Journal of Elementology ISSN 1644-2296

Potarzycki J., Grzebisz W. 2020.
The in-season variability in the calcium concentration in potato organs and its relationship with the tuber yield.
J. Elem., 25(1): 107-124. DOI: 10.5601/jelem.2019.24.3.1801

RECEIVED: 25 January 2019
ACCEPTED: 23 August 2019

ORIGINAL PAPER

THE IN-SEASON VARIABILITY IN THE CALCIUM CONCENTRATION IN POTATO ORGANS AND ITS RELATIONSHIP WITH THE TUBER YIELD*

Jarosław Potarzycki, Witold Grzebisz

Chair of Agricultural Chemistry and Environmental Biogeochemistry
Poznan University of Life Sciences, Poland

Abstract

The assumption of this study was that in-season trends in the calcium concentration (Ca_c) in potato organs allow one to identify the source of this nutrient for the growing tubers. This hypothesis was tested based on the data from field experiments (2006-2008), with sequentially added nutrients (Absolute control – AC, NP, NPK, NPKS, and NPKSMg). The Ca concentration (Ca_c) was measured in potato vines, stolons + roots, and three fractions of potato tubers. Potato plants were periodically harvested in 10-day sequences, starting from BBCH 33 until maturity. The tuber yield, averaged over fertilization treatments, was 33.4, 53.7, and 41.6 t ha^{-1} in 2006, 2007, and 2008, respectively. The Ca_c in-season trends, regardless of the potato part, were governed by the weather and only slightly modified by the applied fertilizers. The Ca_c in potato organs, averaged over the growth season, was in the order: vines > stolons + roots > > tubers. The high Ca_c in potato vines between 89 and 110 DAP, as recorded in 2007, can be treated as the prerequisite of high potato yield. The Ca_c status in potato vines on 99 DAP can be used as the yield predictor. The Ca_c maxima, revealed earlier or later during the potato growth period, as compared to 2007, resulted in the tuber yield decline. The Ca_c in the large-size potato tubers showed a progressive increase in accordance with the phases of potato tuber maturation. The main sources of Ca for the large-size tubers were other potato parts. The Ca_c increase in this potato fraction coincided with its simultaneous drop in the other potato organs, like shoots, stolons, and roots. Intensively expanding tubers created a strong sink for calcium, thus decreasing its concentration in tubers of the smaller size.

Keywords: growing season, vines, stolon + roots, tuber fractions, trends of calcium.

Jarosław Potarzycki, PhD DSc, Chair of Agricultural Chemistry and Environmental Biogeochemistry Poznan University of Life Sciences, Wojska Polskiego 71F, 60-625 Poznań, Poland, e-mail: jarekpo@up.poznan.pl

* Financial source: Statutory research.

INTRODUCTION

The nutritional value of potato tubers is high due to the high input of energy into human diet. Tubers are rich in minerals, mainly in potassium, but not in calcium (Ca). In the European diet, potato delivers only 6% of the daily requirement for Ca by an adult person. The total Ca concentration (Ca_c) in the tuber is low. In addition, its distribution in the tuber is not equal, being several-times higher in the periderm (skin) than in the flesh (7-folds). Peeling potatoes is a typical stage in traditional potato processing. Cooking of potato tubersleads to the subsequent loss of numerous elements, including calcium (Camire et al. 2009, Subramanian et al. 2011).

Calcium impacts numerous processes in potato. In general, Ca is responsible for tissue integrity as a component of the cell wall. Physiological functions of Ca in the potato tuber strongly depend on its concentration in the skin. The black spot bruise of tubers can be limited provided Ca_c in the skin is above 250 mg kg^{-1} DM (Palta 2010). It has been also documented that tubers rich in calcium are less sensitive to mechanical damage during harvest. This is important for farmers because potato tubers with mechanical damage are sensitive to the attack of pathogens during storage (soft rot) (Karlsson et al. 1996). It is well documented that reasonably high Ca_c both in tubers and the whole plant increases its resistance to pathogens (Brown et al. 2013, Tzeng et al. 1990).

One of the most important functions of Ca is its role in the regulation of the potato's hormonal status. It has been recently demonstrated that Ca^{2+} is an accompanying cation which is necessary for auxins to perform cell--to-cell transport. Calcium has been also recognized as a component of a network of signal transduction pathways in plants, known as a secondary messenger. It is activated at the onset of stress, both biotic (pathogen attack) or abiotic one (cold, heat, shortage of water in the soil) (Sanders et al. 1999). One of the most important functions of Ca, but poorly recognized yet, is its role in the tuberization of potato plants. As reported by Vega at al. (2006), the tuberization signal is controlled by the Ca content in the soil zone rooted by a potato. Its induction requires a significant drop in the Ca content in the soil adjacent to the stolon.

Calcium concentration in the plant and its subsequent partitioning between its organs are highly uneven. Calcium ions are taken up by plant roots from the soil solution via the transportation pathway known as mass-flow (Clarkson 1993). The dominating route of Ca ion transportation in the plant and subsequent redistribution is the xylem. The Ca_c in the plant shoot is several-folds higher in leaves than in reproductive organs, i.e. seeds, grains, or in tubers (Kolbe, Stephan-Beckmann 1997*a*,*b*, Rosanoff et al. 2015). The main reason of this huge difference is the low remobilization potential of calcium, subsequently leading to its extremely low concentration in the floem. In addition, the Ca_c in the plant depends on its content in the soil solution and on the plant transpiration rate. Higher air temperature causes higher canopy transpiration, resulting in a higher Ca concentration in plant shoots (Busse, Palta 2006).

There is an information gap in current knowledge concerning the Ca_c in potato plants during the key stages of tuber yield formation. It has been assumed that an analysis of Ca_c trends in potato organs during the growth season can deliver data useful in indicating the sources of this element for the growing tubers.

The key objective of the study was to identify the Ca_c trends during the growing season for potato shoots (vines), stolons + roots, and three fractions of potato tubers: small, medium, and large one. The secondary objective was to assess the usefulness of Ca_c in respective organs and growth stages as a tool for the tuber yield prediction.

MATERIAL AND METHODS

Experimental site

The study is based on data obtained from field trials with potato (*Solanum tuberosum* L.), which were carried out in 2006-2008 at Brody Experimental Farm (Poznan University of Life Sciences, 52°44′N; 16°28′E). The field experiment was established on soil developed from loamy sand, underlain by sandy loam and classified as an Albic Luvisol. The content of available nutrients, measured in the topsoil each year before fertilizer application, was high/very high for phosphorus (80-95 mg P kg^{-1} soil) (double lactate method), medium for potassium (130-150 mg K kg^{-1} soil) (double lactate method), and medium for magnesium (58-62 mg Mg kg^{-1} soil) (Schachtschabel method). The amount of mineral N (N_{min}) was in the range of 23-30 kg ha^{-1} (0.01 mol dm^{-3} $CaCl_2$). The soil pH was 5.6-6.0 (1 mol dm^{-3} KCl). Meteorological data showed concerning highly variable precipitation, especially in June, a critical time for potato tuberization. In June and July 2006 and in July 2008, rainfall deficits were recorded (Figure 1).

