Mineral Nutrition of Two Potato Cultivars Differing in Aluminium Tolerance, as Affected by Liming and Soil Acidity

Boris LAZAREVIĆ [1](✉)
Silvio ŠIMON [2]
Milan POLJAK [1]

Summary

Acid soil is one of the most important limitations in agricultural production worldwide. The application of lime and the growth of Al-tolerant genotypes are the most commonly employed strategies for the amelioration of acidic soil constraints. This study evaluates the effect of soil acidity and liming on the growth and mineral nutrition of Al-tolerant potato cv. Tresor and Al-sensitive potato cv. Canberra (*Solanum tuberosum* L.). Liming increased the total shoot and root dry matter (DM) of cv. Canberra, and the leaf DM of cv. Tresor. 'Tresor' retained a greater ability to acquire nutrients from acidic soil, especially P, Ca, and Mg. In addition, the Al content in the root tips and in other vegetative parts of acidic soil-grown plants indicates, on one hand, the complexity of acidic soil toxicity that was not solely related to Al toxicity and, on the other, the possible involvement of multiple mechanisms of Al tolerance that could be partly related to better nutrient uptake from acidic soil.

Key words

aluminium toxicity and tolerance; amelioration of acidic soils; dry matter production; potato nutrition; *Solanum tuberosum* L.

[1] University of Zagreb, Faculty of Agriculture, Department of Plant Nutrition, Svetošimunska cesta 25, 10000 Zagreb, Croatia
✉ e-mail: blazarevic@agr.hr
[2] University of Zagreb, Faculty of Agriculture, Department of Plant Breeding Genetics, Biometrics and Experimentation, Svetošimunska cesta 25, 10000 Zagreb, Croatia

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Introduction

Acidic soil (soil with a pH of 5.5 or lower) is one of the most important limitations in agricultural production worldwide (Kochian et al., 2004). Acidic soils occupy about 40% of arable and about 50% of potentially arable land in the world (von Uexküll and Mutert, 1995). The low productivity of agricultural crops grown in acidic soils particularly rests on aluminium (Al) toxicity (Foy et al., 1988) and a lack of nutrients (Kochian et al., 2004). The primary response to Al stress in plants occurs in the roots, and this is characterized by reduced elongation at the tip, followed by swelling and distortion of differentiated cells (Foy et al., 1988). Subsequent symptoms also arise related to the decreased uptake of nutrients and water (Samac and Tesfaye, 2003). In order to ameliorate the negative effects of acidic soils on crop production, several strategies have been proposed. Along with soil liming (the application of calcium carbonate), which is the primary method used to raise soil pH and cause the conversion of Al to less toxic forms (Samac and Tesfaye, 2003), many researchers (e.g. Foy et al., 1978; Delhaize and Ryan, 1995; Kochian et al., 2004) have emphasized the use of Al-tolerant cultivars as the most efficient strategy for the production of economically important crops in acidic soils. In addition, considerable genetic variability in Al tolerance was found among different crop species (Foy et al., 1988), as well as among different potato genotypes (Tabaldi et al., 2007; Lazarević et al., 2014).

The potato (*Solanum tuberosum* L.) is one of the most important crops; it is grown worldwide and often in very acidic soils. Moreover, potatoes are generally considered to be highly tolerant of acidic soil conditions (Harris, 1992). However, the negative effects of Al toxicity on potato root growth, dry matter production, mineral nutrition, and photosynthesis parameters were noted in previous experiments (Lee, 1971; Lee, 1972; Tabaldi et al., 2007; Lazarević et al., 2014).

The aim of this study was to investigate the effects of soil acidity and soil liming on the growth and mineral nutrition of two potato cultivars with different levels of Al tolerance.

Materials and methods

Soil preparation

For experimental purposes, the soil material was collected from the topsoil of an arable field (44° 57′ 20″ N, 15° 42′ 17″ E) at a 5–15 cm depth. The soil samples were air-dried, grounded, and passed through a 2 mm sieve prior to physical and chemical characterization (Table 1).

