

# Variation in tuber mineral concentrations among accessions of *Solanum* species held in the Commonwealth Potato Collection

Nithya K. Subramanian · Philip J. White · Martin R. Broadley · Gavin Ramsay

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**Abstract** The variation in tuber mineral concentrations amongst accessions of wild tuber-bearing *Solanum* species in the Commonwealth Potato Collection (CPC) was evaluated under greenhouse conditions. Selected CPC accessions, representing the eco-geographical distribution of wild potatoes, were grown to maturity in peat-based compost under controlled conditions. Tubers from five plants of each accession were harvested, bulked and their mineral composition analysed. Among the germplasm investigated, there was a greater range in tuber concentrations of some elements of nutritional significance to both plants and animals, such as Ca, Fe and Zn (6.7-fold, 3.6-fold, and 4.5-fold, respectively) than others, such as K, P and S (all less than threefold). Significant positive correlations were found between mean

altitude of the species' range and tuber P, K, Cu and Mg concentrations. The amount of diversity observed in the CPC collection indicates the existence of wide differences in tuber mineral accumulation among different potato accessions. This might be useful in breeding for nutritional improvement of potato tubers.

**Keywords** Altitude · Biofortification · Commonwealth Potato Collection (CPC) · Minerals · ICP-MS · *Solanum tuberosum* L. · Tuber

## Introduction

At least 25 mineral elements are considered essential for the normal functioning of human body and mineral malnutrition is considered to be one of the most serious challenges facing the ever-increasing global population (WHO/FAO 2004; White and Brown 2010). The dietary availability of minerals in staple

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food crops depends on the concentration of minerals in edible tissues and their bioavailability for absorption in human body (White and Broadley 2009). The bioavailability of minerals in potato (*Solanum tuberosum* L.) tubers is potentially high, because of the presence of high concentrations of  $\beta$ -carotene, protein cysteine, ascorbate and other organic and amino acids that stimulate micronutrient absorption (White et al. 2009). In addition, potato tubers contain low concentrations of anti-nutritional factors such as phytates (Frossard et al. 2000; Phillippy et al. 2004; White et al. 2016) and oxalates (Bushway et al. 1984). For these reasons, potato tubers make an excellent candidate for biofortification with mineral elements that are lacking in the human diet in populations with this as their staple food. The mineral nutritional status of food crops can be enhanced through genetic (breeding for efficient cultivars) and/or agronomic means (application of mineral fertilisers) (White and Broadley 2009).

Potato germplasm collections are maintained worldwide (Bradshaw 2000), including at the International Potato Centre (CIP, Lima, Peru), the Dutch-German Potato Collection (CGN, Wageningen, the Netherlands), the Groß Lüsewitz Potato Collection (GLKS, IPK, Groß Lüsewitz, Germany), the Potato Collection of the Vavilov Institute (VIR, St Petersburg, Russia), the US Potato Genebank (NRSP-6, Sturgeon Bay, USA), in addition to the Commonwealth Potato Collection (CPC) which is now held at the James Hutton Institute (JHI), Dundee, Scotland. Wild potato species represent a diverse gene pool which might be utilized in breeding programmes as sources of valuable genes [reviewed by Bradshaw and Ramsay (2005)].

There are good prospects for significant improvements using this diverse potato germplasm for many traits (Bradshaw et al. 2006) including, for example, starch and protein content (Jansen et al. 2001), antioxidants (Wegener and Jansen 2010), and mineral traits, such as tuber calcium concentrations (Bamberg et al. 1993, 1998; Paget et al. 2014), and iron and zinc concentrations (Paget et al. 2014). Therefore, it is useful to explore the genetic resources of the wild relatives of potatoes as a source for the genetic enhancement of tuber minerals, because they may harbour an allelic richness for useful traits including tuber mineral concentration. Identifying genes controlling these traits in diverse wild and cultivated populations will allow researchers to extend the range of variation found in modern cultivars.

The CPC is one of the major genbank containing around 1500 potato accessions, of which about two-thirds are wild potato species and the rest are cultivated types from South America (Bradshaw and Ramsay 2005). The objective of this study was to evaluate the variability of tuber mineral concentrations among CPC accessions representing the eco-geographical distribution of wild potatoes under greenhouse conditions.