Experimental design

A field trial consisting of five treatments, with different composition of sequentially added sets of nutrients, arranged in a randomized complete block, and replicated four times, was the source of data for the study. The fertilized treatments were as follows: i) absolute control (AC, no fertilizers added), ii) NP, iii) NPK-MOP (K applied as muriate of potash), NPKS-SOP (K applied as potassium sulfate), NPKSMg (Patentkali). Phosphorus in the dose of 38.7 kg P ha^{-1} was applied as di-ammonium phosphate. Potassium was applied at the dose of 166 kg K ha^{-1}. Both nutrients were applied two weeks before potato planting. The dose of S applied with SOP

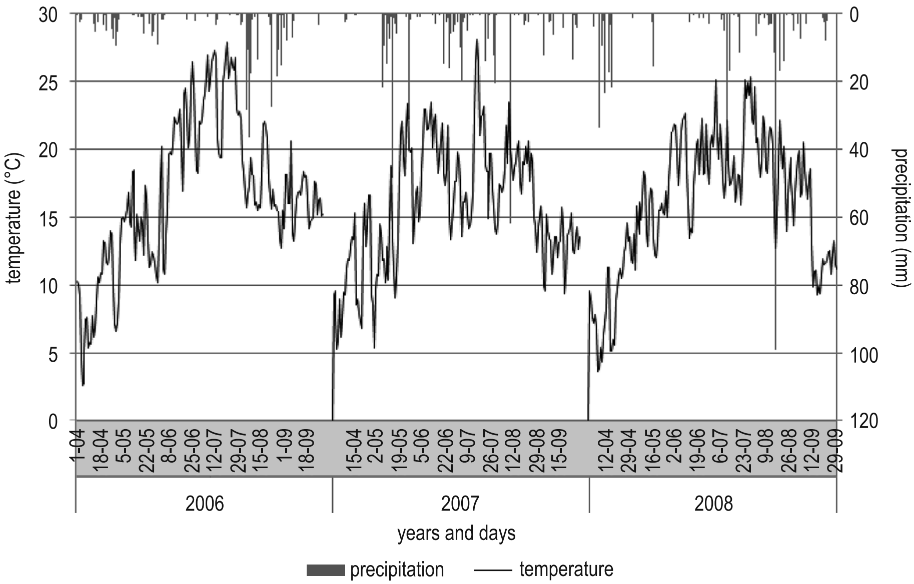

Fig. 1. Monthly mean air temperature and total precipitation at Brody experimental station

and Patentkali was 69.1 and 110.7 kg ha^{-1}, respectively. The dose of Mg was 39.1 kg ha^{-1}. Nitrogen used in the form of ammonium nitrate (34% N) was divided into two sub-doses and applied to potato before planting – 70 kg ha^{-1}, and in BBCH 20 - 60 kg ha^{-1}. The total area of a single plot was 58.5 m^2. An early variety of potato called Korona was planted in the second half of April and harvested from an area of 19.5 m^2 at the end of September.

Soil and plant material and analyses

Plant material used for dry matter determination and determination of the concentrations of nutrients was collected from an area of 1.0 m^2. Each year, plant material was sampled during the growing season in consecutive days after planting (DAP): 57, 68, 78, 89, 99, 110, 121, 131, 141, 152. The sampled material was then divided, depending on the potato stage of growth, into subsamples of vines, stolon + roots. Tubers were divided into three fractions: small (< 3 cm), medium (3.5-5 cm), and large (> 5 cm). For determination of the Ca concentration, the harvested plant sample was dried at 65°C and then mineralized at 600°C. The ash was then dissolved in 33% HNO_3. After dissolving the ash in diluted HNO_3 the concentration of Ca was determined using flame atomic absorption spectrometry. The results are expressed per dry matter.

Statistical analyses

The collected data were subjected to the conventional analysis of variance using Statistica® 10 (StatSoft, Krakow, Poland). Differences between the treatments were evaluated with the Tukey's test. In tables, figures, and developed equations, the results from the *F* test (***, **, *) indicate significance at the $P < 0.001$, 0.01, and 0.05, respectively. In the second step of the diagnostic procedure, stepwise regression was applied to define an optimal set of variables for a given crop's characteristic. In the computational procedure, a consecutive variable was removed from the multiple linear regressions in a step-by-step manner. The best regression model was chosen based on the highest *F*-value for the model and significance of all independent variables.

RESULTS AND DISCUSSION

Vines

The calcium concentration (Ca_c) in the potato vines during the growing season was significantly affected by the weather (Figure 2). The Ca_c course obtained in 2007, a year with the highest yields of tubers, was considered as a model high yielding potato. The experimental data fitted the quadratic regression model the best. The Ca_{cmax} of 8.7 g kg^{-1} DM was recorded on the 103rd DAP. The real maximum was higher by 1.0 g kg^{-1} DM as compared to the Ca_{cmax}. In the period preceding and following the Ca_{cmax}, which lasted for about three weeks, the Ca_c was much lower, between from 4 to 6 g kg^{-1} DM. The model in the first phase is very similar to that presen-

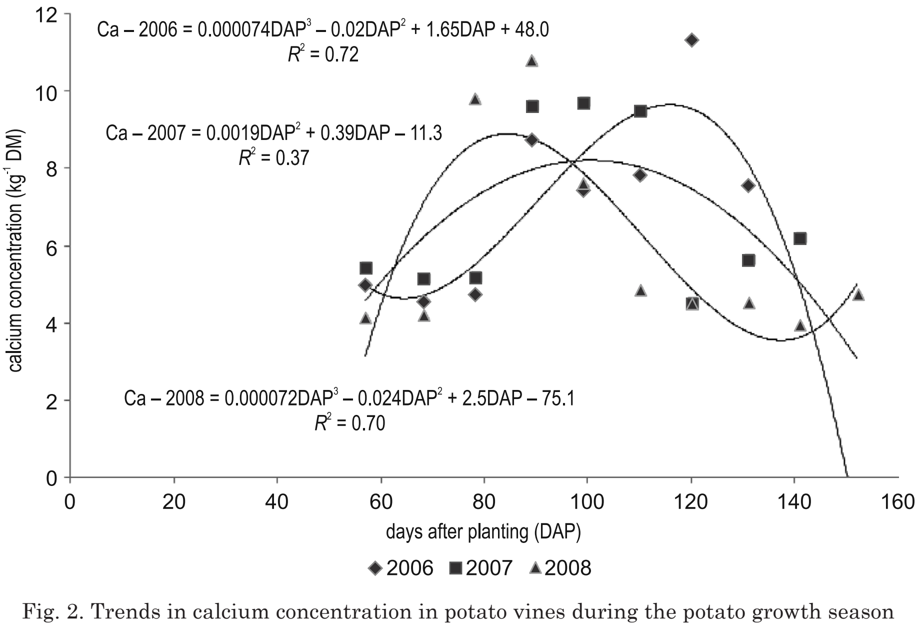

Fig. 2. Trends in calcium concentration in potato vines during the potato growth season in consecutive years

