al), showing reduction in the root system and shoot, higher lipid peroxidation and inhibition of some antioxidant enzymes (Tabaldi et al. 2009).

The anthropogenic activity is leading to the progressive acidification of environments. In these acid soils, soluble Al is found in elevated levels (Magistad 1925; Thomas 1975; Kopittke et al. 2015), limiting the productivity of crops in several countries. Aluminum is the third most abundant element on Earth and the most abundant metal in the Earth's crust. Despite its abundance, Al has no essentiality known to living organisms and is recognized as being highly cytotoxic to plants and animals.

The first toxic effect of Al is apoplastic, which is related to a reduction of individual cell elongation (Kopittke et al. 2015). The strong affinity of Al to phosphate groups of phosphorylated biomolecules (AMP, ADP and ATP) provides a mechanism that explains this toxicity. Aluminum can also impair the function of target metalloproteins by replacing metals that are essential cofactors (mainly Mg^{2+}) in proteins. In addition, Al can trigger oxidative stress and increase the production of reactive oxygen species (ROS) by promoting biological oxidations both *in vivo* and *in vitro* (Mujika et al. 2011).

Several studies have shown that Al caused the production and increase of ROS, as well as the peroxidation of cell membranes, especially in Al-sensitive genotypes (Tabaldi et al. 2009). Reactive oxygen species are agents that cause the inactivation of enzymes and damage to cellular structures such as lipids, proteins and DNA, causing irreversible damages in the cells and their death. Due to the toxicity of ROS, cells are equipped with numerous scavengers in almost every compartment, such as antioxidant enzymes (superoxide dismutase, catalase and ascorbate peroxidase, among others) and also non-enzymatic antioxidants such as ascorbic acid, glutathione S-transferase, tocopherols, carotenoids and anthocyanins. However, Al may inhibit these antioxidant systems, an effect that forces the plant to search for alternatives to mitigate Al effects and/or stimulate its antioxidant system (Mujika et al. 2011).

In this context, silicon (Si) is a beneficial element for some plants and has been effective in reducing the peroxidation of membrane lipids (Etesami and Jeong 2018). This is due to the Si effect on the enzymatic and non-enzymatic antioxidant system of the plant, thus showing potential to be used in the alleviation of stress caused by toxic metals (Farooq and Dietz 2015; Dorneles et al. 2017; Pereira et al. 2018a), mainly Al (Camargo et al. 2014; Haynes 2017; Jesus et al. 2017). This potential is also supported by the high affinity that Si has with various metals, performing a coprecipitation of Si metal complexes in the cell wall. Silicon also promotes a separation of metals bound to organic acids in vacuoles and a more homogeneous distribution of metals, as well as the formation of Si complexes in tissues (Maksimovic et al. 2012).

The hypothesis is that Si is able to reduce the oxidative stress caused by Al in different potato genotypes. Therefore, this research aims to evaluate the potential of Si in alleviating the toxic effects of Al in potato genotypes and whether this behavior is different between two genotypes with different Al sensitivity levels, namely SMIJ319-7 (Al-sensitive) and SMIF212-3 (Al-tolerant), by assessing physiological and biochemical parameters.

MATERIALS AND METHODS

Plant material and growth condition

The experiments were carried out in the Plant Biotechnology Laboratory, the Plant Biochemistry Laboratory and in the greenhouses belonging to the Biology Department of the Federal University of Santa Maria (UFSM). Two potato genotypes differing in aluminum tolerance, SMIJ319-7 (Al-sensitive) and SMIF212-3 (Al-tolerant) (Rossato 2014[6]), from the Genetic and Improvement Program of the UFSM were used.

Nodal segments (1.0 cm long without leaves) of both genotypes were propagated *in vitro* for 25 days in culture medium MS (Murashige and Skoog 1962). After this period,

[6]Rossato L. V. (2014). Physiological and biochemical responses to aluminum and phosphorus stress in potato genotypes (*Solanum tuberosum*) (PhD Thesis). Santa Maria: Universidade Federal de Santa Maria.

the plants were acclimatized in a hydroponic system for five days, with a complete nutrient solution containing the following composition (in μM): 6090.5 of N; 974.3 of Mg; 4986.76 of Cl; 2679.2 of K; 2436.2 of Ca; 359.9 of S; 243.592 of P; 0.47 of Cu; 2.00 of Mn; 1.99 of Zn; 0.17 of Ni; 24.97 of B; 0.52 of Mo and 47.99 of Fe ($FeSO_4$/Na EDTA); and at pH 4.5 ± 0.1 (Tabaldi et al. 2009; Dorneles et al. 2016).

Subsequently, the genotypes were cultivated for 14 days in a nutrient solution, without phosphorus (P) presence and at pH 4.5 ± 0.1 with two different Al concentrations (0 and 1.85 mM as $AlCl_3$) and three different Si concentrations (0, 0.5 and 1.0 mM as Na_2SiO_3). The treatments were as follows: control, 0.5 mM Si, 1.0 mM Si, 1.85 mM Al, 0.5 mM Si + 1.85 mM Al, and 1.0 mM Si + 1.85 mM Al. The control solution was composed of nutrients only, without any Si and Al application; and in the treatments with Si and Al, they were applied in the same nutrient solution as the control treatment. The experiment was conducted in a greenhouse with controlled temperature (25° C ± 3) and relative humidity (80%). A solution without P was used because of the physicochemical interactions between P and Al (Gessa et al. 2005).

The treatments were arranged in a completely randomized design, composed by six treatments, with four replicates per treatment and 15 plants per replicate for each genotype. The nutrient solution was standardized for all treatments, by altering Si and Al concentrations only. The nutrient solution was changed every seven days and the pH checked and adjusted daily.

Plant growth parameter

Before the application of the treatments, the length of shoot and of the main root of the two potato genotypes was measured using a ruler graduated in millimeters. The plants were then placed in the nutrient solution, where the treatments were applied. At the end of the experiment (14 days), the length of shoot and of the main root was measured again. The plant growth during exposure to treatments was evaluated by the difference between the final and initial lengths of shoot and root. Moreover, shoot and roots of the plants were collected and immediately placed in paper bags and dried at 65 °C with forced ventilation until constant weight, when the dry weight was determined using a precision scale (Analytical Balance MS304TS/00).