## Materials and methods

### Plant material and mineral analyses

Forty-nine selected accessions of potato species (Table 1) from the CPC, originating from different habitats and altitudes, were grown in a greenhouse (15–20 plants per accession) in 2007, and tuber samples were obtained from this material for mineral analyses. The individual seedlings obtained from true potato seeds (TPS) of selected CPC accessions were sown in 15 cm diameter pots containing standard peat-based potting compost in April 2007 and the plants were grown to maturity in the greenhouse under natural daylight. The compositions of the potting compost and the base fertilizer Sincrostart (William Sinclair, Lincoln, UK) are given in Supplementary Tables 1 and 2.

Tubers from five randomly chosen CPC plants of each accession were harvested in January 2008 and stored at 4 °C for two days. As the tubers from wild species were smaller than selected cultivated genotypes, the whole tubers (with periderm) were used for mineral analyses. Five medium-sized healthy tubers, one each from the five representative plants, were selected and bulked for mineral analyses. The tubers were washed thoroughly under running tap water, rinsed in deionised water, and briefly air-dried. The air-dried whole tubers were then chopped into pieces measuring <1 cm across and were frozen at –20 °C prior to freeze-drying. Freeze-drying was carried out in a Millitorr S3921 vacuum freeze-drying unit (Millitorr Engineering Ltd., Manchester, UK) for four days. The freeze-dried samples were weighed to determine the dry matter (DM) content and then ground in a coffee blender (De'Longhi, Treviso, Italy) and were stored in re-sealable, air-tight polyethylene bags at –20 °C until analysed for their mineral

**Table 1** Details of the wild and cultivated (\*) species from the Commonwealth Potato Collection (CPC) used in the study

Series	Species <sup>a</sup>	CPC number	Country of origin	Altitude (m)
Acaulia	<i>S. acaule</i> Bitt.	2109	Bolivia	4100
Acaulia	<i>S. acaule</i> Bitt.	2113	Bolivia	4100
Acaulia	<i>S. acaule</i> Bitt.	2456	Argentina	4100
Bulbocastana	<i>S. bulbocastanum</i> Dun.	7638	Mexico	1900
Bulbocastana	<i>S. bulbocastanum</i> subsp. <i>partitum</i> (Corr.) Hawkes	7650	Unknown	1900
Circaeifolia	<i>S. capsicibaccatum</i> Cárđ.	3554	Bolivia	3000
Conicibaccata	<i>S. violaceimarmoratum</i> Bitt.	7782	Bolivia	3300
Cuneolata	<i>S. infundibuliforme</i> Phil.	2477	Argentina	4100
Demissa	<i>S. brachycarpum</i> Corr.	2922	Mexico	2500
Demissa	<i>S. brachycarpum</i> Corr.	7031	Mexico	2500
Demissa	<i>S. brachycarpum</i> Corr.	7027	Mexico	2500
Demissa	<i>S. demissum</i> Lindl.	1126	Mexico	3250
Demissa	<i>S. demissum</i> Lindl.	1345	Mexico	3250
Tuberosa	<i>S. demissum</i> Lindl.	4630	Unknown	3250
Demissa	<i>S. demissum</i> Lindl.	7524	Mexico	3250
Demissa	<i>S. hougasii</i> Corr.	7049	Mexico	2300
Demissa	<i>S. hougasii</i> Corr.	7048	Mexico	2300
Longipedicellata	<i>S. fendleri</i> A. Gray	7214	Mexico	2200
Longipedicellata	<i>S. fendleri</i> A. Gray	2605	USA	2200
Longipedicellata	<i>S. fendleri</i> A. Gray	2601	USA	2200
Longipedicellata	<i>S. hjertingii</i> Hawkes	5697	Mexico	2150
Longipedicellata	<i>S. polytrichon</i> Rydb.	3987	Mexico	2150
Longipedicellata	<i>S. stoloniferum</i> Schlechtd. et Bché.	2639	Mexico	2400
Megistacroloba	<i>S. megistacrolobum</i> Bitt.	3273	Bolivia	4000
Megistacroloba	<i>S. megistacrolobum</i> Bitt.	2482	Argentina	3600
Pinnatisecta	<i>S. cardiophyllum</i> Lindl.	5908	Mexico	2250
Pinnatisecta	<i>S. trifidum</i> Corr.	7124	Mexico	2250
Tuberosa	<i>S. canasense</i> Hawkes	3059	Peru	3500
Tuberosa	<i>S. gourlayi</i> Hawkes	7161	Argentina	3500
Tuberosa	<i>S. kurtzianum</i> Bitt. et Wittm.	6065	Unknown	1950
Tuberosa	<i>S. kurtzianum</i> Bitt. et Wittm.	3783	Argentina	1800
Tuberosa	<i>S. kurtzianum</i> Bitt. et Wittm.	5890	Unknown	1950
Tuberosa	<i>S. microdontum</i> Bitt.	3764	Argentina	3080
Tuberosa	<i>S. microdontum</i> Bitt.	3757	Argentina	2550
Tuberosa	<i>S. microdontum</i> Bitt.	3740	Argentina	1730
Tuberosa	<i>S. multidissectum</i> Hawkes	7180	Peru	4050
Tuberosa	<i>S. multidissectum</i> Hawkes	7171	Peru	4050
Tuberosa	<i>S. marinasense</i> Vargas	6020	Peru	3300
Tuberosa	<i>S. marinasense</i> Vargas	7739	Peru	3250
Tuberosa	<i>S. neocardenasii</i> Hawkes et Hjerting	7612	Unknown	1400
Tuberosa	<i>S. neorossii</i> Hawkes et Hjerting	7628	Unknown	3000
Tuberosa	<i>S. okadae</i> Hawkes et Hjerting	7775	Unknown	3100
Tuberosa*	<i>S. tuberosum</i> Group Phureja Juz. et Buk.	3672	Peru	–
Tuberosa*	<i>S. tuberosum</i> Group Andigena Hawkes	61	Bolivia	–
Tuberosa*	<i>S. tuberosum</i> Group Andigena Hawkes	573	Peru	–