ted by KOLBE and STEPHAN-BECKMANN (1997*a*). In this study, a sudden Ca_c increase was recorded in the same phase of potato tuber enlarging. Then, it reached a plateau, lasting for 45 days. In the cited research, unlike incontrast to the course presented in Figure 2*a* decrease of Ca_c during the maturation phase was very low. A sudden Ca_c drop, which occurred after 110 DAP, can be treated as an indicator of the calcium remobilization effect. The observed Ca_c drop was probably a result of a huge increase in the tuber weight during the maturation phase (data not shown, but available from the authors). This conclusion contradicts the hypothesis which negates the floem transport of Ca to the expanding tuber (BUSSE, PALTA 2006).

In 2006 and 2008, the 3rd degree regression models were obtained. Both models differ significantly in the Ca_{cmax} for respective DAPs and the DAP inflation point (DAP_{ip}). In 2006, the Ca_{max} of 10.2 g kg^{-1} DM was reached on 114 DAP, whereas in 2008, the Ca_{max} of 8.27 g kg^{-1} DM was recorded on 83 DAP. The other characteristics, i.e. the DAP_{ip}, significantly differed in both years. It appeared on 88 and 111 DAP in 2006 and 2008, respectively. In 2006, DAP_{ip} preceded a sudden Ca_c increase, whereas in 2008 it appeared just after the Ca_{cmax}. The key reason of a 30-day difference between the two maxima was the weather. In 2006, June and July were dominated by drought followed by huge rainfall at the end of July. This type of weather resulted in the secondary growth of tubers, leading to an enhanced accumulation of calcium. In 2008, a reverse situation was recorded. The Ca_c in potato shoots increased progressively with the prolonged drought, which prevailed in most of May and June (Figure 1).

The effect of fertilization on the in-season Ca_c changes was considerable in the years of study (Table 1). In 2006, a year with a drought in June and July, the significant impact of applied fertilizers was observed during the entire growing season. As a rule, it resulted in the increase in the Ca_c in potato shoots. The highest differences were revealed on 68 and 120 DAP. On the first date, the Ca_c increased progressively with the input of nutrients. This relation indicates a lack of antagonism between cations applied in fertilizers on Ca uptake. A quite reverse situation was observed on 120 DAP. Firstly, Ca_c values were much higher than on 68 DAP. Secondly, the Ca_c showed a positive response to the application of potassium, but negative one to potato fertilization with sulfur and/or with magnesium.

The observed antagonism was manifested on 99 DAP. In 2007, a year with good distribution of precipitations during the potato growth season, a significant impact of fertilizers on Ca_c was observed on 78 and 99 DAP. On the first date, the applied fertilizers had a positive impact on Ca_c. On the second one, the recorded Ca_c values were slightly below the maxima, which appeared on 89 DAP for the absolute control and NP plot. In 2008, a year with a drought in May and June, a significant impact of fertilization was verified on 99, 131 and 152 DAP. The first event occurred just after the Ca_{cmax}. On all of these sampling dates, significant differences were noted only between the absolute control and fertilized plots.

Table 1

Calcium concentration in potato vines during the growing season in consecutive years (g kg^{-1} DM)

Treatments	Days After Planting (DAP)									
	57	68	78	89	99	110	120	131	141	152
2006										
AC	2.9^{a}	4.1^{a}	4.3^{a}	7.0^{a}	6.3^{a}	5.9^{a}	9.5^{a}	6.8^{a}	-	-
NP	4.7^{c}	4.4^{b}	4.7^{b}	8.9^{b}	7.1^{b}	7.9^{c}	10.1^{b}	7.4^{b}	-	-
NPK	5.0^{c}	4.6^{b}	4.8^{b}	8.8^{b}	7.6^{c}	7.9^{c}	11.2^{c}	7.6^{b}	-	-
NPKS	5.0^{c}	4.9^{c}	4.4^{a}	9.2^{b}	6.6^{a}	6.6^{b}	9.9^{a}	7.2^{ab}	-	-
NPKS Mg	3.6^{b}	5.0^{c}	4.4^{a}	8.4^{b}	6.6^{a}	6.6^{b}	9.9^{a}	7.3^{ab}	-	-
F value	118***	35.2***	18.5***	13.6***	26.6***	39.2***	26.6***	20.6***	-	-
2007										
AC	4.2^{a}	4.7	3.4^{a}	9.4	7.9^{a}	8.8	3.9	5.2	6.0	-
NP	5.6^{b}	5.3	4.6^{ab}	10.0	9.2^{ab}	9.8	4.5	5.8	6.8	-
NPK	5.4^{b}	5.2	5.2^{b}	9.7	9.7^{ab}	9.5	4.5	5.7	6.2	-
NPKS	5.5^{b}	4.9	5.3^{b}	9.4	9.3^{b}	9.5	4.8	5.6	6.4	-
NPKS Mg	5.6^{b}	4.9	5.0^{b}	9.4	9.1^{ab}	9.3	5.4	5.4	6.8	-
F value	6.5**	2.0	6.5**	0.2	3.6*	0.4	1.6	0.3	1.0	-
2008										
AC	3.8	4.1	9.1	10.5	6.9^{a}	4.2	4.1	3.0^{a}	3.4	3.7^{a}
NP	4.3	4.4	10.1	11.8	8.0^{ab}	4.7	4.7	4.0^{ab}	3.9	4.9^{b}
NPK	4.1	4.2	9.8	10.8	7.6^{ab}	4.9	4.5	4.5^{b}	3.9	4.7^{b}
NPKS	4.1	4.1	9.8	11.1	8.1^{b}	4.6	4.4	4.6^{b}	4.2	4.8^{b}
NPKS Mg	4.0	4.1	9.4	11.8	7.9^{ab}	4.7	4.3	4.3^{b}	4.7	4.9^{b}
F value	0.4	0.2	0.3	1.0	3.6*	2.3	2.0	6.5**	1.6	6.5**

***, **, * significant at $p < 0.001$, < 0.01, <0.05, respectively, n.s. – not significant;
^{a} the same letter indicates a lack of significant differences within the treatment.

The predictive worth of Ca_c in potato shoots was significant on 99 DAP. As shown below, any increase in Ca_c in this phase of potato growth resulted in a tuber yield (Y) increase:

$$Y = 11.98Ca_c - 52.4 \text{ for } n = 15, R^2 = 0.75, \text{ and } P \leq 0.001.$$

This equation clearly shows that at the beginning of the tuber growth phase, high Ca_c is required to reach a high yield of tuber. The Ca_c obtained in 2007 demonstrates that the optimum range for this stage of potato development was between 9.5 and 9.8 g kg^{-1} DM.