The lime requirement for the neutralization of soil acidity (pH target: 6.0) was determined by incubation of the moistened soil samples (300 g) with different levels of $CaCO_3$ (ranging from 0–3000 mg kg^{-1}) for 15 days at room temperature. Following the incubation period, the soil samples were air-dried and the soil pH was measured with a glass electrode. Based on the results obtained in the described experiment, half of the soil samples were limed via the application of 1200 mg of $CaCO_3$ kg^{-1}. After the lime application, the soil samples were moistened to field capacity and incubated for two months at room temperature. Prior to planting, the soil was fertilized with monoammonium phosphate (multi-MAP 12-61-0; Haifa Chemicals Ltd.) in concentration of 0.25 g kg^{-1} of soil.

Experimental design

The experiment was conducted under controlled conditions in a greenhouse at the University of Zagreb, Faculty of Agriculture from May 2011 to July 2011. Tubers (an average of 50 g of fresh mass) of two potato cultivars, cv. Canberra (Al-sensitive) and cv. Tresor (Al-tolerant), were grown in plastic pots (5 L) in a completely randomised design consisting of three replications of two soil treatments: acidic and limed soil. Each cultivar was

Table 1. Physical and chemical properties of the soil used in the study

Sand[a]	Silt[a]	Clay[a]	pH[b]	C_{org}[c]	N[d]	P[f]	ECEC[g]	Ca	Mg	K	Al	Al[h]
	%		H_2O	%		mg kg^{-1}			cmol(+) kg^{-1}			Sat (%)
11.0	69.0	20.0	4.7	2.7	0.4	17.0	4.21	1.20	0.54	0.62	1.85	43.9

Basic soil characteristics were determined using standard methods: [a]the soil particle size distribution was determined via the pipette method with sieving and sedimentation (HRN ISO 11277:2011); [b]pH was measured potentiometrically (HRN ISO 10390:2005); [c]organic carbon content (C_{org}) was determined after dry combustion (HRN ISO 11277:2004); [d]total nitrogen was assessed using the modified Kjeldahl method (HRN ISO 11261:1995); [f]phosphorus was evaluated using the ammonium lactate method in accordance with Egner-Riehm-Domingo (Egner et al. 1960); [g]effective cation exchange capacity (ECEC = Ca + Mg + K + Na + Al) and base saturation level were determined in barium chloride extracts (HRN ISO 11260:2004); the determination of exchangeable acidity was also performed in barium chloride extracts (HRN ISO 14254:2001). [h]Al sat – Al saturation =100 × (exchangeable Al)/(ECEC).

Table 2. Exchangeable cations, Al saturation, and pH of the acidic and limed soils after potato harvesting

Soil treatment	pH[a] H_2O	ECEC[b]	Ca	Mg	K	Al	Al[c] Sat (%)
				cmol(+) kg^{-1}			
Acidic soil	4.7	3.80	1.01	0.46	0.54	1.80	47.35
Limed soil	5.8	4.01	3.14	0.38	0.37	0.12	3.33

[a]pH was measured potentiometrically (HRN ISO 10390:2005); [b]effective cation exchange capacity (ECEC = Ca + Mg + K + Na + Al) and base saturation level were determined in barium chloride extracts (HRN ISO 11260:2004); the determination of exchangeable acidity was also performed in barium chloride extracts (HRN ISO 14254:2001). [c]Al sat – Al saturation =100 × (exchangeable Al)/(ECEC).

Table 3. Dry matter (g plant^{-1}) means, and analysis of variance at harvest for potato cultivars Tresor and Canberra grown in acidic and limed soil

Soil treatment	Total Shoot		Leaf		Stem		Root		Shoot:root	
	Can.	Tres.	Can.	Tres.	Can.	Tres.	Can.	Tres.	Can.	Tres.
Acidic	4.46b	5.68a	2.03b	3.01b	2.43b	2.74a	6.38b	5.20a	0.86a	1.15a
Limed	6.86a	6.07a	3.64a	3.33a	3.22a	2.67a	8.04a	5.30a	0.70a	1.10a
(S) Soil treatment	***		***		**		*		*	
(CV) Cultivar	NS		***		NS		***		***	
S × CV	***		***		**		*		NS	

Can. cv. Canberra (Al sensitive); Tres. cv. Tresor (Al tolerant); * Significant at the 0.05 probability level; ** Significant at the 0.01 probability level; *** Significant at the 0.001 probability level; NS: Not significant; The letters indicate the mean differences of the soil treatments within a given cultivar based on Tukey's HSD test.

represented with six plants/pots per treatment × replication combination. Plants were grown for 56 days after planting (DAP). The average temperature in the greenhouse was 27°C; the midday photosynthetic active radiation (PAR) averaged from 800–1000 µmol photons m^{-2} s^{-1}, and the average humidity was 70%.