**Table 1** continued

Series	Species <sup>a</sup>	CPC number	Country of origin	Altitude (m)
Tuberosa*	<i>S. tuberosum</i> Group Andigena Hawkes	7617	Unknown	–
Tuberosa*	<i>S. tuberosum</i> L. Group Stenotomum Juz. et Buk.	7699	Peru	–
Yungasensa	<i>S. chacoense</i> Bitt.	3732	Argentina	850
Yungasensa	<i>S. chacoense</i> Bitt.	3504	Unknown	1200

<sup>a</sup> Scientific authority according to Hawkes (1992)

**Table 2** Mean values and ranges for tuber dry matter (DM) and mineral concentrations observed in CPC accessions

Trait <sup>a</sup>	Unit	Mean	Range	Ratio <sup>b</sup>
DM	%	28.9	17.3–48.4	2.8
Ca	mg/g	0.2	0.1–0.7	6.7
K	mg/g	19.6	15.0–26.9	1.8
Mg	mg/g	1.4	0.8–2.2	2.5
P	mg/g	3.6	2.4–5.2	2.1
S	mg/g	1.6	1.0–2.8	2.9
Cu	µg/g	5.6	2.6–10.8	4.0
Fe	µg/g	22.0	12.2–43.6 <sup>c</sup>	3.6
Mn	µg/g	7.1	3.9–11.7	3.0
Zn	µg/g	13.6	5.9–26.9	4.5

<sup>a</sup> Mineral concentrations presented on a DW basis

<sup>b</sup> Maximum/minimum trait value

<sup>c</sup> Excluding one outlier (*S. bulbocastanum* CPC 7650) with a value 3.8-fold higher than the preceding highest value

concentration. Tuber mineral concentrations were determined on acid-digested material using inductively coupled plasma mass spectrometry (ICP–MS; ELAN DRCe; PerkinElmer, Waltham, MA, USA), following the method reported by Subramanian et al. (2011).

#### Data analyses

Differences among taxonomic groups were not tested for statistical significance because some of the series and species used in this study contained only a few accessions. Principal component analysis (PCA, based on correlation matrix) and Spearman's correlation analysis were performed in GenStat version 13.2 (VSN International Ltd., Hemel Hempstead, UK) to determine the correlations between tuber DM content and mineral concentrations. In the PCA plot, the

accessions were coded according to molecular groupings of *S. acaule*, *S. demissum*, series Tuberosa (northern species), series Tuberosa (southern species) and others, and taxonomic series according to Hawkes (1990).