Photosynthetic parameters

After the period of exposure to the treatments, the evaluations of photosynthetic parameters were carried out in the fourth fully expanded leaf of two plants per repetition, using an infrared gas analyzer portable photosynthesis system LI-6400XT (LI-COR). The evaluated parameters were photosynthetic rate (A – μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$); stomatal conductance (Gs – mol $H_2O \cdot m^{-2} \cdot s^{-1}$); internal CO_2 concentration (Ci – $\mu mol \cdot m^{-2} \cdot s^{-1}$); transpiration rate (Trmmol – mol $H_2O \cdot m^{-2} \cdot s^{-1}$) and water use efficiency (WUE – mol $CO_2 \cdot mol^{-1}$ of H_2O) obtained by the ratio between the amount of CO_2 fixed by photosynthesis and the amount of transpired water (A.Trmmol^{-1}). The evaluations were determined at an ambient CO_2 concentration of 400 $\mu mol \cdot mol^{-1}$, at 20 to 25 °C and a photon flux density of 1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ conducted in the period between 8 a.m. and 11 a.m.

Chlorophyll and carotenoids content

Samples of the same leaves used for the photosynthetic parameters were taken in the form of discs with a paper puncher. Samples were immediately frozen in liquid nitrogen and afterwards incubated at 65 °C with dimethylsulfoxide (DMSO), until the complete extraction of the pigments. Chlorophyll *a* and *b* and carotenoids were extracted according to the Hiscox and Israelstam (1979) method and estimated using the equation of Lichtenthalerz (1987).

Determination of lipid peroxidation

Lipid peroxidation was measured in samples of leaves (0.5 g) and roots (1.5 g) by the malondialdehyde (MDA) quantification, according to El-Moshaty et al. (1993).

Determination of antioxidant enzymes activity

Leaves and roots samples macerated in liquid nitrogen were used for enzymatic analysis, in which 0.5 g of samples were homogenized in 3 ml of sodium phosphate buffer (pH 7.8) 0.05 M, containing 1 mM EDTA and 2% (w/v) polyvinylpyrrolidone. After centrifugation at 13,000 × *g* for 20 min at 4 °C, the supernatant was collected to determine enzyme activity and protein concentration. Guaiacol →

peroxidase activity was determined according to Zeraik et al. (2008), using guaiacol as substrate.

The superoxide dismutase (SOD) activity was measured according to the spectrophotometric method, described by Giannopolitis and Ries (1977).

Statistical analysis

The results were analyzed according to a two-way ANOVA (genotypes × treatments) and Scott Knott test ($p \leq 0.05$) error probability, using Sisvar software.

RESULTS

With the help of Visual MINTEQ 3.1 software, it was possible to calculate the availability percentage of Si and Al in both concentrations used. Si had approximately 100% availability in both concentrations used, even when applied with Al. Aluminum presented 73.3% availability as Al^{+3} and 22.79% as $AlOH^{+2}$, both readily absorbed forms, thus totaling 96.09% of Al available (data not shown).

Plant growth parameter

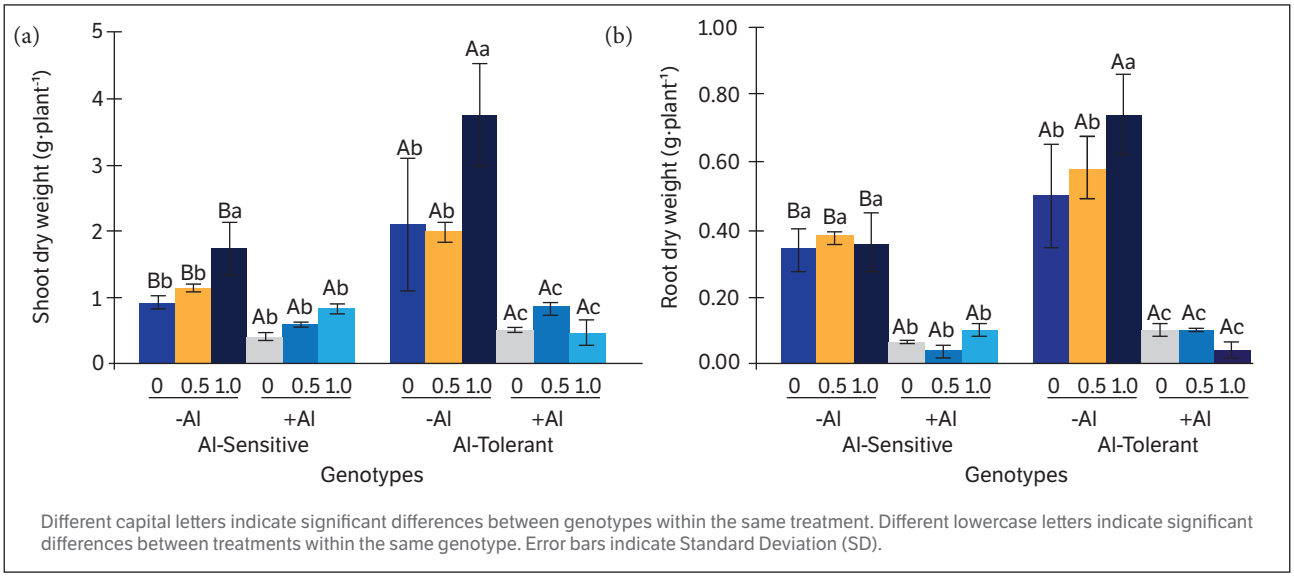
The data of dry weight accumulation allow affirming the beneficial effects of Si for both genotypes (Fig. 1). The concentration of 1.0 mM stimulated higher dry weight accumulation in the shoot of both genotypes (Fig. 1a) and in the roots of the Al-sensitive genotype (Fig. 1b). However, Si was not effectively beneficial for the mitigation of Al toxicity in both genotypes.

After 14 days of exposure to the treatments, shoot growth increased with increasing Si concentration in plants not exposed to Al from the Al-sensitive genotype (SMIJ319-7) (Fig. 2a), while for the Al-tolerant genotype (SMIF212-3) this effect was not observed. In addition, both genotypes showed growth inhibition of both shoot and roots in the presence of Al when compared with the control (Fig. 2). In the presence of Al, the increased Si concentration did not alleviate the toxic effect of Al in either genotype in the shoot (Fig. 2a). However, in the roots of the Al-tolerant genotype, Si at both concentrations (0.5 and 1.0 mM) mitigated the toxic effects of Al in comparison to the treatment in which only Al was present in the growth medium (Fig. 2b).