Measurement of aluminium content in the root tips

At 14 DAP, three plants from each cultivar per treatment were harvested in order to determine the Al concentration in the root tips. The roots were washed from soil and five young root tips (10 mm in length) per root system were excised. The Al content in the root tips was determined using a method described by Yang et al. (2005). The root tips were washed under running distilled water for 10 minutes, followed by washing in a $CaCl_2$ solution for a total of three times (pH 4.5). The root tips were placed in a 1.5 mL microcentrifuge tube containing 1.0 mL of 2 M HCl. After 24 hours of Al extraction, the apoplasmic Al concentration was determined using graphite furnace atomic absorption spectrometry (Thermo Fisher Scientific-SOLAAR M Series AA Spectrometer).

Dry matter and mineral composition measurements

At harvest (56 DAP), the plants from each pot were separated into the root, stem, old leaves (leaves from the basal and central parts of the haulm), and young leaves (upper four youngest leaves). The plant material was dried in an air-forced oven at 105°C until it reached a constant mass; it was weighed to determine the dry matter content of the selected organs. Dried tissue samples were grounded and homogenized using a sample grinder (IKA® Werke M 20). The total nitrogen (N) content was determined using the micro-Kjeldahl procedure following plant material decomposition at 420°C in the presence of sulphuric acid. After digestion of the plant material in a microwave oven with nitric and perchloric acid (6:1), phosphorus (P) and potassium (K) contents were determined using a spectrophotometer and flame photometer, respectively, while the contents of calcium (Ca), magnesium (Mg), iron (Fe), zinc (Zn), copper (Cu), manganese (Mn), and Al were determined via flame atomic absorption spectrometry (Thermo Scientific-SOLAAR M Series AA Spectrometer). The characteristics of the soil samples were analysed after the harvest and are presented in Table 2.

Data Analysis

The data were analysed using the SAS® 9.2 statistical package (SAS Institute, Cary, NC, USA). Analysis of variance was performed for each plant part to determine the dry matter production and concentrations of mineral nutrients, as well as to assess the concentration of apoplasmic Al in the root tips. When no interactions were found between soil treatments and cultivars, the means of the main effects were compared using Tukey's honestly significant difference (HSD) test. In the case of a significant soil treatment × cultivar interaction, pairwise differences were calculated using the Tukey–Kramer method.

Results

Dry matter production

Plants grown in limed soil had higher vegetative organ dry matter production when compared with the acidic soil-grown plants (Table 3). When the average dry matter production of the cultivars was compared across both soil treatments, higher dry matter production in the roots occurred in cv. Canberra, while cv. Tresor had higher dry matter production in its leaves and a higher shoot-to-root ratio (Table 3). In addition, the dry matter production of all vegetative organs was affected by a significant soil treatment × cultivar interaction (Table 3). Soil liming increased the leaf dry matter production of both cultivars; however, this effect was more pronounced for cv. Canberra (+79.3%) when compared to cv. Tresor (+10.6%). Soil liming did not affect the dry matter production of any of the other vegetative organs of cv. Tresor; in contrast, the total shoot, stem, and root dry matter production of limed soil-grown cv. Canberra increased by +53.8%, +32.5%, and +26.0%, respectively (Table 3).

Mineral composition

The results of the analyses of variance of the nutrient contents in the different plant parts (roots, stems, old leaves, and young leaves) at harvest (56 DAP) for potato cultivars Tresor and Canberra grown in acidic and limed soil are presented in Table 4; the mean values are indicated in Figure 1.