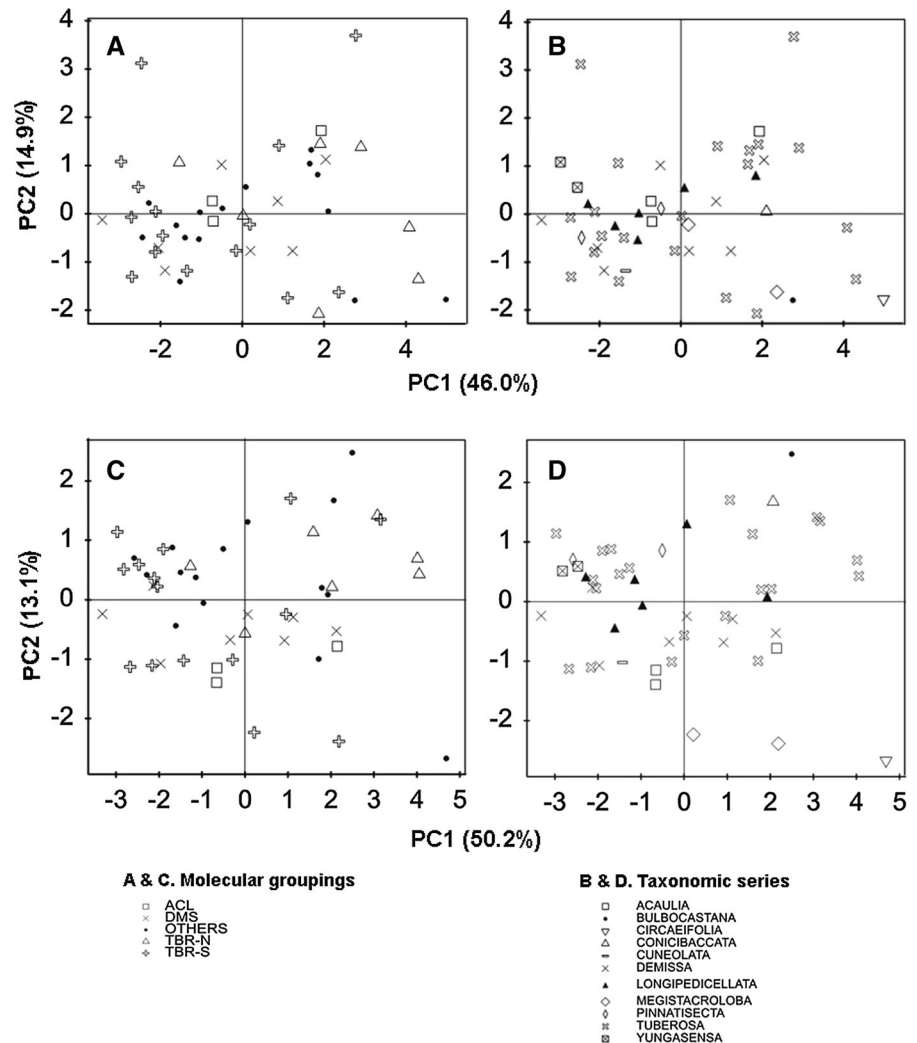
#### Results

The CPC accessions grown in the greenhouse showed a wide variation for tuber DM and mineral concentrations (Table 2). A detailed summary of the mineral composition of 44 wild accessions and five cultivated taxa is presented in Supplementary Table 3. Among the germplasm investigated, there was a greater range in the concentration of some mineral nutrients of nutritional significance (Ca, Fe and Zn; 6.7, 3.6, and 4.5-fold respectively) than others (e.g. K, P and S all less than threefold, Table 2).

To explore the patterns of variation amongst the 49 different accessions, a PCA analysis was carried out opting for the correlation matrix method using all the ten variables (DM and nine mineral elements). The first two principal components (PC1 and PC2) accounted for 60.9% (46.0 and 14.9% respectively for PC1 and PC2) of the total variability found among the 49 accessions (Fig. 1A, B). The contributions of each variable (tuber DM and mineral concentrations) to the first two PC scores are shown in the biplot in Fig. 2A.