There were no significant differences between genotypes in most treatments for shoot growth (Fig. 2a), except for the highest Si concentration (1.0 mM) without Al, in which the Al-sensitive genotype showed higher shoot growth compared with the Al-tolerant genotype. Furthermore, the shoot of the Al-tolerant genotype showed higher growth than the Al-sensitive genotype in the concentration of 0.5 mM Si with Al.

Photosynthetic parameters

There were significant differences in the photosynthetic rate (Fig. 3a) between treatments within each genotype. →



Different capital letters indicate significant differences between genotypes within the same treatment. Different lowercase letters indicate significant differences between treatments within the same genotype. Error bars indicate Standard Deviation (SD).

Figure 1. (a) Shoot and (b) Root dry weight of two potato genotypes, SMIJ319-7 (Al-sensitive) and SMIF212-3 (Al-tolerant), cultured in the presence (+Al, 1.85 mM) or absence of Al (–Al) and three levels of silicon (0, 0.5 and 1.0 mM).

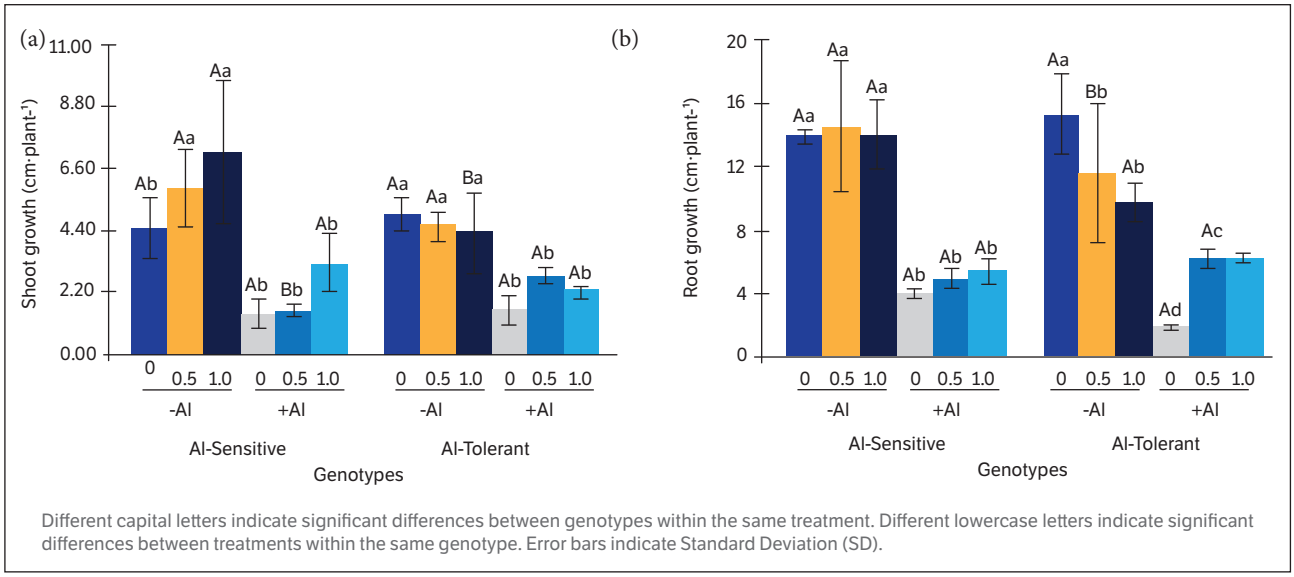


Figure 2. Silicon effects (0, 0.5 and 1.0 mM) on (a) shoot and (b) roots growth in two potato genotypes, SMIJ319-7 (Al-sensitive) and SMIF212-3 (Al-tolerant), cultured with the presence (+Al; 1.85 mM) or absence of Al (–Al).

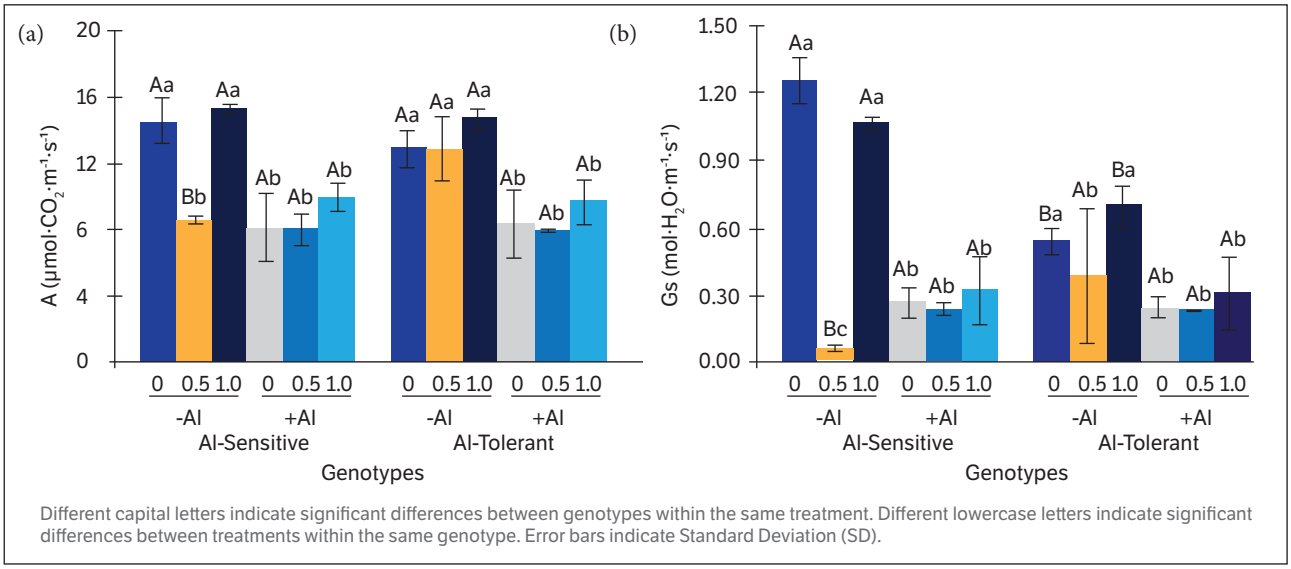


Figure 3. Silicon effects (0, 0.5 and 1.0 mM) on (a) photosynthetic rate, and (b) stomatal conductance in two potato genotypes, SMIJ319-7 (Al-sensitive) and SMIF212- 3 (Al-tolerant), cultured with the presence (+Al; 1.85 mM) or absence of Al (–Al).