The N content in the roots, stems, old leaves, and young leaves was significantly affected by the cultivar. The N content in the young leaves was also affected by the soil treatment and the soil treatment × cultivar interaction (Table 4). When compared to cv. Tresor, cv. Canberra had higher average N content in the roots (21.0 vs. 18.9 mg g^{-1}), stems (12.9 vs. 8.5 mg g^{-1}), old leaves (37.7 vs. 26.7 mg g^{-1}), and young leaves (46.4 vs. 36.6 mg g^{-1}), respectively. Soil liming caused a significant increase (+23.5%) in the N content of young leaves for cv. Canberra, while there were no

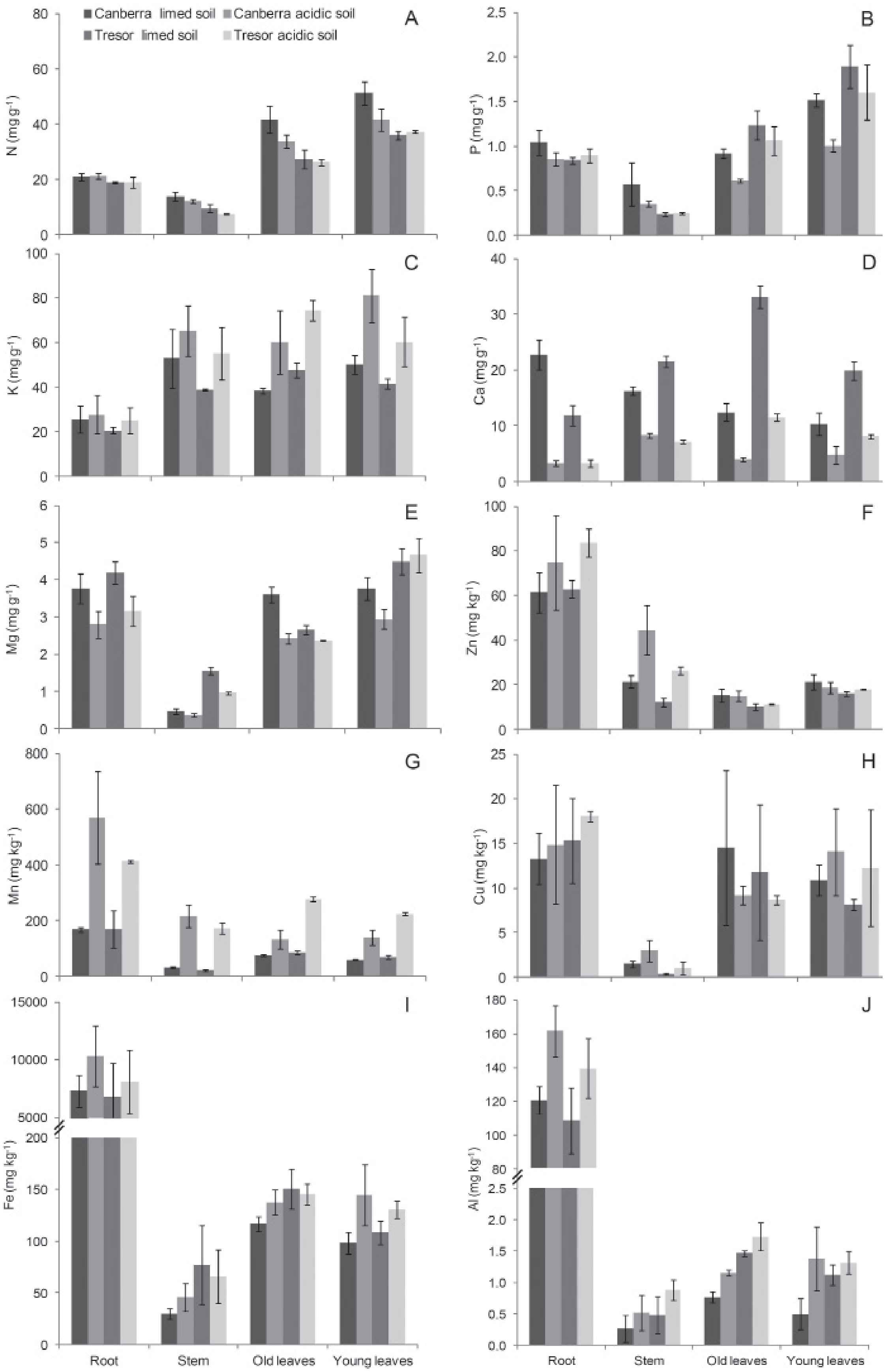

Figure 1. Content of the mineral nutrients in the roots, stems, old leaves, and young leaves of potato cv. Tresor and cv. Canberra grown for 56 days in acidic and limed soil. The vertical bars represent the means ± standard deviations

