Genetic differences in macro-element mineral concentrations among 52 historically important tomato varieties

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Abstract

Tomato (*Solanum lycopersicum*) fruit quality and yield are highly dependent on adequate uptake of nutrients. Potassium, magnesium and calcium are essential elements that influence fruit quality traits such as colour, uniformity of ripening, hollow fruit, fruit shape, firmness and acidity. Sodium is not an essential element for tomato and can detrimentally compete with the absorption of potassium and calcium. Daily intakes of potassium, magnesium and calcium in human diets are typically below healthful levels, while sodium intake is often excessive. The objective of this study was to compare 52 diverse commercially important varieties of tomato for concentrations of potassium, magnesium, calcium and sodium in fruits. The tomatoes were produced in replicated plots in Geneva, NY in 2010 and 2011. Multiple fruits per plot were harvested vine-ripe, homogenized and assayed for cations. Analysis of variance showed significant differences among the 52 varieties for all four traits, i.e. cation concentrations (df = 51, $P < 0.0001$–0.0034) and no significant differences between years for any trait (df = 1, $P = 0.3432$–0.6770). Factor analysis showed a strong interrelationship between potassium and magnesium that was independent of calcium and sodium. Potassium and magnesium were highly significantly correlated with each other ($r = 0.64$, $P < 0.0001$). No other correlations between pairs of traits were observed. Results supported a genetic basis for potassium, magnesium, calcium and sodium concentrations that was consistent across environments (i.e. years). Results can contribute to the development of cultivars with favourable cation profiles in terms of human health and fruit quality.

Keywords: calcium, genetic variation, magnesium, multivariate analysis, nutrients, potassium, sodium

Introduction

Nutrient levels will influence both yield and fruit quality in tomato production. Uptake and use of potassium, magnesium, calcium and sodium is a complex process that is dependent on environmental factors such as light, temperature, humidity, moisture, soil pH and the levels of other nutrients (Davies *et al.*, 1981; Adams, 1986). Potassium, magnesium and calcium are essential elements that influence fruit quality traits such as colour, uniformity of ripening, hollow fruit, fruit shape, firmness and acidity (Adams, 1986 and references therein, Hartz *et al.*, 2005).

Potassium is an essential element that helps regulate many metabolic processes (Adams, 1986). Measured as % dry matter in parts of a tomato plant, the highest potassium content was associated with the fruit, while % calcium and magnesium were relatively lowest in the fruit (Kidson *et al.*,

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1953). Fruit titratable acidity, and hence flavour, is dependent on potassium (Davies et al., 1981). Magnesium is the central atom of a chlorophyll molecule, is involved in phosphate transfer and is an activator for certain enzymatic reactions. Magnesium has not been directly associated with fruit quality except under conditions of severe deficiency, which will reduce the size and overall attractiveness of the fruit (Passam et al., 2007). Calcium is an important constituent of cell membranes and cell walls. A localized calcium deficiency in the distal end of the fruit can cause blossom end rot, a blackening around the stylar scar (Adams, 1986; Adams, 2002). Sufficient calcium levels can help prevent shoulder check crack (Lichter et al., 2002; Huang and Snapp, 2004). Sodium is not an essential nutrient although in some tomato genotypes it can serve to compensate for potassium deficiency (Walker et al., 2000).

Micronutrients and minerals provided by fruits and vegetables are important to human health and nutrition. A survey of 13 essential elements in 20 diverse human diets showed that on average, sodium was consumed at the highest levels, followed by potassium, calcium and magnesium (Mir-Marqués et al., 2016). Many physiological and pathological processes in the body are dependent and influenced by electrolytes such as sodium and potassium (Pohl et al., 2013). Blood pressure and cardiovascular health are closely connected to sodium, potassium, calcium and magnesium intake (Karppanen et al., 2005). Tomatoes serve as a major source of nutrients in human diets because they are widely cultivated and consumed in many forms (e.g. fresh, canned, sundried, paste, sauce, juice and soup).