The PC1 was positively associated with mineral elements (Mn, Cu, Fe, Zn, S, Mg, P, K and Ca), and negatively with DM. The PC2, on the other hand, was positively associated with DM, Cu, Fe and Mn and negatively with Ca and K. The Spearman's correlation analysis conducted on these accessions also established the negative relationships between DM, and Ca and K (Table 3). This trend was clearly evident when the accessions that fall within 15% of low and high

**Fig. 1** PCA plots for 49 CPC accessions based on tuber DM and mineral concentrations (**A, B**) and mineral concentrations only (**C, D**). The accessions are coded based on **A, C** molecular groupings, and **B, D** taxonomic series, as per Hawkes (1990). *TBR-S* *Solanum* series Tuberosa Southern Group (Argentina and Bolivia), *TBR-N* *Solanum* series Tuberosa Northern Group (Peru), *DMS* Mexican hexaploids in series Demissa, *ACL* series Acaulia. Mineral concentrations based on dry weight basis



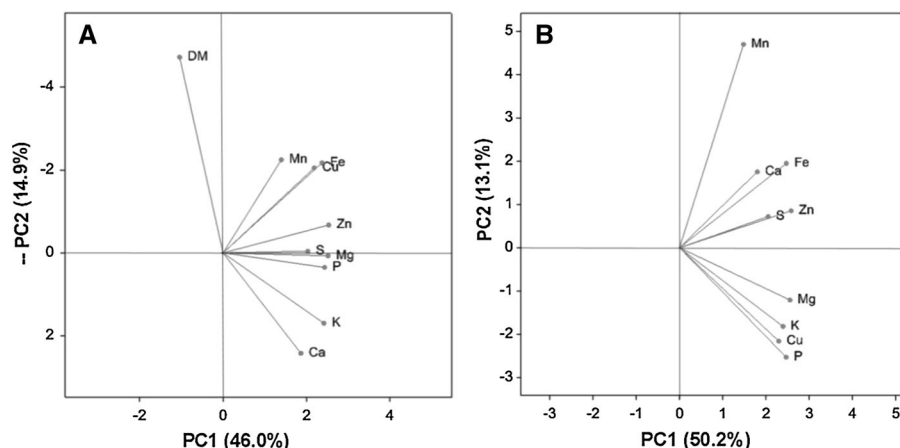
extreme values for tuber Ca, K and DM were sorted (Supplementary Table 4).

In addition, PCA analysis was also performed among the nine mineral elements excluding DM (Figs. 1C, D, 2B). In this case, the first two principal components explained 63.3% of the total variability found among the 49 accessions, with PC1 alone accounting for 50.2% of the variability (Fig. 2B). The loadings plot indicated that all minerals were positively associated with PC1, whereas PC2 was positively associated with Mn, Ca, Fe, S and Zn, and negatively with Mg, K, Cu and P. Comparing the loadings plot with and without DM, the relative positions of most minerals are similar with the exception of Ca and Cu which showed an exchange of positions with each other. Correlations coefficient

matrix (Table 3) show a negative relationship between Ca and DM, which may explain the shift in the loadings plot position of Ca. Weak separation of groups of accessions was observed in the PCA plots constructed using all mineral traits with (Fig. 1A, B) and without (Fig. 1C, D) DM as a variable. There was a strong tendency for the northern and southern series Tuberosa species to separate into two groups, and the Acaulia (ACL) and Demissa (DMS) groups also form their own space shared with a broad spread of other accessions (Fig. 1C, D).

No clear groupings of accessions were observed in the PCA plot for tuber mineral concentrations based on altitude (Fig. 3). However, significant positive correlations between altitude and tuber P, K, Cu and Mg concentrations were evident in the Spearman's

**Fig. 2** Biplots from PCA analysis for 49 CPC accessions based on (A) tuber DM and mineral traits, and (B) mineral traits alone



**Table 3** Spearman's correlation coefficients among the DM content and nine mineral elements for 49 accessions of CPC potatoes

	DM	Ca	K	Mg	P	S	Cu	Fe	Mn	Zn
DM	–									
Ca	–0.44***	–								
K	–0.37**	0.38**	–							
Mg	–0.13 ns	0.51***	0.62***	–						
P	–0.10 ns	0.34**	0.60***	0.60***	–					
S	–0.22*	0.28*	0.50***	0.32**	0.41***	–				
Cu	0.15 ns	0.16 ns	0.49***	0.62***	0.61***	0.34**	–			
Fe	–0.02 ns	0.54***	0.38**	0.63***	0.48***	0.51***	0.61***	–		
Mn	0.05 ns	0.16 ns	0.15 ns	0.28*	0.12 ns	0.33**	0.15 ns	0.46***	–	
Zn	–0.09 ns	0.44***	0.40***	0.53***	0.53***	0.53***	0.50***	0.72***	0.44***	–