Stolons + roots

The true roots of potato, according to BUSSE and PALTA (2006), are the main transportation means of calcium ions from the soil solution into the growing potato tubers. Therefore, it can be assumed that the Ca_c in the roots reflects the size of Ca soil resources and environmental conditions of its uptake. As it is suggested by GUNTER and PALTA (2008), the uptake of Ca^{2+} from soil occurs along the mass flow path, and is closely related to the transpiration rate of the plant. Consequently, the Ca_c in a potato tuber should be considered as a product of both the content of Ca ions and water in the soil solution.

The Ca_c in stolons + roots were significantly lower than the values recorded for potato shoots (3.5 to 5.5 g kg^{-1} DM versus 4.5 - 9.7 g kg^{-1} DM). In all years of the study, the smallest differences in Ca_c between the fertilization treatments were recorded at the beginning of the potato growth season. The in-season changes of Ca_c in the stolons + roots were significantly governed by the weather, as demonstrated for the NPK plot (Figure 3). The regression model obtained in 2007 was described by the 4th degree polynomial function. Its course was characterized by one distinct maximum, and two minima. The Ca_{cmax} which appeared around 110 DAP was concurrent with the period of the highest Ca_c in potato shoots (Figure 2). The lowest Ca_c values in stolons + roots were recorded in two distinct stages of potato growth, i.e. between 68 - 89 DAP and from 110 to 131 DAP. The observed Ca_c minima are closely linked to the tuber intensive growth periods (KOLBE, STEPHAN-BECKMANN 1997*b*). The determined pattern corroborates the claim

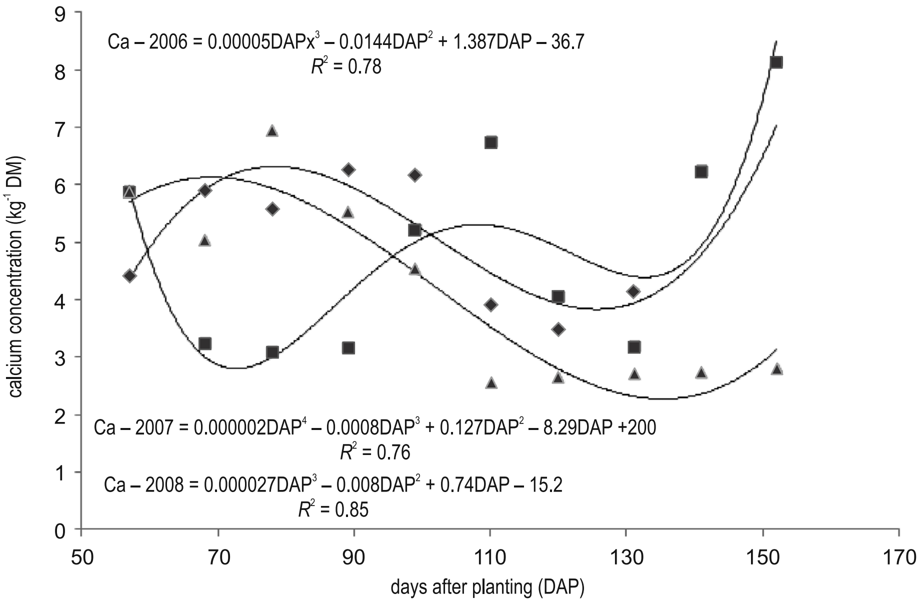

Fig. 3. Trends in calcium concentration in potato stolons + roots during the potato growth season in consecutive years

that the weather has a considerable impact on the Ca uptake by potatoes (Busse, Palta 2006). In the other two years, the Ca_c trend was described best by the cubic function. In years with water shortage, the maxima of both functions occurred on nearly the same DAP, indicating high similarity in the Ca_c course in stolons + roots. In 2006, the Ca_{cmax} of 6.1 g kg^{-1} DM was achieved on 76 DAP. At the same time, the DAP_{ip} was recorded on 102 DAP. In 2008, the Ca_{cmax} of 6.4 g kg^{-1} DM was recorded on 71 DAP. The DAP_{ip} took place on 100 DAP.

The effect of fertilization treatments on the Ca_c in stolons + roots was highly variable in the consecutive years of the study (Table 2). In 2006, a significant increase in the Ca_c for fertilized treatments with respect

Table 2

Calcium concentration in potato stolons + roots during the growing season in consecutive years (g kg^{-1} DM)

Treatments	Days After Planting (DAP)									
	57	68	78	89	99	110	120	131	141	152
2006										
AC	3.6^a	4.3	4.2^a	5.0	3.8^a	3.6^a	3.4^a	3.6^a	-	-
NP	4.1^{ab}	4.8	5.2^{ab}	6.2	6.1^b	3.8^{ab}	3.5^a	3.8^b	-	-
NPK	4.5^{ab}	5.9	5.6^{ab}	6.3	6.2^b	4.0^{ab}	3.5^a	4.2^{ab}	-	-
NPKS	6.0^c	6.2	5.8^{ab}	6.6	6.5^b	4.4^{ab}	5.4^b	4.8^b	-	-
NPKS Mg	6.0^c	6.0	6.1^b	6.1	4.9^{ab}	4.6^b	5.7^b	4.8^b	-	-
F value	6.6^{**}	2.8	3.7^{*}	1.2	5.9^{**}	1..0	89.9^{***}	5.4^{**}	-	-
2007										
AC	5.7	2.5^a	2.8	2.0^a	4.8^a	5.3	3.7^{ab}	2.4	7.2^{ab}	-
NP	6.0	3.4^b	3.2	3.3^b	5.5^{ab}	6.8	3.8^{ab}	2.7	8.1^b	-
NPK	5.9	3.3^b	3.1	3.2^b	5.2^{ab}	6.8	4.1^b	3.2	6.3^a	-
NPKS	5.7	3.3^b	3.0	3.2^b	5.6^b	6.5	2.8^a	2.9	7.0^{ab}	-
NPKS Mg	5.7	3.4^b	2.7	3.0^b	5.5^{ab}	5.6	2.9^a	3.2	5.8^a	-
F value	0.4	6.5^{**}	2.0	13.6^{***}	3.6^{*}	2.2	6.1^{**}	2.6	5.5^{**}	-
2008										
AC	4.7	5.0	6.5^{ab}	6.2^{ab}	4.1^a	2.6^{ab}	2.5	1.8^a	2.1^a	2.2^a
NP	5.8	5.1	6.4^{ab}	7.1^b	4.9^b	2.9^{ab}	2.8	2.9^b	2.4^{ab}	2.9^b
NPK	5.9	5.1	7.0^b	5.5^a	4.6^{ab}	2.6^{ab}	2.7	2.7^b	2.8^{ab}	2.8^b
NPKS	5.7	5.1	5.1^a	6.1^{ab}	5.0^b	2.4^a	2.6	2.9^b	2.6^{ab}	3.0^b
NPKS Mg	4.8	4.8	5.2^a	5.1^a	4.7^b	2.9^b	2.4	2.7^b	3.0^b	2.9^b
F value	2.1	0.6	6.4^{**}	5.2^{**}	7.9^{**}	3.8^{*}	1.8	37.1^{***}	3.7^{*}	9.2^{***}