A better understanding of the genetic diversity of mineral concentrations in tomato cultivars will help breeders to improve their content to benefit human health and plant health (Stommel, 2007; Capel et al., 2017). The objectives of this study were to (i) characterize a diverse set of 52 USA commercially important tomato varieties for their macro-element content (K^+, Ca^{2+}, Mg^{2+}, Na^+) using replicated trials across two environments; (ii) gain insight regarding the interrelationships among K^+, Ca^{2+}, Mg^{2+} and Na^+ concentrations; and (iii) identify those varieties useful for developing new cultivars with enhanced macro-element profiles or for exploring the genetic basis controlling the accumulation of macro-elements in tomato fruits.

Materials and methods

Plant materials

Fifty-two phenotypically diverse tomato varieties (Table 1, online Supplementary Table S1) were sampled from the USDA-ARS Plant Genetic Resources Unit (PGRU) germplasm collection. The varieties were commercially important

Table 1. Germplasm of 52 varieties of tomato (*Solanum lycopersicum*) accessions grown in field trials and sampled for fruit cation concentrations

Accession identifier: Accession name	Accession identifier: Accession name
PI 645398: 466 Jungs Improved Wayahead	PI 270234: Loran Blood
PI 601411: 71–75	PI 270236: Manalucie
PI 601342: 888	PI 309669: Manapal
PI 584456: Allure	PI 600930: Moran 3053
PI 265955: Anahu	PI 601192: Mystro
PI 601136: Baxter's Early Bush Cherry	PI 600906: NC 50-7
PI 601449: Beall's Gourmet	PI 601512: NC 8288
PI 341132: Campbell 1327	PI 270239: Ohio WR Brookston
PI 279565: Caro Red	PI 559912: Pink Mozark
PI 600927: Castlerock	PI 270241: Pinkshipper
PI 600907: Cherokee	PI 601396: Ramsay
PI 341124: Chico Grande	PI 647513: Red Pear
PI 645390: CMVF 232	PI 647316: Rosa
PI 339914: Coldset	PI 451967: Sub-Arctic Maxi
PI 601629: Colusa	PI 601450: Sun 1643
PI 601165: DNAP-9	PI 270249: Sunray
PI 270228: Fireball	PI 601177: Tioga
PI 645214: Floradel	PI 451970: Trimson
PI 601601: Florida 7060	PI 638513: UC 82B
PI 645391: Florida MH-1	PI 270212: Valiant
PI 645389: H 2990	PI 645361: Vendor
PI 341133: Heinz 1350	PI 645370: Venus
PI 647122: High Crimson	PI 370091: Vision
PI 601178: Horizon	PI 636302: Wabash
PI 309672: Hotset	G 33008: Walter
PI 452018: Jubilee	
PI 303749: KC 146	

in the USA between the 1930s and 1990s. Seventeen were considered highly unique based on PVP (plant variety protection) certificates (http://www.ars-grin.gov/cgi-bin/npgs/html/pvplist.pl; online Supplementary Table S1) as processing, fresh market or breeding types. The tomatoes were produced in experimental trials in Geneva, NY in 2010 and 2011. Two plots of five plants of each entry were planted in a randomized complete block design. Fully ripe fruits were harvested from random positions on the vines, rinsed with reverse osmosis water and blotted dry. Pieces of one to ten fruits per plot were homogenized in a Waring Commercial blender (model 51BL30 7010*, Torrington, CT) after removing scars and any diseased or damaged tissue. Homogenates were immediately flash-

frozen in 15 ml aliquots using liquid nitrogen and a SPEX SamplePrep 2600 Cryo-Station (NJ), stored at −80°C and shipped overnight on dry ice to Albany, CA for analysis. Additional details of field conditions and sample preparation were reported in Breksa et al. (2015).

Materials and chemicals

Methanesulfonic acid was obtained from Sigma-Aldrich (St. Louis, MO). Standard solutions used for the cation determinations by HPLC were purchased from Thermo Scientific (Waltham, MA, USA) and Inorganic Ventures (Christiansburg, Virginia). Water was deionized to ≥18.1 MΩ/cm resistance using a Barnstead NANOpure Deionization System (Dubuque, IA). Water was further filtered through a 0.45 μm-type HA membrane filter (Millipore, Billerica, MA) prior to use.