Photosynthetic rates were reduced in the presence of Al in both genotypes and in the treatment with 0.5 mM Si without Al to the Al-sensitive genotype. Although the photosynthetic rate increased with the increase of Si concentration in the presence of Al, it was not statistically significant, i.e. Si could not attenuate the damage caused by Al on the photosynthetic rate in both genotypes. When comparing the genotypes, the Al-sensitive genotype showed lower photosynthetic rate in the presence of 0.5 mM Si compared to the Al-tolerant genotype.

Responses in stomatal conductance (Fig. 3b) were similar to those observed for photosynthetic rate in the Al-sensitive genotype. However, the Al-sensitive genotype showed a higher conductance in the control treatment and in the presence of 1.0 mM of Si when compared to the Al-tolerant genotype. At a lower Si concentration without Al (0.5 mM), the Al-sensitive genotype showed lower stomatal conductance when compared to the Al-tolerant genotype. Both genotypes showed a decrease in stomatal conductance (Fig. 3b) at 0.5 mM Si concentration and in the →

presence of Al, and Si failed to alleviate this negative effect of Al for this parameter.

Silicon at the 0.5 mM concentration promoted a reduction in internal CO_2 concentration (Ci) and in the transpiration rate in both genotypes and increased water use efficiency (WUE) in the Al-sensitive genotype (Table 1). The presence of Al also favored a reduction in the transpiration rate in both genotypes (Table 1). The Al-sensitive genotype showed a lower internal CO_2 concentration and transpiration rate in the presence of 0.5 mM Si without Al and higher WUE than the Al-tolerant genotype.

Chlorophylls and carotenoids content

In the control treatment without Al or Si, the Al-tolerant genotype showed the highest concentration of chlorophyll *a* (Fig. 4a) compared to the Al-sensitive genotype. For the Al-tolerant genotype, there was lower chlorophyll *a* content at both Si concentrations in the absence and presence of Al, compared to the control. In the Al-sensitive genotype, there was no significant difference between treatments, and chlorophyll *a* showed no sensitivity to Al in this genotype.

For chlorophyll *b* content (Fig. 4b), the treatment with 1.0 mM Si provided an increase in the content of this pigment in the Al-tolerant genotype, when compared to the control. For the Al-sensitive genotype, the treatment with 1.0 mM Si with Al promoted a reduction in chlorophyll *b* content when compared to the control, whereas the treatment with 0.5 mM Si without Al promoted an increase in the content of this pigment. In the treatments where Si was present with Al, chlorophyll *b* levels were statistically similar to the control and different from the treatment where only Al was present in both genotypes. However, in this study, Al did not cause a reduction in chlorophyll *b* content.

For the content of total chlorophyll (Fig. 4c), there was a significant difference between treatments only in the Al-sensitive genotype (SMIJ319-7), in which treatments with 1.0 mM Si without Al and 0.5 mM Si + Al promoted a reduction in the content of total chlorophyll. When comparing genotypes, the Al-sensitive genotype showed lower content of total chlorophyll in the treatments with 1.0 mM Si without Al and 0.5 mM Si with Al, compared to the Al-tolerant. However, the treatment with 0.5 mM Si promoted a reduction in the total chlorophyll content when compared to the Al-tolerant genotype.

Regarding the content of carotenoids (Fig. 4d), there was a difference between treatments only for the Al-sensitive genotype, in which the treatment with 1.0 mM Si induced a reduction in the content of carotenoids. There was no alteration in levels of carotenoids among treatments for the Al-tolerant genotype.

Table 1. Silicon effect (0. 0.5 and 1.0 mM) on internal CO_2 concentration (IC – $\mu mol \cdot m^{-2} \cdot s^{-1}$). Transpiration rate (Trmmol – mmol $H_2O \cdot m^{-2} \cdot s^{-1}$) and Water use efficiency (WUE – mol $CO_2 \cdot mol^{-1} H_2O$) in two potato genotypes, SMIJ319-7 (Al-sensitive) and SMIF212- 3 (Al-tolerant), cultured with presence (+Al; 1.85 mM) or absence of Al (–Al).

Genotype	Treatments	IC	Trmmol	WUE
SMIJ319-7	Control	349.49 ± 2.45 Aa*	5.73 ± 0.03 Aa	2.56 ± 0.22 Ab
	0.5 Si	134.36 ± 36.5 Bb	0.88 ± 0.20 Bc	10.6 ± 2.95 Aa
	1.0 Si	344.05 ± 1.51 Aa	5.31 ± 0.06 Aa	2.88 ± 0.08 Ab
	Al	360.74 ± 35.8 Aa	3.53 ± 0.54 Ab	1.94 ± 1.47 Ab
	0.5 Si + Al	319.56 ± 9.93 Aa	2.34 ± 0.15 Ab	3.46 ± 0.60 Ab
	1.0 Si + Al	310.79 ± 24.7 Aa	2.81 ± 0.97 Ab	3.90 ± 1.06 Ab
SMIF212-3	Control	328.06 ± 2.99 Aa	4.07 ± 0.29 Ba	3.20 ± 0.05 Aa
	0.5 Si	281.02 ± 52.6 Ab	2.98 ± 1.66 Ab	4.77 ± 1.67 Ba
	1.0 Si	333.29 ± 2.67 Aa	4.59 ± 0.23 Aa	3.20 ± 0.03 Aa
	Al	341.80 ± 50.0 Aa	3.28 ± 0.84 Ab	2.69 ± 2.09 Aa
	0.5 Si + Al	321.34 ± 1.86 Aa	2.40 ± 0.01 Ab	3.30 ± 0.05 Aa
	1.0 Si + Al	315.68 ± 22.6 Aa	2.85 ± 1.06 Ab	3.63 ± 0.89 Aa

*Different lowercase letters indicate significant differences between treatments in the same genotype. Different capital letters indicate significant differences between genotypes in the same treatment.