Significance of the effects is given in three levels: \*  $P \leq 0.05$ ; \*\*  $P \leq 0.01$ ; \*\*\*  $P \leq 0.001$

ns non-significant

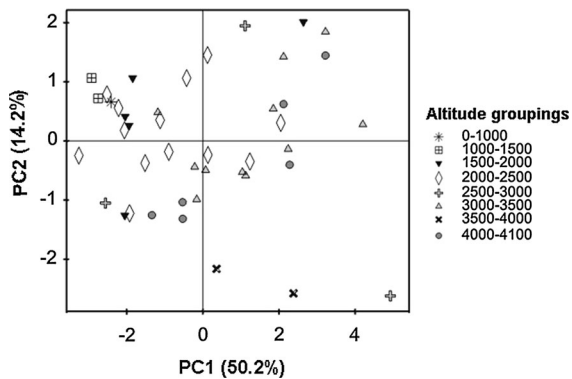
correlation analysis (Table 4). The highest correlation between tuber mineral concentration and altitude was for phosphorus.

## Discussion

The CPC accessions used in this study represented different taxonomic series and diverse geographical origins within South and Central America (Table 1), making them valuable resources for investigating the genetic variation in mineral accumulation in wild potatoes adapted to different environments. The greenhouse study demonstrated considerable variability among the wild CPC accessions for tuber DM and mineral concentrations (Table 2). The range of values

(Table 2) shows a relatively narrow spread for some minerals, such as Mg, K, P and S, and a greater spread for others, such as Ca, Fe and Zn. This suggests that breeding for high tuber Ca, Fe and Zn concentrations might have potential. Furthermore, the heritability of tuber mineral concentrations in potato were found to be moderately high (Brown et al. 2010, 2011, 2012, 2013, 2014; Haynes et al. 2012; Paget et al. 2014; Zorrilla et al. 2014), indicating the possibility of mineral biofortification by plant breeding.

Principal component analysis biplots of the accessions for tuber DM and mineral traits (Fig. 1) showed much overlap of accessions based on molecular groups and taxonomic series. However, when PCA analysis was performed using only mineral elements (Fig. 1C, D), although there was some overlap among



**Fig. 3** PCA plots for wild species CPC accessions based on tuber mineral concentrations. The accessions are grouped on the altitude of the site of collection or the mean altitude of the range for the species

accessions based on molecular grouping, some groups of accessions did form separate clusters. The Mexican hexaploids in series DMS and series ACL accessions formed separate groups. Also, the two main molecular groups within series *Tuberosa* sensu Hawkes (1990), the Peruvian species (*Solanum* series *Tuberosa* Northern group, TBR-N) and the Bolivian and Argentinian species (*Solanum* series *Tuberosa* Southern group, TBR-S), also occupied different areas in the biplot of PC1 and PC2.

Genetic variation was observed in the CPC germplasm collection for tuber DM, Ca and K, and these data corroborate those of McCann et al. (2010), Bamberg et al. (1993, 2008) and Paget et al. (2014). In the present study, tuber DM content varied from 17 to 48% (Table 2), which is in agreement with the range reported by McCann et al. (2010) in wild *Solanum* species (18–35% DM) and by Paget et al. (2014) in a breeding population of Andean landrace cultivars (13–36% DM). Research by Bamberg et al. (1993) suggests that there is a great genetic variation within *Solanum* germplasm for the ability to accumulate Ca in tubers. Bamberg et al. (1993) screened wild *Solanum* species at adequate (solution Ca concentrations—80 mg/kg) and high (800 mg/kg) Ca levels in 21 *Solanum* species (three accessions per species) in a

greenhouse study. They found that the tuber Ca concentrations ranged from 0.16 to 0.74 mg/g DW with an adequate supply of Ca, which is similar to the range reported in this study (0.10–0.67 mg/g DW, Table 2) with a comparable Ca supply, and by Paget et al. (2014; 0.04–0.78 mg/g DW). Among the *Solanum* species investigated in the current study, *S. bulbocastanum* (CPC 7638) and *S. chacoense* (CPC 3504) exhibited the highest and the lowest tuber Ca concentrations, respectively (Supplementary Table 3). Considering the species that were common between the present study and those evaluated by Bamberg et al. (1993), the ranking of genotypes were similar such that *S. chacoense* and *S. kurtzianum* had low tuber Ca concentrations and *S. gourlayi* and *S. tuberosum* Group *Stenotomum* (as *S. stenotomum*) showed high tuber Ca concentrations (Supplementary Table 4; Bamberg et al. 1993). Recently, Chung et al. (2016) reported SSR markers associated with high tuber Ca content in an F<sub>2</sub> population derived from a high-Ca accumulating wild relative, *S. microdontum* and a low-Ca accumulating, *S. kurtzianum*.