Determination of cation concentrations

Cryopreserved tomato homogenates were thawed in a 20°C water bath for 30 min and then transferred to centrifuge tubes to be clarified by centrifugation at 38,729 g (4°C) for 10 min using a Sorvall RC 5 Plus centrifuge (Thermo Scientific, Waltham, MA, USA). The clarified liquid was collected and filtered through a 0.2 μm Nalgene syringe filter (Thermo Fisher Scientific, Fair Lawn, NJ) and used for ion chromatography (IC) analysis. The filtered solution was diluted 2× with water prior to IC analysis.

The HPLC system consisted of a Paradigm MS-4 pump (Michrom Bioresources, Inc., Auburn, CA) and HP 1050 Series Autosampler (Agilent, Foster City, CA). The separation of cations was performed using a Dionex IonPac CS12A column (250×2 mm^2) and a guard column of the same material maintaining at 40°C, with an isocratic mobile phase of 18 mM methanesulfonic acid. The eluant was directed into a Dionex CSRS 300 2 mm suppressor (self-regenerating suppressor) to remove the conductive eluant. A Dionex SRC-1 SRS controller controlled the suppressor. A Pharmacia Biotech Conductivity Monitor (GE Health Care Piscataway, NJ) equipped with 0.2 μl conductivity flow cell was used to perform the detection and quantification of the cations. The flow was 0.250 ml/min and an injection volume of samples and standards was 2.5 μl. Total runtime for each sample was 20 and 17 min for the standards, blank and controls. The system was controlled using Xcalibur (version 1.4) and an SS-420× A/D converter was used to capture the signal from the conductivity detector. Integration of individual peak areas was done using Xcalibur and quantification was based on external calibration curves of each cation (3.125–1500 mg/l). Values are reported as mg/l ± SD and represent the average of a triplicate analysis with a standard curve.

Statistical analyses

Statistical analyses were performed in SAS ver. 9 (SAS Institute Inc, 2011). To test for significant differences in cation concentration among entries, PROC GLM was used for an analysis of variance (ANOVA) with cation concentration used as the dependent variable (208 observations per cation). Because genotype × environment (G × E) (i.e. entry × year) was non-significant, the G × E term was pooled with the error term for significance testing to improve statistical power. Differences between environments were tested using 'replication within a year' as the error term.

Principal components analysis (PCA) was used to find the number of components (combinations of variables) that explained as much of the total variance as possible. Correlations (PROC CORR) were performed between the principal components (PCs) and their original variables to illustrate which variables contributed the most to the major PCs. PCA results of 52 entries by two environments were plotted using a 95% prediction ellipse. A prediction ellipse defines a region for predicting a new observation in a population. It also approximates a region containing a specified percentage of the population (SAS Institute Inc, 2011). We used the prediction ellipses to identify potential outliers and to visualize the consistency of an accession's cation profile between the two environments.

Factor analysis (PROC FACTOR) was performed to find the factors, which are combinations of the four cation variables that explained interrelationships among the original variables. Pearson correlation (PROC CORR) was used to test whether two traits varied together for the six possible pairwise comparisons among the four cations.

The STANDARD procedure was used to standardize the four cation variables to mean = 0 and variance = 1 and fast cluster (PROC FASTCLUS) was used to perform cluster analysis of the 52 entries. This method uses an algorithm to assign each observation into one and only one cluster based on distance from the mean. This is a good method to detect outliers (cluster of one). Hierarchical clustering of the 52 entries based on their means was performed using PROC CLUSTER and the average linkage method.

A two-sample t-test assuming unequal variances (Sokal and Rohlf, 1981) was used to test for significant differences between mean concentrations of K$^+$, Ca^{2+}, Mg^{2+} and Na$^+$ in fresh market versus processing types.