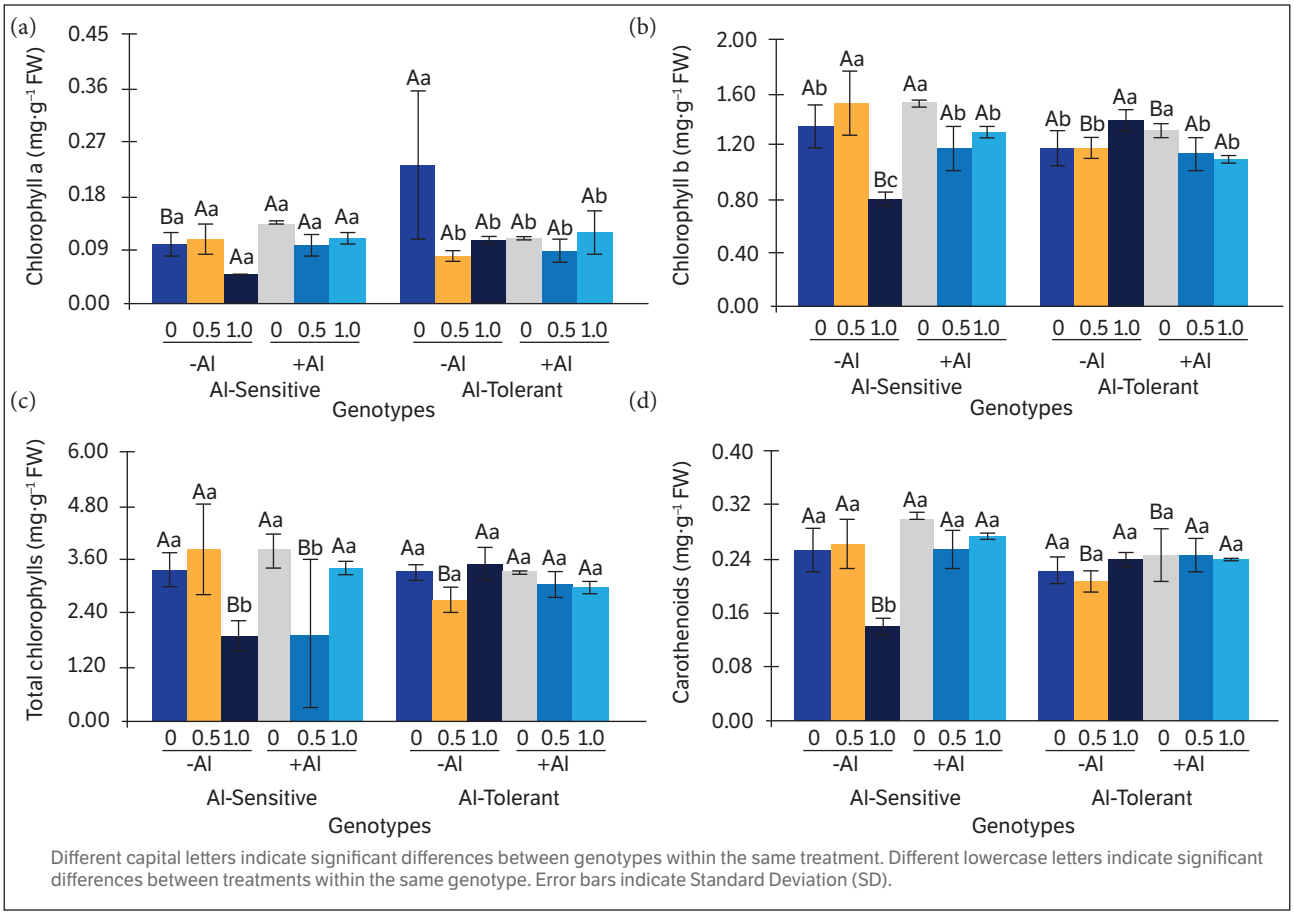


Figure 4. Silicon effects (0, 0.5 and 1.0 mM) on (a) chlorophyll *a*, (b) chlorophyll *b*, (c) total chlorophyll, and (d) carotenoids in two potato genotypes, SMIJ319-7 (Al-sensitive) and SMIF212- 3 (Al-tolerant), cultured with the presence (+Al; 1.85 mM) or absence of Al (–Al).

Lipid peroxidation

Malondialdehyde (MDA) concentration in the shoot of the Al-sensitive genotype was reduced in the treatment with the highest Si concentration without Al (Fig. 5a). However, there was no significant difference between the control plants and those exposed to both Si concentrations for the MDA content in the Al-tolerant genotype. With increasing Si concentration in the presence of Al, there was a decrease in the MDA concentration in the shoot of both genotypes.

In the roots (Fig. 5b), contrary to that observed in the shoot, there was an increase in the MDA concentration in both genotypes when plants were exposed to the highest concentration of Si in the absence of Al. For both the Al-sensitive and Al-tolerant genotypes, the exposure to Al promoted an increase in the concentration of MDA in the roots compared to the control, and the Al-sensitive genotype had the highest percentage of increase (130%).

In the presence of Al, Si application caused a reduction in the concentration of MDA in roots in the Al-sensitive genotype (1.0 mM Si) and in the Al-tolerant genotype (0.5 mM Si) (Fig. 4b). Overall, the Al-tolerant genotype showed lower peroxidation of membrane lipids, both in roots and shoot, when compared to the Al-sensitive genotype (SMIJ319-7).

Antioxidant enzymes activity

In the shoot (Fig. 6a), superoxide dismutase (SOD) activity was reduced with the application of Si in the absence of Al in the Al-sensitive genotype. However, this reduction for the Al-tolerant genotype was only observed with the application of 0.5 mM Si. For both genotypes, in general, the exposure to Al induced the inhibition of SOD enzyme in the shoot when compared to the control. However, for the Al-sensitive genotype (SMIJ319-7) treated with 1.0 mM Si + Al, there was an increase in the activity of this enzyme, equal to control →