***, **, * significant at $p < 0.001$, < 0.01, <0.05, respectively, n.s. – not significant;
[a] the same letter indicates a lack of significant differences within the treatment.

to the absolute control (AC) was found in five of the eight sampling dates. The Ca_c increase in response to the progressive input of nutrients was most visible at the beginning of the potato growth (57 DAP). At this phase of potato growth, no antagonism between the applied nutrients and Ca_c was recorded. The antagonistic impact of magnesium was detected only at 99 DAP. In 2007, a positive impact of the applied fertilizers continued during the whole growing season. The negative impact of the applied magnesium occurred first at 120 DAP and persisted up to the harvest. In 2008, a decrease in Ca_c in the NPK and NPKSMg treatments with respect to NP was observed since the beginning of the potato growth.

The small-size tubers

The Ca_c in the small-size potato tubers was by 10-folds lower than the values recorded for stolons + roots (Tables 2 and 3). The Ca_c trend during the potato growth period was year-to-year variable (Figure 4). The proven Ca_c trends were recorded only in years with a drought, i.e. 2006 and 2008. In 2006, the Ca_{cmax} of 0.33 g kg^{-1} DM was achieved on 94 DAP, and the DAP_{ip} took place on 120 DAP. In 2008, the Ca_{cmax} was much lower, amounting to 0.24 g kg^{-1} DM. It occurred on 90 DAP and the DAP_{ip} was noted on 117 DAP.

The effect of fertilization treatments on the Ca_c in the small-size tubers was most pronounced in 2006 (Table 3). In that year, a significantly higher Ca_c in tubers from the the fertilized plots was found in four of the eight sampling dates. However, the real differences between treatments tended to be

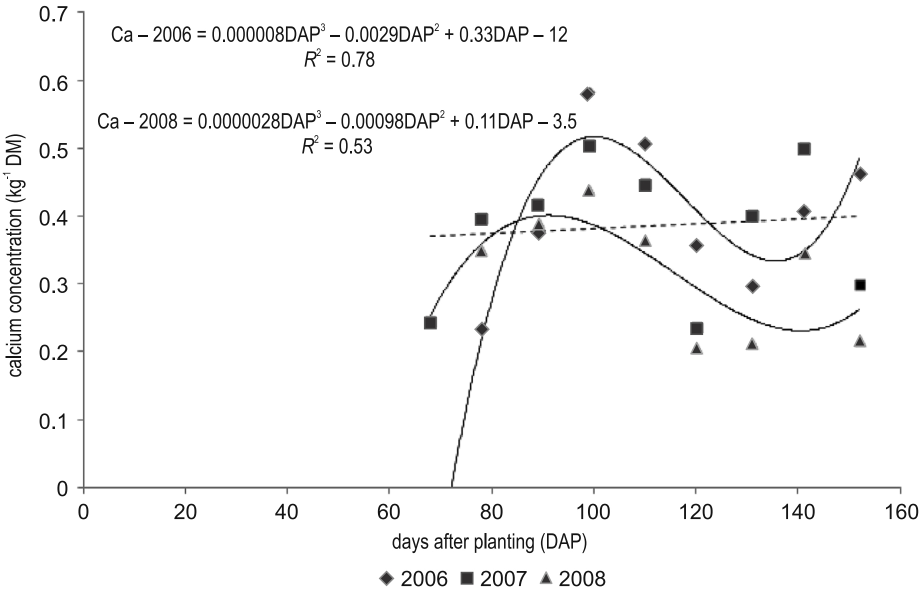

Fig. 4. Trends in calcium concentration in the small-size tubers during the potato growth season in consecutive years

Table 3

Calcium concentration in the small-size (< 3cm) tubers during the growing season in consecutive years (g kg^{-1} DM)

Treatments	Days After Planting (DAP)								
	68	78	89	99	110	120	131	141	152
2006									
AC	-	0.22^{a}	0. 35	0.53^{a}	0.46^{a}	0.35	0.24^{a}	0.39	0.42
NP	-	0.25^{b}	0.33	0.58^{b}	0.54^{bc}	0.35	0.29^{b}	0.40	0.45
NPK	-	0.24^{ab}	0.38	0.59^{b}	0.51^{b}	0.36	0.30^{b}	0.41	0.47
NPKS	-	0.25^{b}	0.37	0.58^{b}	0.55^{c}	0.36	0.31^{b}	0.37	0. 47
NPKS Mg	-	0.24^{ab}	0.33	0.59^{b}	0.51^{b}	0.34	0.30^{b}	0.39	0.46
F value	-	3.6^{*}	1.7	35.7^{***}	20.1^{***}	0.3	11.3^{***}	2.7	1.1
2007									
AC	0.18	0.15^{a}	0.48	0.50	0.33	0.30	0.41	0.51	0.28^{b}
NP	0.20	0.21^{ab}	0.51	0.48	0.33	0.28	0.34	0.42	0.21^{ab}
NPK	0.24	0.40^{b}	0.42	0.51	0.45	0.24	0.40	0.50	0.30^{b}
NPKS	0.11	0.21^{ab}	0.43	0.49	0.28	0.41	0.31	0.39	0.13^{a}
NPKS Mg	0.20	0.24^{ab}	0.45	0.47	0.36	0.21	0.31	0.39	0.20^{ab}
F value	1.4	3.9^{*}	0.8	0.2	2.7	0.6	2.4	2.4	6.4^{**}
2008									
AC	-	0.36	0.28	0.44	0.41	0.27	0.15	0. 13^{a}	0.25
NP	-	0.30	0.29	0.42	0.44	0.24	0.18	0.18^{ab}	0.19
NPK	-	0.35	0.39	0.44	0.37	0.21	0.21	0.35^{b}	0.22
NPKS	-	0.27	0.24	0.42	0.37	0.38	0.10	0.19^{ab}	0.12
NPKS Mg	-	0.27	0.31	0. 41	0.39	0.17	0.18	0.021^{ab}	0.18
F value	-	2.3	2.7	0.2	0.8	2.3	1.4	3.9^{*}	2.3

***, **, * significant at $p < 0.001$, < 0.01, <0.05, respectively, n.s. – not significant;
^{a} the same letter indicates a lack of significant differences within the treatment.