Results

Cation concentrations

All concentration estimates for the four cations are reported in online Supplementary Table S2. Concentrations of K$^+$ ranged from 1378.4 mg/l (CMVF 232) to 2960.0 mg/l
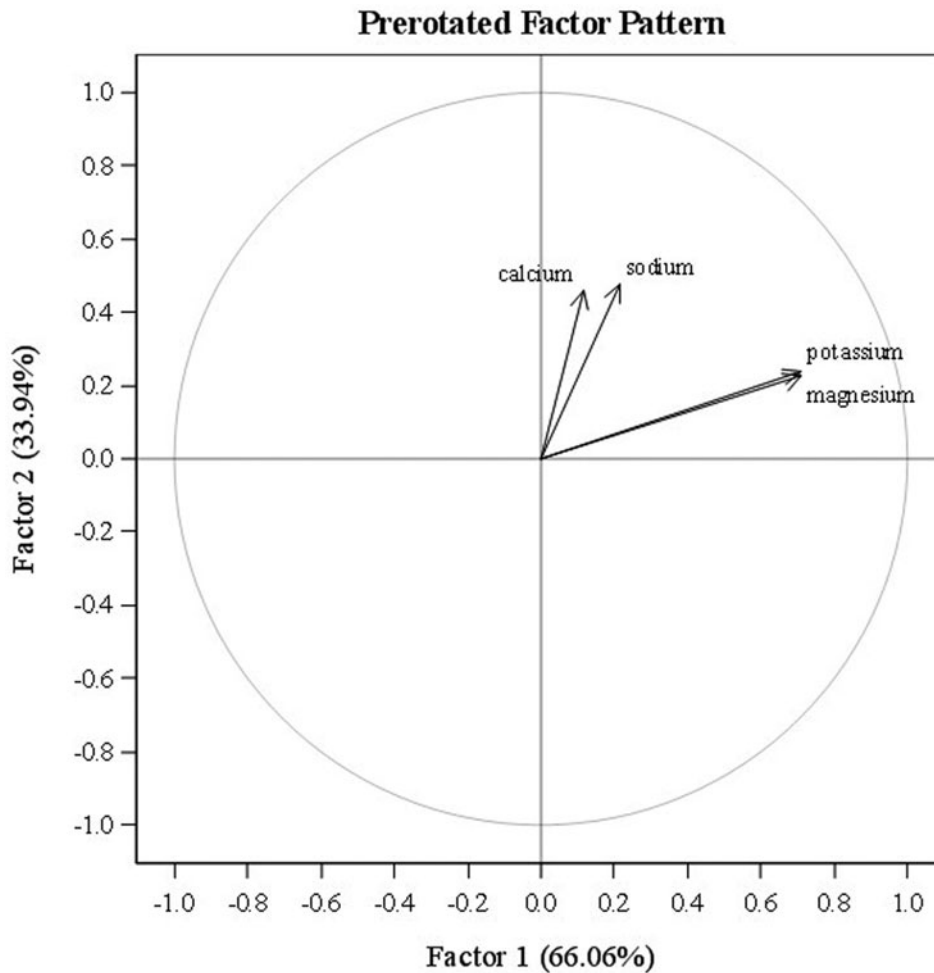
Prerotated Factor Pattern

Fig. 1. Factor analysis of four cation traits (sodium, potassium, magnesium and calcium) for 52 tomato accessions grown in replicated plots in two environments ($n = 208$). Prerotation method: varimax.

(Walter) in 2010, and from 1337.1 mg/l (Wabash) to 2628.7 mg/l (UC 82B) in 2011. The averages for 2010 (1993.1 ± 305.16 mg/l) and 2011 (2043.5 ± 249.50 mg/l) were not significantly different. Averaged across all four experimental replicates, Wabash (1565.9 ± 180.99 mg/l) and Jubilee (2401.4 ± 290.30 mg/l) were the samples with the lowest and highest K^+ concentrations, respectively. Cultivars with the least and greatest variability were Coldset (2.3% CV) and 466 Jung's Improved Wayahead (27.6%CV), respectively.

Mg^{2+} concentrations were 16–50-fold less than K^+ concentrations and ranged from 51.4 mg/l (Vision) to 135.1 mg/l (High Crimson) in 2010, and from 44.7 mg/l (Venus) to 145.1 mg/l (Cherokee) in 2011. The averages for 2010 (87.3 ± 19.33 mg/l) and 2011 (82.42 ± 17.72 mg/l) were not significantly different. Averaged across all four experimental replicates, Baxter's Early (62.6 ± 10.77 mg/l) and Rosa (62.6 ± 9.13 mg/l) were the samples with the lowest Mg^{2+} concentrations. Sunray (112.5 ± 10.77 mg/l) had the highest average

Mg^{2+} concentration. Cultivars with the least and greatest variability were Colusa (6.0% CV) and Venus (38.7% CV).