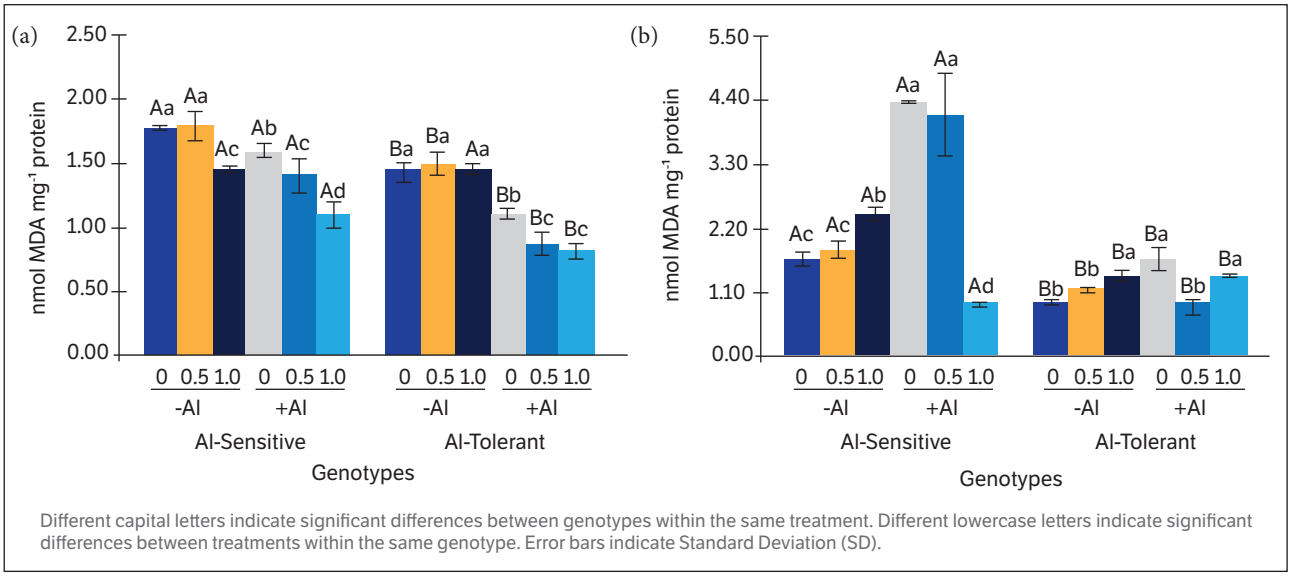


Figure 5. Silicon effects (0, 0.5 and 1.0 mM) on MDA content in (a) shoot and (b) roots in two potato genotypes, SMIJ319-7 (Al-sensitive) and SMIF212- 3 (Al-tolerant), cultured with the presence (+Al; 1.85 mM) or absence of Al (–Al).

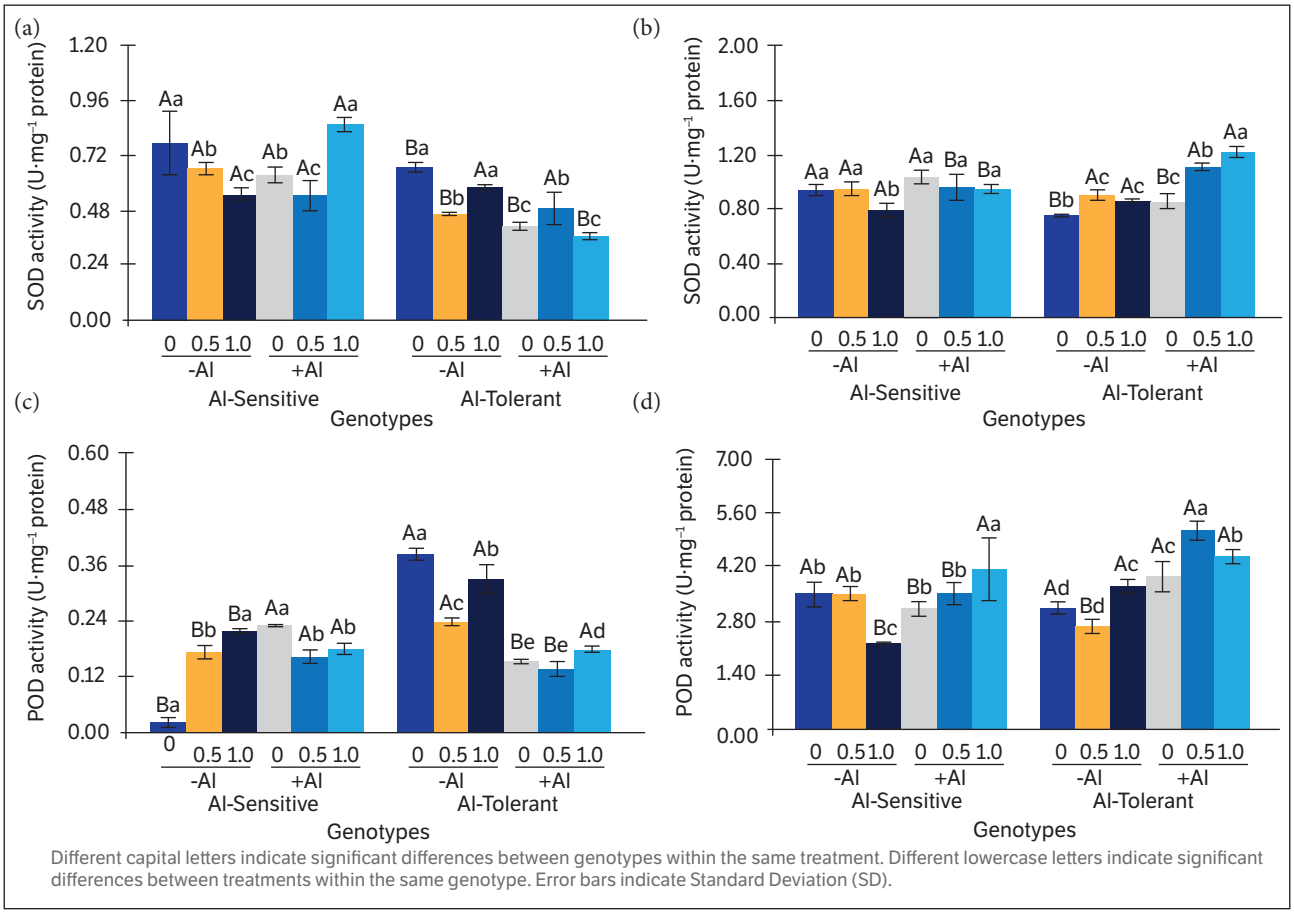


Figure 6. Silicon effects (0, 0.5 and 1.0 mM) on (a) SOD activity in shoot and (b) roots, (c) POD activity in shoot and (d) roots in two potato genotypes, SMIJ319-7 (Al-sensitive) and SMIF212- 3 (Al-tolerant), cultured with the presence (+Al; 1.85 mM) or absence of Al (–Al).

levels (Fig. 6a). For the Al-tolerant genotype (SMIF212-3), the treatment with 0.5 mM Si + Al promoted an increase in SOD activity (Fig. 6a), when compared to the treatment where only Al was present. In the roots (Fig. 6b), the application of 1.0 mM Si in the absence of Al reduced SOD activity for the Al-sensitive genotype. However, Si promoted an increase of SOD activity in roots of the Al-tolerant genotype (Fig. 6b).