Table 4. Analysis of variance for the mineral composition of the different plant organs of potato cv. Tresor and cv. Canberra grown in acidic and limed soil

Plant organ	Source of variability	Plant nutrient									
		N	P	K	Ca	Mg	Fe	Zn	Mn	Cu	Al
Root	(S) Soil treatment	NS	NS	NS	***	**	NS	*	***	NS	**
	(CV) Cultivar	*	NS	NS	***	NS	NS	NS	NS	NS	NS
	S × CV	NS	NS	NS	***	NS	NS	NS	NS	NS	NS
Stem	(S) Soil treatment	NS	NS	NS	***	***	NS	**	***	NS	**
	(CV) Cultivar	**	*	*	**	***	NS	**	NS	*	**
	S × CV	NS	NS	NS	***	***	NS	NS	NS	NS	NS
Old leaves	(S) Soil treatment	NS	*	**	***	***	NS	NS	***	NS	*
	(CV) Cultivar	**	**	*	***	**	*	*	***	NS	**
	S × CV	NS	*	NS	***	***	NS	NS	**	NS	NS
Young leaves	(S) Soil treatment	**	**	**	***	NS	**	NS	***	NS	*
	(CV) Cultivar	*	**	*	***	**	NS	NS	**	NS	NS
	S × CV	*	*	NS	*	*	NS	NS	**	NS	*

* Significant at the 0.05 probability level; ** Significant at the 0.01 probability level; *** Significant at the 0.001 probability level; NS: Not significant

difference in the N content of young leaves for cv. Tresor grown in acidic (37.3 mg g^{-1}) and limed soil (36.0 mg g^{-1}) (Fig. 1A).

The P content in the stems was significantly affected by the cultivar, whereas a significant effect for cultivar, soil treatment, and a soil treatment × cultivar interaction was determined for P content in the old and young leaves (Table 4). When compared to cv. Tresor, cv. Canberra had a higher average content of P in the stems (0.46 vs. 0.24 mg g^{-1}), and lower P content in the old leaves (0.75 vs. 1.15 mg g^{-1}) and young leaves (1.30 vs. 1.75 mg g^{-1}), respectively (Fig. 1B). Soil liming caused an increase in the P content in the old leaves and young leaves; however, this increase was not significant for cv. Tresor (16.3% for old leaves and 18.1% for young leaves). Conversely, this increase was significant for cv. Canberra (50.0% for old leaves and 50.7% for young leaves) (Fig. 1B).

The K content in old and young leaves was affected by both the cultivar and soil treatment, while the K content in the stems was affected only by the cultivar (Table 4). Consequently, plants grown in acidic soil had a higher average K content in the old (67.4 mg g^{-1}) and young leaves (70.7 mg g^{-1}) when compared to plants grown in limed soil (43.0 and 45.8 mg g^{-1}, respectively) (Fig. 1C). Cultivar Canberra had higher levels of K content in its stems (59.1 vs. 46.9 mg g^{-1}) and young leaves (65.6 vs. 50.9 mg g^{-1}), but lower K content in its old leaves (49.3 vs. 61.1 mg g^{-1}) when compared to the findings of cv. Tresor (Fig. 1C).

The Ca content in all investigated plant parts was influenced by a significant soil treatment × cultivar interaction (Table 4). No significant differences were found in the Ca content in the roots, stems, and young leaves between the acidic soil-grown cv. Canberra and cv. Tresor (3.23 vs. 3.23 mg g^{-1}, 8.2 vs. 7.2 mg g^{-1}, and 4.7 vs. 8.1 mg g^{-1}, respectively). Soil liming increased the Ca content in the roots, stems, and young leaves for both potato cultivars. Moreover, in the case of Ca content in the roots, liming had a more pronounced effect on cv. Canberra (+603%) when compared to cv. Tresor (+255%), whereas in the stems and young leaves, liming had a more pronounced effect on cv. Tresor (+201% and +145%, respectively) when compared to cv. Canberra (+96% and +119%, respectively) (Fig. 1D). Cultivar Tresor had higher Ca content in the old leaves when compared to cv. Canberra when grown in acidic soil (11.5 vs. 4.0 mg g^{-1}), and this difference was even more pronounced when the cultivars were grown in limed soil (33.1 vs. 12.4 mg g^{-1}) (Fig. 1D).