Concentrations of Ca^{2+} ranged from 9.0 mg/l (Horizon) to 47.7 mg/l (H 02990) in 2010, and from 6.9 mg/l (Rosa) to 33.6 mg/l (Sub-artic Maxi) in 2011. The averages for 2010 (19.9 ± 7.37 mg/l) and 2011 (19.0 ± 5.52 mg/l) were not significantly different. Averaged across all four experimental replicates, Tioga (11.0 ± 2.32 mg/l) and H 2990 (30.8 ± 11.36 mg/l) were the samples with the lowest and highest Ca^{2+} concentrations, respectively. Cultivars with the least and greatest variability were Vendor (5.9% CV) and Manapal (48.6% CV), respectively.

Concentrations of Na^+ ranged from 5.2 mg/l (Allure) to 27.7 mg/l (H 1350) in 2010, and from 5.8 mg/l (NC 50-7) to 22.5 mg/l (466 Jung's Improved Wayahead) in 2011. The averages for 2010 (12.4 ± 3.99 mg/l) and 2011 (11.4 ± 2.79 mg/l) were not significantly different. Averaged across all four experimental replicates, NC 50-7 (7.4 ± 1.47 mg/l) and H 1350 (19.4 ± 6.52 mg/l) were the samples
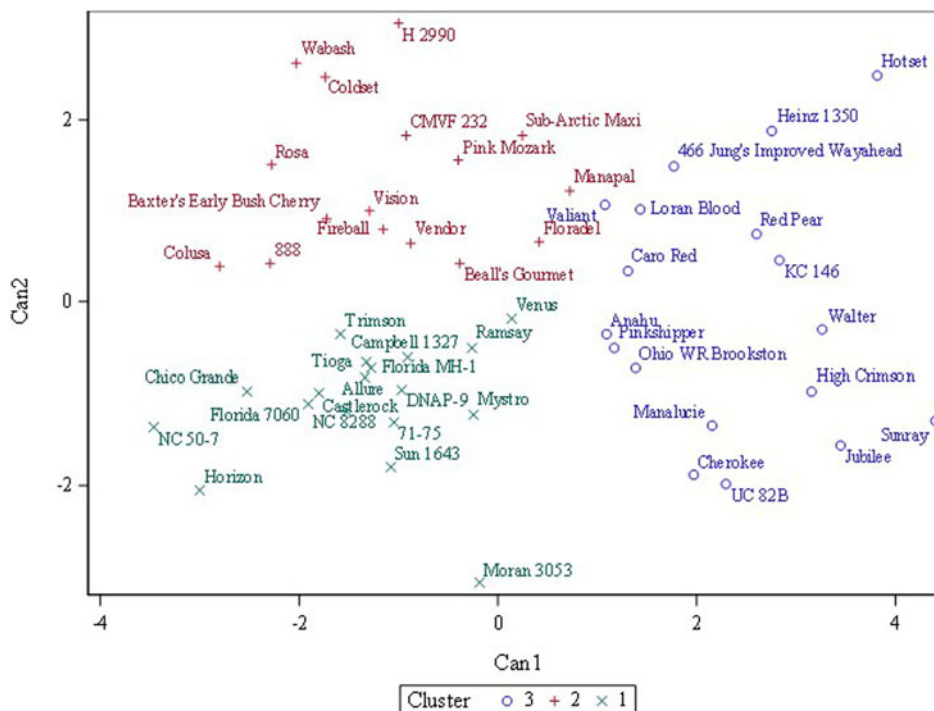
Fig. 2. Fast cluster results for three clusters of 52 tomato accessions grown in replicated plots in two environments ($n = 208$) based on four cation traits (sodium, potassium, magnesium and calcium). The statistical method identifies initial predefined number of clusters and then applies an iterative algorithm that minimizes the sum of squared distances from the cluster means.

with the lowest and highest Na^+ concentrations, respectively. Cultivars with the least and greatest variability were Colusa (5.9% CV) and Vision (46.7% CV), respectively.