For the Al-sensitive genotype, guaiacol peroxidase (POD) activity in the shoot was stimulated by Si both in the absence and presence of Al, when compared to the control (Fig. 6c). However, for the Al-tolerant genotype, this enzyme presented high activity in the control treatment, and reduced activity in the presence of Si, as much in the absence as in the presence of Al. The application of Al promoted an even greater reduction in the POD activity. However, the application of the highest Si concentration (1.0 mM) increased the activity of this enzyme when compared to the treatment with Al only.

In roots (Fig. 6d), the exposure to high concentrations of Si in the absence of Al promoted a reduction in POD activity for the Al-sensitive genotype. However, in the presence of Al, there was an increase in POD activity only with the application of the highest concentration of Si, when compared with the control. For the Al-tolerant genotype, there was an increase of POD activity in the absence of Al only with the application of the highest concentration of Si. For this genotype, the exposure to Al alone promoted an increase in POD activity in comparison to the control, which may be related to its Al-tolerance. In addition, Si application in the presence of Al promoted a more pronounced increase in the POD activity.

DISCUSSION

The potential of silicon (Si) in alleviating the toxic effects of aluminum (Al) in two potato genotypes with different sensitivity to Al (SMIJ319-7, Al-sensitive, and SMIF212-3, Al-tolerant) was assessed. After 14 days of exposure to the treatments, potato plants showed an increase in shoot growth and dry weight accumulation with increasing Si concentration in plants not exposed to Al (Figs. 1 and 2). This beneficial effect of Si on plant growth was reported by several studies in the literature (Shi et al. 2010; Gu et al. 2012; Pereira et al. 2018b). This increase in the growth of shoot may be related to the Si effect on mineral absorption, resulting in increased availability of some nutrients to plants and hence increasing biomass production (Pavlovic et al. 2013). Furthermore, the promotion of growth induced by Si may be due to an increase in cell wall extensibility (Hattori et al. 2003; Gu et al. 2012).

On the other hand, the presence of Al promoted growth inhibition and decreased dry weight of both shoot and roots for both genotypes, when compared with the control (Figs. 1 and 2). This reduction in root growth has been observed in several studies with other plant species (Pereira et al. 2008; Liu et al. 2012; Freitas et al. 2017). Because of the inhibition in root growth, shoot growth is negatively affected and this leads to a reduction in dry weight. Moreover, this reduction in shoot growth might be possibly related to limited uptake of water and other nutrients such as Ca and Mg by Al (Meriño-Gergichevich et al. 2010).

Several studies have shown the effect of Si in increasing plant tolerance to biotic and abiotic stresses (Ma 2004; Gu et al. 2012). For the Al-tolerant genotype, shoot growth was higher with the presence of Si and Al in the treatment, when compared to the Al-sensitive genotype. One possibility is that hydroxyaluminosilicate complexes may have formed in large quantities in the roots of this genotype, thereby preventing the translocation of Al to the shoot. As observed by Dorneles et al. (2016), Si promoted a significant reduction in Al content in the shoot of potato plants. This Al reduction promoted by Si in the shoot can reduce the toxic effects of Al in source tissues.

Within each genotype, the increased Si concentration did not alleviate the toxic effect of Al in the shoot. However, in the roots of the Al-tolerant genotype, Si mitigated the toxic effects of Al in comparison to the treatment in which only Al was present in the nutrient solution. Probably, Si is operating on the chelation and/or internal Al compartmentalization in this genotype, as the acid pH of the nutrient solution used in this study (pH 4.5) impedes the formation of hydroxyaluminosilicate complexes in the solution, because only low concentrations of Al hydroxide are found in solutions with low pH (Kidd et al. 2001). The role of Si in the tolerance of plants to biotic and abiotic stresses can be attributed to changes in the properties of the cell wall. The esterification of cell wall components by Si can reduce the Al bond in the cell wall, causing a minor negative effect of this metal on the roots. Also, it has been reported that the inhibition of root growth of corn plants exposed to Al was lower in plants pre-treated with Si (Kidd et al. 2001).

The photosynthetic rates were reduced in the presence of Al for both genotypes (Fig. 3). Jiang et al. (2008) showed that →

a smaller electron transport capacity on the photosynthetic apparatus accompanied by a lack of reducing equivalents were the main factors contributing to lower CO_2 assimilation in plants exposed to Al. Although the photosynthetic rate increased with the increase of Si concentration in the presence of Al, this increase was not significant. Thus, Si failed to reduce the damage caused by Al on the photosynthetic rate in both genotypes, although studies in the literature show an alleviator effect of Si on photosynthetic parameters in other plant species under metal stress (Song et al. 2014; Vaculík et al. 2015). This may be a dose-dependent response or variable between species.

At the lowest concentration tested (0.5 mM), Si promoted a reduction in photosynthetic rate and stomatal conductance in both genotypes. Furthermore, a lower stomatal conductance was observed in the Al-sensitive genotype exposed to the highest content of Si used in this study. This reduction may be associated with thickening of the wax layer in leaves treated with Si (Pozza et al. 2015), which covers the stomata and negatively influences photosynthesis, by hindering the diffusion process in gas exchange, thereby limiting the internal CO_2 concentration, as observed in this study.

The results of this study showed that Al promoted reduction in photosynthetic rates of both potato genotypes and Si failed to mitigate the toxic effects of Al. However, these reductions in photosynthetic rates and stomatal conductance may be related to lower transpiration rate, which was decreased at 0.5 mM Si in the absence of Al, for the Al-sensitive genotype, although the Al-tolerant genotype showed higher growth than the Al-sensitive, possibly due to greater efficiency of this genotype in the use of absorbed CO_2.

Takahashi (1995) reported increased photosynthetic rates induced by Si due to better leaf architecture provided by this element, allowing improved light absorption. Gong et al. (2005) reported that the increase in the photosynthetic rate in wheat plants treated with Si was due to higher Rubisco and glyceraldehydes-3-phosphate dehydrogenase activities. The factors mentioned above may have influenced trends in the capability of Si to attenuate the effects of Al. Although Si did not increase photosynthetic rates when compared to the control in the presence of Al, plants that were treated with Al and Si showed a trend of increasing these rates in the highest Si concentration (1.0 mM) used in this study.