The Mg content in the roots was affected by soil treatment. In addition, a significant soil treatment × cultivar interaction was found for the Mg content observed in the stems, old leaves, and young leaves (Table 4). Soil liming increased the Mg content in the roots of both potato cultivars (+32.6% for cv. Tresor and +34.5% for cv. Canberra). No significant difference was found in the Mg content of the stems between the acidic and limed soil-grown cv. Canberra (0.38 vs. 0.47 mg g^{-1}), whereas increased (+60.5%) Mg content in the stems was found for limed soil-grown (as compared to acidic soil-grown) cv. Tresor. Soil liming caused a significant increase in the Mg content in old (+49%) and young (27.8%) leaves for cv. Canberra, while there was no difference in the Mg content in either the old or young leaves in the acidic (2.36 and 4.66 mg g^{-1}, respectively) and limed soil-grown (2.66 and 4.49 mg g^{-1}, respectively) cv. Tresor (Fig. 1E).

The Fe content in old leaves was affected by cultivar, while the Fe content in young leaves was affected by soil treatment (Table 4). Cultivar Tresor (148.1 mg kg^{-1}) had higher average Fe content in the old leaves when compared to cv. Canberra (127.1 mg kg^{-1}). Plants grown in acidic soil (137.6 mg kg^{-1}) had higher average Fe content in the young leaves when compared to limed soil-grown plants (103.3 mg kg^{-1}) (Fig. 1I).

Soil treatment affected the Zn content in the roots and stems, while cultivar affected the Zn content in the stems and old leaves (Table 4). Soil liming decreased the average Zn content in the roots (–21.6%) and stems (–52.4%) when compared to the acidic soil-grown plants. Cultivar Canberra had higher average Zn content in the stems (32.3 vs. 28.3 mg kg^{-1}) and old leaves (15.3 vs. 12.6 mg kg^{-1}) when compared to cv. Tresor (Fig. 1F).

Soil treatment had a significant effect on the Mn content in the roots and stems, while a significant cultivar × soil treatment interaction was found for the Mn content in old and young leaves (Table 4). Soil liming decreased the average Mn content in the roots (–65.6%) and stems (–86.3%) when compared to the acidic soil-grown plants. There were no differences in the Mn content

Table 5. Aluminium content in the root tips (10 mm), and analysis of variance for potato cv. Tresor and cv. Canberra grown in acidic and limed soil for 14 days

Soil treatment	Al content (nmol root tip^{-1})	
	Canberra	Tresor
Acidic soil	3.40a	3.60a
Limed soil	1.08b	1.18b
(S) Soil treatment	**	
(CV) Cultivar	NS	
S × CV	NS	

* Significant at the 0.05 probability level; ** Significant at the 0.01 probability level; *** Significant at the 0.001 probability level; The letters indicate the mean differences in the soil treatments within a given cultivar based on Tukey's HSD test

in either the old or young leaves between the limed soil-grown cv. Tresor (85.8 and 69.1 mg kg^{-1}, respectively) and cv. Canberra (75.8 and 60.8 mg kg^{-1}, respectively); however, acidic soil-grown cv. Tresor had higher Mn content in its old (277.5 vs. 133.2 mg kg^{-1}) and young leaves (224.8 vs. 139.8 mg kg^{-1}) when compared to acidic soil-grown cv. Canberra (Fig. 1G).

The Cu content in stems was significantly affected by cultivar (Table 4). Namely, cv. Canberra had higher average Cu content in its stems when compared to cv. Tresor (2.23 vs. 0.70 mg kg^{-1}) (Fig. 1H).

The Al content in the roots, stems, old leaves, and young leaves was affected by soil treatment; cultivar also had a significant effect on the Al content in the stems and old leaves, while a significant soil treatment × cultivar interaction was found for the Al content in young leaves (Table 4). Soil liming decreased the average Al content of the roots (–16.7%), stems (–45.5%), old leaves (–22.7%), and young leaves (–39.8%) when compared to the acidic soil-grown plants. Compared to cv. Canberra, cv. Tresor had a higher average amount of Al content in its stems (0.49 vs. 0.39 mg kg^{-1}) and old leaves (1.31 vs. 0.96 mg kg^{-1}), respectively (Fig. 1J).