Calcium was the only cation that showed a significant difference in concentration (df = 28, $P < 0.0001$) between fresh market ($n = 34$, mean = 20.9 mg/l) and processing ($n = 14$, mean = 15.5 mg/l) accessions. However, the ranges of the means were similar for the two groups (11.9–30.6 versus 11.0–24.6, respectively).

Multivariate statistical analyses

The 52 tomato accessions consisted of 14 processing, 34 fresh market or garden types, three lines developed primarily for breeding (888, CMVF 232 and H 2990) and one ornamental type (Allure) (online Supplementary Table S1), although these descriptive categories were not mutually exclusive. Average concentrations of K^+, Ca^{2+}, Mg^{2+} and Na^+ varied widely among the 52 tomato accessions (online Supplementary Table S3). ANOVA showed significant differences among accessions for all four traits (df = 51, $P < 0.0001$–0.0034) and no significant differences between years for any trait (df = 1, $P = 0.3432$–0.6770).

The first two PCs explained 75.4% of the total variation among the 52 replicated plots (online Supplementary Fig. S1). All four cations were significantly correlated with

PC1 ($r = 0.57$ to 0.83, $P < 0.0001$) and with PC2 ($r = -0.41$–0.61, $P < 0.0001$) (online Supplementary Fig. S2). The negative r values for K^+ and Mg^{2+} indicated that PC2 was correlated with decreasing levels of those two cations. Of 104 observations, only four (H 2990, Heinz 1350, Hotset and Wabash) fell slightly outside of the 95% prediction ellipse in the PCA plot (online Supplementary Fig. S1). No extreme outliers were observed.

Factor analysis showed a strong interrelationship between K^+ and Mg^{2+} that was independent of Ca^{2+} and Na^+ (Fig. 1). K^+ and Mg^{2+} were highly significantly correlated with each other ($r = 0.64$, $P < 0.0001$). No other correlations between pairs of traits were observed.

Three or four clusters were used in fast cluster analysis to discover whether *a priori* designated categories (fresh, processing, other) or (fresh, processing, breeding, ornamental) clustered together. Three clusters gave the best separation although the categories did not cleanly separate (Fig. 2). Fresh-consumption types were widely dispersed across the x and y-axes while processing types mostly clustered in the lower left-hand quadrant (Fig. 3). Online Supplementary Fig. S3 showed that when visualized as a hierarchical set of clusters, H 2990, Heinz 1350 and Hotset were most distinct (consistent with the 95% prediction ellipse), but no pattern of fresh-consumption versus processing types was observed.
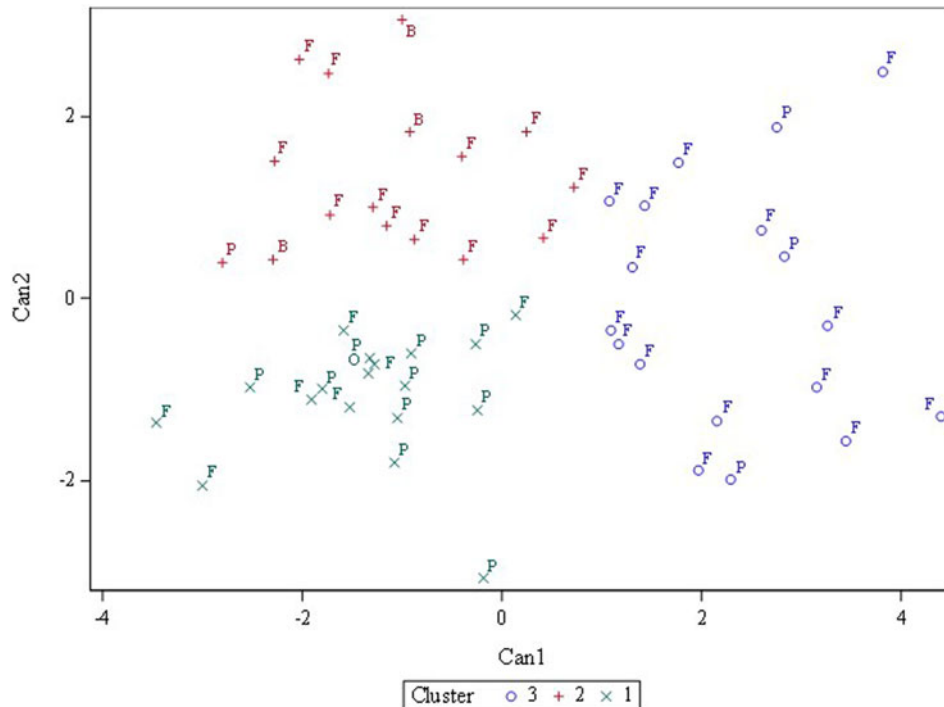
Fig. 3. Fast cluster results for three clusters with accessions labelled based on primary usage: P, processing; F, fresh market; B, breeding; O, ornamental.