small, being the highest on 110 DAP. In 2007, significant differences between treatments were recorded on 78 and 152 DAP. On the first sampling date, Ca_c reached the highest values for tubers grown on the NPK plot. Significantly lower values were recorded on plots fertilized with NPKS and NPKSMg, which clearly demonstrated an antagonism between Mg and Ca. The same pattern was found at harvest. The key reason of the observed antagonism was probably a good supply of potassium (Grzebisz et al. 2018). In 2008, significant differences between treatments were recorded only on 141 DAP. The Ca_c was twice as high in tubers grown on the NPK plot as in to all other plots. The antagonism of Mg against Ca was revealed first on 120 DAP. The yield of tubers can be predicted based on the Ca_c status in the small-size tubers on 99 DAP:

$$Y = -128.6Ca_c + 103.5 \text{ for } n = 15,\ R^2 = 0.44 \text{ and } P \leq 0.01.$$

The regression model clearly indicates that Ca_c above 0.4 g kg^{-1} DM at this particular stage of the potato growth led to a tuber yield decrease. In the studied case, the cause of the elevated Ca_c was a drought, which disturbed relationships between main cations, subsequently resulting in a yield drop.

The medium-size tubers

The Ca_c in-season trends for the medium-size tubers were significantly driven by the weather (Figure 5). The most regular trend was obtained in 2007. As seen from the developed equation, the Ca_{cmax} of 0.52 g kg^{-1} DM

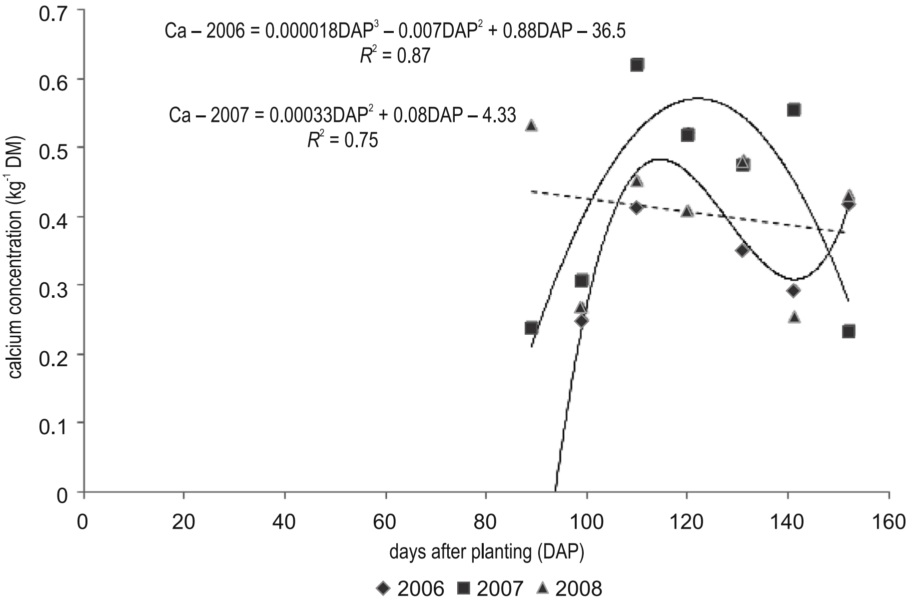

Fig. 5. Trends in calcium concentration in the medium-size tubers during the potato growth season in consecutive years

was recorded on 121 DAP. Just afterwards, a significant drop in the Ca_c took place. Quite a different pattern of Ca_c was observed in 2006. The regression model was described by the 3rd degree polynomial function. The Ca_{cmax} of 0.45 g kg^{-1} DM was achieved on 111 DAP and the DAP_{ip} occurred on 135 DAP. The late occurrence of the DAP_{ip} in that year was a result of the disturbed Ca supply due to a heavy rainfall event, which took place at the end of July. This caused a secondary growth of potato tubers. The Ca_c pattern in 2008 was not consistent. The main reason for the enormous Ca_c variability was a severe drought in May and June (Figure 1).

The effect of the applied fertilizers on the Ca_c in-season variability tended to be significant during most of the potato growth season in 2006 (Table 4). The highest differences between treatments were most visible on 131 DAP. On that sampling date, the Ca_c increase was correlated with the number of the applied nutrients. The same, although a much weaker trend was observed on 99 DAP. The coincidence of Ca_c on both sampling dates is an indicator of the secondary growth of potato tubers. In 2007, significant differences in Ca_c between fertilization treatments were recorded at the beginning and at the end of the potato growth season. In spite of the high Ca_c variability during the growing season, no antagonism between Ca and other main cations was recorded. In 2008, significant impact of the applied fertilizers on Ca_c was demonstrated on 99 and 120 DAP. On the latter sampling

Table 4

Calcium concentration in the medium-size (3.5 - 5 cm) tubers during the growing season in consecutive years (g kg^{-1} DM)

Treatments	Days After Planting (DAP)						
	89	99	110	120	131	141	152
2006							
AC	-	0. 23^{a}	0.42^{a}	0.53^{a}	0.29^{a}	0.27	0.39^{a}
NP	-	0.29^{b}	0.43^{a}	0.52^{a}	0.33^{ab}	0.29	0.40^{a}
NPK	-	0.25^{b}	0.42^{a}	0.52^{a}	0.35^{bc}	0.30	0.42^{ab}
NPKS	-	0.27^{b}	0.45^{ab}	0.58^{ab}	0.39^{c}	0.29	0.44^{b}
NPKS Mg	-	0.29^{b}	0.49^{b}	0.060^{b}	0.40^{c}	0.30	0.39^{a}
F value	-	3.5*	7.0**	6.5*	17.7***	0.7	3.3*
2007							
AC	0.50^{c}	0.50^{b}	0.57	0. 59	0.38	0.41	0.13^{a}
NP	0. 47^{bc}	0.48^{b}	0.57	0.63	0.35	0.41	0.18^{ab}
NPK	0.24^{ab}	0.31^{a}	0.62	0.52	0.18	0.56	0.24^{abc}
NPKS	0.19^{a}	0.28^{a}	0.69	0.53	0.23	0.35	0.31^{bc}
NPKS Mg	0.20^{a}	0.48^{b}	0.54	0.56	0.25	0.45	0.34^{c}
F value	7.3**	8.9***	0.9	0.8	1.6	2.7	6.4**
2008							
AC	0.51	0.30^{ab}	0.52	0.44^{c}	0.35	0.33	0.45
NP	0.51	0.42^{b}	0.55	0.41^{bc}	0.36	0.30	0.37
NPK	0.53	0.27^{ab}	0.45	0.21^{ab}	0.49	0.26	0.44
NPKS	0.50	0.25^{a}	0.46	0.51^{c}	0.30	0.20	0.34
NPKS Mg	0.50	0.42^{b}	0.49	0.18^{a}	0.39	0.22	0.34
F value	0.2	5.7**	0.8	9.3***	2.7	0.8	2.4

***, **, * significant at $p < 0.001$, < 0.01, <0.05, respectively, n.s. – not significant;
[a] the same letter indicates a lack of significant differences within the treatment.

date, a significant Ca_c decline was found on plots with K and Mg, thus indicating a potential antagonism of both nutrients versus Ca. The observed nutritional status of the medium-size tubers continued until the end of the potato growth season.