For the Al-tolerant genotype in the control treatment, it was observed a higher concentration of chlorophyll *a* (Fig. 3), which can provide higher absorption of light energy, leading to greater biomass production. On the other hand, under Si and Al presence there was a lower chlorophyll *a* concentration for the Al-tolerant genotype. Therefore, Si failed to alleviate the oxidative damage caused by Al in this genotype. Shi et al. (2010) found no significant effect of Si on the chlorophyll content in coffee plants. Pereira et al. (2010) reported a reduction in pigment content in cucumber plants with increased Al concentrations. This reduction in chlorophyll content with Al may be acting to inhibit enzymes related to the synthesis of these pigments. For chlorophyll *b*, Al did not cause a reduction in content of this pigment, indicating that there may be a protective mechanism against the damage by Al in these genotypes.

For carotenoids, there was no difference in levels of Si between treatments for the Al-tolerant genotype. This response in the Al-tolerant genotype may be due to a possible constitutive expression of these molecules, which may be one of the factors leading this genotype to be more tolerant to Al. Moreover, the reduction in chlorophyll b, total chlorophyll and carotenoids for the Al-sensitive genotype (SMIJ319-7) exposed to higher Si concentration in the absence of Al may be due to a dilution effect. For this genotype, shoot growth (Fig. 2a) and the number of leaves and leaf area (Dorneles et al. 2016) were increased in plants exposed to 1.0 mM Si, suggesting a reduction in the concentration of pigments with increased leaf biomass.

Malondialdehyde (MDA) results from lipid peroxidation in cells and this product remains an important indicator of oxidative stress in several studies with plants (Chen et al. 2017). The increase in Si concentration in the presence of Al decreased shoot MDA concentration in both genotypes (Fig. 5). Thus, Si significantly mitigated the damage caused by Al in the lipid membrane, suggesting that plants growing in the presence of Si operate with metabolic pathways that remove more oxygen radicals in this organ. Shi et al. (2010) observed that Si promoted a decrease in peroxidation of membrane lipids by the activation of the enzymatic and non-enzymatic antioxidant system, possibly by preventing MDA accumulation in shoots. Si caused lower reduction in the growth of this organ. These data also suggest that Si application in potato plants can effectively increase the defense capability of potato plants against oxidative stress induced by Al toxicity.

On the other hand, Al promoted an increase in the concentration of MDA in the roots for both Al-sensitive and Al-tolerant genotypes, and the Al-sensitive genotype had the →

highest percentage of increase (130%). This result is possibly due to the characteristic of Al in indirectly promoting ROS formation (Mujika et al. 2011). Aluminum can change the arrangement of membrane lipids, thus facilitating lipid peroxidation caused by Fe (II), which may lead to changes in the permeability of membranes. Chaffai et al. (2005) showed that Al promotes a change in the level of unsaturation of fatty acids, leading to a reduction in the fluidity of the membrane lipids. In the presence of Al, Tabaldi et al. (2009) reported a greater accumulation of MDA as Al concentrations were increased in Al-sensitive potato plants. Besides, in the presence of Al, Si application promoted a reduction in the concentration of MDA in roots for both genotypes (Fig. 5b). The alleviation effect of Si has been associated with an increase in the antioxidant defense mechanisms in plants. Overall, the Al-tolerant genotype (SMIF212-3) showed lower peroxidation of membrane lipids, both in roots and shoot, when compared to the Al-sensitive (SMIJ319-7), indicating that the Al-sensitive genotype presented higher oxidative damage in the presence of Al.

As a protection against ROS, plant cells harbor several antioxidant enzymatic-scavenging systems. Superoxide dismutase (SOD) and guaiacol peroxidase (POD) are among the main enzymes involved in this defense system of the plants. For both genotypes, in general, the exposure to Al induced the inhibition of SOD enzyme in the shoot when compared to the control (Fig. 6). The SOD enzyme requires metal ions such as iron, manganese, zinc and copper. Thus, it may be suggested that Al may interfere with the absorption or binding of these ions to the active site of the enzyme. High concentrations of Al also caused inhibition of SOD in cucumber and blueberry plants (Pereira et al. 2010; Inostroza-Blancheteau et al. 2011).

On the other hand, for both genotypes, in the Si + Al treatments, there was an increase in the SOD activity in the shoot, when compared to the treatment with Al only. Therefore, the results for SOD activity suggest that Si has a role in alleviating Al toxicity in the shoot through the activation of this antioxidant enzyme. As seen in this study, in plants exposed to Al, the presence of Si caused a more significant decrease in the peroxidation of membrane lipids. This may be an indication that the damage caused by ROS under the stress of Al was ameliorated by the addition of Si, partly due to an increase in SOD activity. Therefore, these results suggest that the Si application can effectively increase the defense capability of potato plants against the oxidative stress induced by Al, especially in the shoot.

In the roots of the Al-tolerant genotype, Si promoted an increase in SOD activity. This shows that Si potentially stimulates the activity of SOD in the Al-tolerant genotype. This response is observed in the presence of Al, where there is an increase in SOD activity with increasing Si concentration.

Overall, Si promoted an increase in the guaiacol peroxidase (POD) activity in roots and shoot in the presence of Al, mainly in the Al-sensitive genotype, indicating that Si has the potential to activate the antioxidant system. Besides, for the Al-tolerant genotype, the exposure to Al alone promoted an increase in POD activity when compared to the control, which may be related to its Al-tolerance. In addition, the application of Si in the presence of Al promoted a more pronounced increase in the POD activity.

Despite many studies on Si in plants, it is still not understood how it acts on physiological and biochemical processes. The effects of silicon may involve cellular changes that stimulate alteration of biochemistry by determining oxidative stress as performed in this study, but also alterations in gene synthesis, protein structure and transport of molecules across the membranes (Moldes et al. 2013).

CONCLUSION

Silicon effectively ameliorated the toxic effects of Al through the activation of the antioxidant system and the reduction of harm to membrane lipids. The results obtained in this study show the ability of Si to promote the tolerance of potato genotypes to Al stress. In addition, the SMIF212-3 (Al-tolerant) genotype is more Si-responsive than the SIMJ319-7 (Al-sensitive) genotype. This indicates the possibility that genotypes with more efficient Si uptake and translocation may also be more tolerant to Al. Thus, this study shows the potential use of Si as a strategy to mitigate Al stress in plants.

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