Discussion

Vegetable crops are potentially rich sources with which to improve nutritional components of diets, and biochemical profiling of GeneBank collections can support these efforts (Akundabweni *et al*., 2010; Kaushik *et al*., 2015; Rahim, 2015). Cations K^+, Mg^{2+}, Ca^{2+} and Na^+ were at measureable concentrations in all of the sampled tomato varieties in our study. The difference between the lowest and highest average concentrations of each cation was approximately two- to threefolds (Table 2). K^+ was the most abundant cation. Comparisons of ranges of concentrations showed that Mg^{2+} levels were 3–7% those of K^+, and Ca^{2+} levels were 10–49% those of Mg^{2+} (Table 2). Overall, Na^+ concentrations were slightly more than half the concentration Ca^{2+} (64% on average, online Supplementary Table S3). Samples with the highest average K^+ concentrations did not contain the highest average concentrations of the other three cations.

Calcium and magnesium are well known as mineral elements that are frequently deficient in human diets (White and Broadley, 2009). Calcium was reported to be inadequately supplied for 3.5 billion people globally (Kumssa *et al*., 2015). Potassium has also been reported to be grossly deficient due to processing and preparation practices that increase sodium and consequently decrease natural levels of potassium in foods. Daily sodium consumption

exceeded recommended amounts in an estimated 99% of the adult population globally (Powles *et al*., 2013; Webb *et al*., 2017).

In pounds of vegetables consumed on average per capita per year, tomato ranks second in the USA, after potato and followed by onion and lettuce (Economic Research Service/USDA, 2017). Although calcium content in fresh tomato was estimated to be approximately one-quarter of the amounts found in lettuce and onion (Mayer, 1997), the tomato is consumed at greater than fourfold level relative to lettuce or onion (32₤ versus 7₤ per capita) (Economic Research Service/USDA, 2017). Tomato ranked slightly higher relative to lettuce and onion in magnesium and potassium (Mayer, 1997). Tomato paste and juice are both recognized as rich sources of dietary potassium (Weaver, 2013), and nutrients are concentrated in these processed forms relative to fresh fruit. Compared with two other major solanaceous crops, eggplant and pepper, the tomato was higher in potassium and similar in calcium, magnesium and sodium content (online Supplementary Table S4).

Mineral deficiencies in the human diet are a problem in both developing and industrialized nations. Fruits and vegetables with low mineral contents are aggravating this problem (Sands *et al*., 2009), and even in situations where consumers are obtaining sufficient caloric intake, they are not in many cases obtaining sufficient minerals.

Table 2. Means, sample sizes, standard deviations, and ranges of each of four cations measured in 52 tomato accessions

Trait	n	Mean	Std dev	Minimum mean	Maximum mean
Sodium	52	11.9	2.12	7.4	19.4
Potassium	52	2018.3	180.72	1565.9	2401.4
Magnesium	52	84.9	11.28	62.6	112.5
Calcium	52	19.5	4.57	11.0	30.8

Concentrations were measured in mg/l.