The Ca_c recorded on the 120th DAP can be used as a predictor in a tuber yield forecast. The regression model obtained is as follows:

$$Y = 114.1Ca_c - 17.4 \text{ for } n = 15,\ R^2 = 0.45 \text{ and } P \leq 0.01.$$

This equation clearly shows that a Ca_c increase in the medium-size tubers at this particular stage of the potato growth indicates a higher tuber yield.

The large-size tubers

The Ca_c in-season trends for the large-size tubers were similar to the ones detected for the previously described tuber fractions (Fig. 6). In 2006,

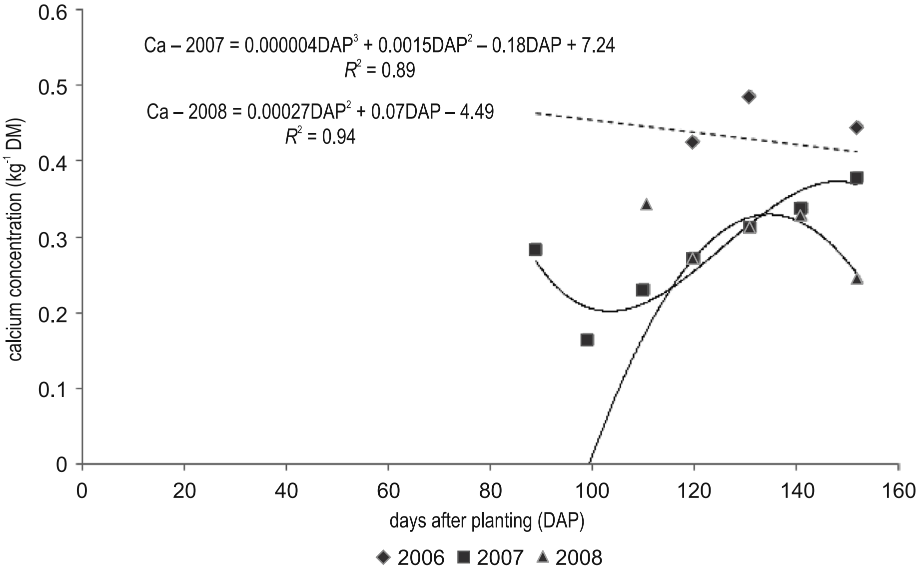

Fig. 6. Trends in calcium concentration in the large-size tubers during the potato growth season in consecutive years

it was impossible to develop a regression model reflecting the Ca_c trend in potato tubers. In 2007, this trend was best described by the 3rd degree polynomial equation. The Ca_c increased progressively in the period extending from 100 DAP to 150 DAP, finally reaching 0.38 g kg^{-1} DM. This value is much higher than recorded on 150 DAP for the small- and the medium--size tubers (Figures 4 and 5). The model explains the observed decline in Ca_c in tubers of much smaller diameter. It stresses a higher sorption potential of large-size tubers for Ca ions, inducing a decrease in Ca_c of the small- and the medium-size tubers. In 2008, the Ca_c pattern was described by the quadrate regression model. The Ca_{cmax} of 0.33 g kg^{-1} DM was achieved on 132 DAP.

The effect of the applied fertilizers on Ca_c was variable, clearly stressing the impact of the weather (Table 5). In 2006, the strongest differences between fertilization treatments were recorded at harvest. The key reason was the huge rainfall at the end of July, resulting in the secondary regrowth of tubers. The lower Ca_c in tubers on the NPKSMg plot indicates the antagonistic effect of magnesium. In 2007, the Ca_c differed significantly between the absolute control and the other fertilized plots. A slight antagonism between Ca and Mg was observed at the end of the potato growth. In 2008,

Table 5

Calcium concentration in the large-size (> 5 cm) tubers during the growing season in consecutive years (g kg^{-1} DM)

Treatments	Days After Planting (DAP)						
	89	99	110	120	131	141	152
2006							
AC	-	-	-	0.44	0.43^{a}	0.27^{a}	0.36^{ab}
NP	-	-	-	0.44	0.47^{ab}	0.31^{ab}	0.41^{cd}
NPK	-	-	-	0.43	0.49^{b}	0.34^{ab}	0.45^{d}
NPKS	-	-	-	0.43	0.50^{b}	0.40^{b}	0.39^{bc}
NPKS Mg	-	-	-	0.39	0.46^{ab}	0.37^{b}	0.33^{a}
F value	-	-	-	1.6	4.9^{*}	39.5^{***}	26.2^{***}
2007							
AC	0.24^{a}	0.19	0.23	0.23	0.26^{a}	0.23^{a}	0.30^{a}
NP	0.31^{b}	0.22	0.20	0.30	0.35^{b}	0.35^{b}	0.40^{b}
NPK	0.28^{ab}	0.16	0.23	0.27	0.31^{ab}	0.34^{b}	0.38^{ab}
NPKS	0.31^{b}	0.12	0.21	0.25	0.32^{ab}	0.36^{b}	0.39^{b}
NPKS Mg	0.30^{ab}	0.22	0.19	0.30	0.27^{a}	0.37^{b}	0.36^{ab}
F value	10.1^{***}	1.2	0.2	0.4	5.5^{**}	20.4^{***}	4.2^{*}
2008							
AC	-	-	-	0.21^{a}	0.21^{a}	0.22^{a}	0.21^{a}
NP	-	-	-	0.30^{b}	0.31^{b}	0.35^{b}	0.27^{b}
NPK	-	-	-	0.28^{b}	0.32^{b}	0.33^{b}	0.25^{b}
NPKS	-	-	-	0.27^{b}	0.32^{b}	0.34^{b}	0.27^{b}
NPKS Mg	-	-	-	0.28^{b}	0.33^{b}	0.32^{b}	0.27^{b}
F value	-	-	-	10.8^{***}	28.2^{***}	39.2^{***}	10.1^{***}

***, **, * significant at $p < 0.001$, < 0.01, <0.05, respectively, n.s. – not significant;
[a] the same letter indicates a lack of significant differences within the treatment.

Ca_c was low compared to the both previous years. The positive impact of the applied fertilizers on Ca_c was only significant with respect to the absolute control.