Al content in the root tips

The Al content in the root tips is shown in Table 5. Soil treatment had a significant effect on the Al content in the root tips. Namely, soil liming decreased the average amount of Al content in the root tips (–67.7%) of both potato cultivars.

Discussion

The soil used in this study can be characterized as acidic with a high degree of Al saturation and a low pH level (Table 1). Despite the fact that exchangeable Al in soil is a poor indicator of Al toxicity (e.g. Delhaize and Ryan, 1995), the acidic and chemical properties of used soil, along with low exchangeable Ca and Mg saturation and low P content, could have detrimental effects on plant root growth and on the response of the potato cultivars to the application of lime and fertilization. Liming increased soil pH and decreased Al saturation (Table 2) which should, in turn, reduce the negative effects of soil acidity and Al toxicity on the root growth, dry matter production, and mineral uptake of the investigated potato cultivars.

Dry matter production, especially of Al-sensitive cv. Canberra, responded strongly to soil liming (Table 3), as there were sharp increases in the production of leaf, stem, and root dry matter. The primary response to Al stress in plants occurs in the roots, which is characterized by reduced elongation of the root tip and a subsequent reduction of the root system (Hossain et al., 2005). The lack of a significant soil treatment × cultivar interaction for the shoot to root ratio indicates that there was a similar reaction of the root and shoot dry matter production among both cultivars to liming. Namely, soil liming caused an increase in the total shoot and root dry matter production of cv. Canberra, while it did not affect the dry matter production of cv. Tresor. A similar reduction in the dry matter production of Al-sensitive potato genotypes in conditions of Al toxicity were previously obtained by Lee (1972) and Tabaldi et al. (2007). In addition, Lazarević et al. (2014) found that growth in acidic soil caused a reduction in the chlorophyll content and photosynthetic rate of cv. Canberra, while it did not affect cv. Tresor. However, the results of the evaluation of Al content in the various plant parts did not confirm the idea that Al toxicity is the only reason behind the reduction of dry matter production and C partitioning. Namely, growth in acidic soil caused a significant increase in the Al content across all investigated plant parts for both potato cultivars, although, Al-tolerant cv. Tresor contained more Al in the stems and old leaves when compared to cv. Canberra (Fig. IJ). Moreover, the observed Al content in the upper parts of the acidic soil-grown plants (1.15 to 1.73 mg kg^{-1} in the young leaves, and 1.31 to 1.37 mg kg^{-1} in the old leaves of cv. Tresor and cv. Canberra, respectively) is probably not enough to independently cause Al toxicity-related symptoms. As a point of comparison, the threshold concentrations of Al that cause Al toxicity-related symptoms is 30 mg kg^{-1} in the leaves of the soybean (*Glycine max* L.) (Wallace and Rommey 1977). However, when compared to the threshold Al content in rice (*Oryza sativa* L.) roots (20 mg kg^{-1}) (Wallace and Rommey, 1977), the total Al content in the roots could potentially cause toxic effects in plants grown in acidic soil (138.9 and 160.9 mg kg^{-1} in the roots of cv. Tresor and cv. Canberra, respectively). However, given that 99.99% of the total Al content may be found in the apoplasts of root cells, and since Al does not enter into the simplast (Reid et al., 1996; Rengel and Reid, 1997), the Al content in the roots, as well as its potential toxicity, should be taken with caution.

In addition, the results of the Al content analysis of the root tips showed no difference between acidic soil-grown cv. Canberra and cv. Tresor (Table 5). Measurement of the Al content in the root tips can be used as an indicator of the Al exclusion mechanism. The most recognized physiological mechanism conferring Al tolerance in plants involves exclusion of Al from the root tip (Miyasaka et al., 1991; Delhaize and Ryan, 1995; Kochian, 1995); thus, Al-tolerant genotypes contain less Al in the root tips when compared to Al-sensitive genotypes. The lack of significant differences in the Al content of the root tips of Al-sensitive and Al-tolerant potato cultivars grown in acidic soil points to aforementioned fact that Al toxicity is not the sole reason for the dry matter reduction in cv. Canberra; conversely, it also points to the possible existence of Al tolerance mechanisms that are not based on Al exclusion from the root tip. Theories and evidence for the idea that Al exclusion from the root tip cannot fully explain the Al tolerance mechanisms were previously published for maize (Piñeros et al., 2005) and rice (Famoso et al., 2010).