With regard to K accumulation, *S. capsibaccatum* (CPC 3554) exhibited the highest tuber K concentrations, whereas *S. chacoense* (CPC 3504) showed the lowest K concentration (Supplementary Table 3), a 1.8-fold range for tuber K concentrations (Table 1). In a study assaying tuber K concentrations in different *Solanum* species, Bamberg et al. (2008) found large tuber K concentrations in *S. acaule*, *S. chacoense*, *S. okadae* and *S. pinnatisectum*.

In general, accessions with small tuber DM content had large concentrations of Ca and K and vice versa (Supplementary Table 4). A negative correlation between tuber DM content and Ca, Fe, and Zn concentrations, expressed on a dry weight basis, was reported by Paget et al. (2014). About 65–75% of DM content in tubers is made up of starch (Burton 1989). Tuber mineral concentrations (including Ca and K) have been found to decrease following DM (starch) accumulation during tuber bulking (Kolbe and Stephan-Beckmann 1997). Within the tuber, Ca is

**Table 4** Spearman's correlation coefficients between the altitude (m) and nine mineral elements for wild species CPC accessions

	Ca	K	Mg	P	S	Cu	Fe	Mn	Zn
Altitude	0.35**	0.54***	0.51***	0.65***	0.29**	0.52***	0.37**	−0.10 ns	0.37**

Significance of the effects is given in three levels: \*  $P \leq 0.05$ ; \*\*  $P \leq 0.01$ ; \*\*\*  $P \leq 0.001$

ns non-significant

concentrated around the periphery and decreases towards the centre (Subramanian et al. 2011). As Ca is relatively immobile in the phloem (Kärenlampi and White 2009), its concentration tends to decrease with increasing DM accumulation. On the other hand, K is mobile in the phloem and its concentration was found to be higher at the bud end than the stem end of the tuber (Subramanian et al. 2011). Within cells K is required for many physiological functions, including osmoregulation, enzyme activation and membrane transport processes (White and Karley 2010). Nitsos and Evans (1969) first observed that starch synthesizing enzymes have a specific requirement for K and about 1.8% of K (as a proportion of DM) is critical for high starch concentrations in potatoes (Forster and Beringer 1983; Lindhauer and De Fekete 1990). However, tuber K concentrations above 2% DM were found to reduce starch content (Marschner and Krauss 1980), which could be explained in terms of an osmotic optimum for starch synthesis (Oparka and Wright 1988).

The association of S and Zn, as evident from PCA plots, might be attributed to the similar phloem mobility of these elements (Kärenlampi and White 2009). On the other hand, neither Fe nor Ca have high phloem mobility (Kärenlampi and White 2009), and the association of Fe and Ca might be due to the high entrapment of these minerals by periderm of the potato tuber, since the surface layers of potato tubers contain 55 and 34% of total tuber Fe and Ca concentrations, respectively (Subramanian et al. 2011).

Potatoes are adapted to grow in different habitats including high altitudes. There are no studies reported on mineral concentrations in potato tubers grown at different altitudes. Results from this study showed that tuber P, K, Mg and Cu concentrations increased as the altitude of the habitat of a species increased, and that phosphorus is the mineral found to be most strongly linked with altitude. Kitayama and Aiba (2002) suggest that trees on Mount Kinabalu, Borneo, maintain net assimilation rate with increasing altitude by increasing foliar N and P, where soil P deficiency does not inhibit this process. Work in the Andes suggests that P availability may not be strongly linked to altitude (Fisher et al. 2013), which would support a mechanism for P accumulation which is not driven by adaptation to low P availability. However, whatever the adaptive forces driving this trend, the higher concentrations of tuber minerals in high altitude species provide useful variation for breeding for these

traits. These minerals include those of greatest importance to human nutrition (Ca, Fe and Zn) as well as P which has importance for productivity and sustainable production.

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#### Compliance with ethical standards

**Conflict of interest** The authors declare no conflict of interest.

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