As pointed out by numerous researchers, Ca_c depends on a potato variety, soil content and supply of exchangeable Ca, and on the weather (Brown et al. 2012, Gunther, Palta 2008). The measured Ca_c were much lower than data presented by others, e.g. Klikocka and Głowacka (2013) or Šrek et al. (2010). This discrepancy can be explained by the tested potato varieties. Mineral composition of potato tubers as reported by Luis et al. (2011) and Brown et al. (2013) is highly variable between varieties. In the light of our study, the key reason of differences is the level of harvested yield. In a study by Šrek et al. (2010) the tuber yield was between 15 and 32 t ha^{-1} and Ca_c ranged from 0.9 to 1.2 g kg^{-1} DM. In our study, the tuber yield was twice as high, ranging from 29 to 64 t ha^{-1}, but the Ca_c in the large-size tubers was 3(4)-folds lower, ranging from 0.2 to 45 g kg^{-1} DM. These findings corroborate the hypothesis of White et al. (2009), relating the yield of tubers to nutrient concentrations in tubers. Nevertheless, the Ca_c recorded on the fertilized plots were above 250 mg kg^{-1} DM, i.e. in the range sufficient to prevent any Morphological Disorder (Palta 2010). The Ca_c in potato tubers at harvest, irrespective of their fraction, was considerably dependent on the weather, corroborating the hypothesis by Busse and Palta (2006) about the dominating impact of a water supply. However, the final Ca_c was modified by the applied fertilizers, which induced a Ca_c increase. The lowest Ca_c as obtained in 2008 was a classic example of the dilution effect. In 2007, a year with a good amount and distribution of precipitation, the Ca_c in tubers increased up to harvest. The highest Ca_c in 2006 cannot be considered as reliable data due to the secondary growth of tubers which took place in that year.

CONCLUSIONS

1. The calcium concentration (Ca_c) trends in potato organs during the potato growth season were significantly governed by the changeable weather.

2. The antagonistic effect of the applied fertilizers containing potassium and or/magnesium on the Ca_c was observed in years with water shortage.

3. The Ca_c in potato organs, averaged over the growth season, declined in the order: vines > stolons + roots > tubers.

4. The tuber yield variability can be predicted based on the Ca_c in a particular potato organ, taking into account a specific sampling date, i.e. DAP: vines – 99, small-size tubers – 120, medium-size tubers – 120.

5. The progressive increase in Ca_c along the potato growth season in

large-size tubers, concurrent with a simultaneous decline in other potato organs, points to shoots and stolons as important sources of this nutrient to the growing tubers.

REFERENCES

Brown C.R., Haynes K.G., Moore M., Pavek M.J., Hane D.C., Love S.L., Novy R.G., Miller Jr J.C. 2013. *Stability and broad-sense heritability of mineral content in potato: calcium and magnesium*. Am. J. Potato. Res. 89: 255-261. DOI: 10.1007/s12230-012-9240-9

Busse J.S., Palta J.P. 2006. *Investigating the in vivo calcium transport path to developing tuber using 45Ca: a new concept in potato tuber calcium nutrition*. Physiol. Plant., 128: 313-323. DOI: 10.1111/j.1399-3054.2006.00741.x

Camire M.E., Kubov S., Donnelly D.J. 2009. *Potatoes and human health*. Crit. Rev. Food Sci. Nutr., 49: 823-840. DOI: 10.1080/10408390903041996

Clarkson D.T. 1993. *Roots and the delivery of solutes to the xylem*. Philosophical Transactions of the Royal Society of London, Ser. B, 341: 5-17. DOI: 10.1098/rstb.1993.0086

Grzebisz W., Potarzycki J., Biber M. 2018. *The early prognosis of tuber yield based on nitrogen status in potato tops*. Plant Soil Environ., 64(11): 539-545. DOI: 10.17221/388/2018-PSE

Gunter Ch.C., Palta J.P. 2008. *Exchangeable soil calcium may not reliably predict in-season calcium requirements for enhancing potato tuber calcium concentration*. Am. J. Potato. Res., 85: 324-331. DOI: 10.1007/s12230-008-9025-3

Karlsson B.H., Palta J.P., Crump P.M. 2006. *Enhancing tuber calcium concentration may reduce incidence of blackspot bruise injury in potatoes*. HortScience, 41: 1213-1221.

Klikocka H., Głowacka A. 2013. *Does the sulphur fertilization modify magnesium and calcium content in potato tubers (Solanum tuberosum* L.*)?* Acta Sci. Pol. Hortorum Cultus, 12(5): 41-53.

Kolbe H., Stephan-Beckmann S. 1997*a*. *Development, growth and chemical composition of the potato crop (Solanum tuberosum* L.*)*. I. *Leaf and stem*. Potato, Res., 40: 111-129.

Kolbe H., Stephan-Beckmann S. 1997*b*. *Development, growth and chemical composition of the potato crop (Solanum tuberosum* L.*). Tuber and whole plant*. Potato, Res., 40: 135-153.

Luis G., Rubio C., González-Weller D., Gutierrrez A.J., Revert C., Hardisson A. 2011. *Comparative study of the mineral composition of several varieties of potatoes (Solanum tuberosum* L.*) from different countries cultivated in Canary Islands (Spain)*. Int. J. Food Sci. Tech., 46: 774-780. DOI: 10.1111/j.1365-2621.2011.02556.x

Palta J.P. 2010. *Improving potato tuber quality and production by targeted calcium nutrition: the discovery of tuber roots leading to a new concept in potato nutrition*. Potato Res., 53: 267-275. DOI: 10.1007/s11540-010-9163-0

Rosanoff A., Capron E., Barak Ph., Mathews B., Nielsen F. 2015. *Edible plant tissue and soil calcium: magnesium ratios: data too sparse to assess implications for human health*. Crop Pasture Sci., 66(12): 1265-1277. DOI: 10.1071/CP15085

Sanders D., Brownlee C., Harper J.F. 1999. *Communicating with calcium*. Plant Cell, 11: 691-706. DOI: 10.1105/tpc.11.4.691

Šrek P., Hejcman M., Kunzova E. 2010. *Multivariate analysis of relationship between potato (Solanum tuberosum* L.*) yield, amount of applied elements, their concentration in tubers and uptake in a long-term fertilizer experiment*. Field Crops Res., 118: 183-193. DOI: 10.1016/j.fcr.2010.05.009

Subramanian N.K., White Ph.J., Broadley M.R., Ramsay G. 2011. *The three-dimensonial distribution of minerals in potato tubers*. Ann. Bot., 107: 681-691. DOI: 10.1093/aob/mcr009

Tzeng K.C., Mcguire R.G., Kelman A. 1990. *Resistance of tubers from different potato cultivars to soft rot caused by Erwinia carotovora subsp. atroseptica*. Am. Potato J., 67: 287-305.

Vega S.E., Bamberg J.B., Palta J.P. 2006. *Root zone calcium can modulate GA-induced tuberization signal*. Am. J. Potato Res., 83(1) :135.

White, P.H., Bradshaw J.F., Finlay M., Dale, B., Ramsay G., Hammond J.P., Broadley M.R. 2009. *Relationships between yield and mineral concentrations in potato tubers*. HortScience, 44(1): 6-11. DOI: 10.21273/HORTSCI.44.1.6