Results from the analysis of historic micronutrient content of foods in the USA (Davis *et al.*, 2004) and UK (Mayer, 1997) suggested that nutritional and mineral content of commercial cultivars decreased over the last 60 years. The authors of these reports hypothesized that the apparent decrease may be an unintended consequence of modern agricultural practices (reliance on chemical fertilization and intensive cultivation), as well as breeding programmes directed at improving yield, appearance, and shelf-life, at the cost of other characteristics.

We grouped the cultivars in our study by decade (1940–1990) using their approximate date of release or commercial introduction to see if our results supported a trend in decline in nutrient content over time as was observed in similar studies (Mayer, 1997; Davis *et al.*, 2004). We found no relationship between decade and K^+, Mg^{2+}, Ca^{2+} and Na^+ content (results not shown). It is possible that a larger sample size is needed to detect a correlation. Alternatively, the results may depend on sample selection (e.g. cultivar, harvest season, location) or analytical methods. This possibility is supported by an investigation of mineral levels in 44 types of Australian fruits and vegetables in which it was reported that no significant differences or changes occurred over time from 1980 and 2000 (Cunningham *et al.*, 2001).

Regardless of measurable trends, there is an opportunity to improve the mineral content of fruits and vegetables through the development of new varieties through breeding or optimized production methods, or a combination of both. Biofortification of fruits and vegetables may be accomplished through breeding targeting higher mineral contents or varieties that uptake minerals placed in the soil with higher efficiency. In an analysis of modern soyabean cultivars, Kusano *et al.* (2015) reported that seed mineral profile was a discerning factor for identifying varieties and the environment in which they were grown.

The nutritional content of tomato fruits is influenced by both genotype and environment. An overabundance of other cations will lead to the reduced uptake of more desirable cations. For example, excessive ammonium concentrations were shown to reduce calcium, but not potassium and magnesium contents of tomato fruits (Barker and Ready, 1994), and excessive potassium uptake can reduce calcium and magnesium uptake (Adams, 1986). Sodium can inhibit adequate absorption of potassium and calcium and is generally studied in terms of salt stress and improvement of salt tolerance (Apse and Blumwald, 2002; Giuffrida *et al.*, 2009). Kleiber (2014) recently reported increasing levels of manganese resulted in reduced fruit levels of potassium (up to 30% reduction), magnesium (two to threefold decrease) and calcium (three to fourfold decrease). Organic production of tomatoes was associated with the increased content of calcium, magnesium and potassium (Zoran *et al.*, 2014). However, cultivar was a greater factor than growing conditions when comparing organic versus conventional production methods (Ordóñe-Santos *et al.*, 2011; Zoran *et al.*, 2014).

Based on all evidence, surveying tomato germplasm for nutrient content is a useful strategy to identify varieties with alleles that markedly alter the relative levels found in fruit. Many tomato QTL or association mapping studies have benefitted from diversity between species, which circumvents the lack of genetic variation within *Solanum lycopersicum* (e.g. Capel *et al.*, 2017), however, intraspecific variation can be successfully used if a broad array of genotypes is sampled (Chaïb *et al.*, 2006; Prarthana *et al.*, 2014; Zhang *et al.*, 2016). In the current study, Wabash, a fresh market type adapted to the Midwestern USA, was very low in K^+ relative to the other accessions (online Supplementary Fig. S4). Breeding line H 2990 and fresh market type Hotset were high in Ca^{2+}, and processing type Heinz 1350 was high in Na^+ (online Supplementary Fig. S4). Although our study revealed a strong interrelationship between K^+ and Mg^{2+} concentrations, other cultivars in other environments revealed different patterns of relative ratios or correlations among K^+, Mg^{2+}, Ca^{2+} and Na^+ (Fernández-Ruiz *et al.*, 2011; Nour *et al.*, 2013; Ozturkoglu-Budak and Aksahin, 2016; Watanabe *et al.*, 2016; Sager, 2017). These studies have all shown that nutrient contents fall below concentrations required to easily consume daily recommended levels of fresh fruit. However, the differences among genotypes can serve as a tool with which to study genes and regulatory factors necessary for the development of biofortified cultivars (Watanabe *et al.*, 2016; Capel *et al.*, 2017).

Supplementary material

The supplementary material for this article can be found at https://doi.org/10.1017/S1479262117000417

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