The results of this study highlight the possible mitigating effects of other plant nutrients on the Al toxicity in cv. Tresor. They also point to the additional possible causes that underlie the reduction of dry matter production in acidic soil-grown cv. Canberra. Namely, according to the results found for the root dry matter, cv. Tresor had a smaller root system when compared to cv. Canberra (Table 3); however, according to the results of the nutrient content analysis of the different plant parts, it appears that cv. Tresor was better able to acquire nutrients from acidic soil, especially nutrients such as P, Ca, and Mg (Fig. 1B, 1D, and 1E), which are known to have mitigating effects on Al toxicity. Interactions of Al with P, Ca, and Mg have long been implicated in Al phytotoxicity because the symptoms of severe Al toxicity in the field resemble those of P, Ca, and/or Mg deficiency (e.g. see reviews by Foy, 1988; Samac and Tesfaye, 2003; Bose et al., 2011).

The high affinity of Al^{3+} to displace essential nutrients such as Ca^{2+} from the apoplast is presumed to be a primary mechanism of Al toxicity (Blamey and Dowling, 1995). The frequent explanations behind the effects of Ca and Mg on reductions in Al toxicity include increases in thee ionic strength of the soil solution, and reductions in the activity of rhizotoxic Al species (Wheeler and Edmeades, 1995). Thus, in order to achieve such an effect, soil liming (with different Ca and Mg materials) is employed. However, several authors (Lazof and Holland, 1999; Silva et al., 2001) reported the ameliorative effect of Ca or Mg on rhizotoxicity upon constant Al activity in a solution. In addition, the researchers' results suggested that Mg may be more effective than Ca at ameliorating Al rhizotoxicity (Yang et al., 2000; Silva et al., 2001).

Bose et al. (2011) stated that one possible approach used to engineer Al^{3+}-resistant plant genotypes could rely on improved Mg^{2+} transport and/or accumulation. Some of the proposed mechanisms for the Mg-induced alleviation of Al toxicity in plants include better carbon partitioning from the shoots to roots and enhanced acid phosphatase activity (Bose et al. 2011). Indeed, our results showed that growth in acidic soil severely affected the Mg content in old and young leaves, as well as the production of root dry matter in cv. Canberra, while it did not affect the root dry matter production and Mg content in the old and young leaves of cv. Tresor (Table 3; Fig. 1E). In addition, soil acidity significantly reduced the P content of the aboveground vegetative parts of cv. Canberra (Fig. 1B). In fact, the minimal concentrations of P in the diagnostic leaf (the fourth leaf from the top) of potato plants during tuber bulking were observed to be 0.15%–0.25% (White et al., 2007), which indicates that acidic soil-grown cv. Canberra suffered from P deficiency (0.08% in old leaves and 0.012% in young leaves). In addition to Al toxicity, P deficiency might be an additional reason for the reduction in dry matter production obtained from acidic soil-grown cv. Canberra. A similar reaction of the dry matter production to the P supply in the potato was previously obtained by Fleisher et al. (2012).

The results of this study showed the positive effects of soil liming on the mineral nutrition of both Al-sensitive and Al-tolerant potato cultivars. In addition, liming prevented acidic soil-caused reductions in the dry matter production of Al-sensitive cv. Canberra. However, the results of this experiment should be further investigated under field conditions. One should also assess whether liming has an effect on the tuber yield of these two potato cultivars. Moreover, their susceptibility to the common scab (*Streptomyces scabies*) under limed soil conditions should be included in subsequent studies.

The results of the Al content analyses in the root tips and other vegetative organs of the investigated potato cultivars, as well as the concentrations of nutrients such as P, Mg, and Ca, indicate that acidic soil toxicity is not solely attributed to Al toxicity. Moreover, the physiological reactions to acidic soil toxicity may involve multiple mechanisms that are related to higher-efficiency nutrient utilization under specific conditions, which are associated with low soil pH and high concentrations of mobile Al.

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