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Delving into the Bioactive and Nutritional Compounds in Bolivian Accessions of Tomato (*Solanum lycopersicum* L.) Fruits: Relationship with Genetic, Phenotypic, and Origin Indicators

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ABSTRACT: Bolivia is one of the centers of origin of tomatoes. As a result, a wide array of tomatoes exists in the country, containing a variety of bioactive compounds that are beneficial for plants and human consumption. Here, we evaluated, by the use of high performance liquid chromatography−diode array detection−mass spectrometry (HPLC−DAD−MS), 29 accessions from the Bolivian gene bank for content and effects of indicators on polyamines, carotenoids, vitamin C, and their relationships. The content of the bioactive compounds varied significantly (2−500-fold) among accessions with the exception of lutein, spermidine, and spermine. Among the indicators, specifically, the 'genotype group' and the 'locality of origin' had a relationship with the content of carotenoids and vitamin C. However, despite the large variation in bioactive compounds among the genotypes, few determinants of this phenomenon were identified in the present study. Therefore, to distinguish genotypes that produce large amounts of bioactive compounds for breeding purposes or product development, broad-based screening is necessary instead of focusing on indicators or determinants.

KEYWORDS: *carotenoids, lycopene, polyamines, vitamin C, Bolivian tomato germplasm, quality traits*

INTRODUCTION

Tomato (*Solanum lycopersicum*) is regarded as a fruiting vegetable[1] because tomato fruits are eaten as vegetables. Among the vegetables, tomato has the second largest production volume annually, and it is a major vegetable produced in most countries around the globe.[2] Tomato is consumed both fresh and processed, and is known to have a high content of nutritional and bioactive compounds, as well as a wide range in aroma, flavor, and color.[3] Nutritional compounds present in tomatoes are sugars, vitamin C, pro-vitamin A, and minerals.[4] Bioactive compounds reported in tomatoes are carotenoids and polyamines, suggested to have specific health benefits. Some carotenoids are also known as vitamin A precursors.[5]

Carotenoids have been categorized as potent antioxidants and bioactive compounds, which is a result of their carbon−carbon double bond system with the ability to scavenge free radicals.[6] In tomato, the content of carotenoids such as β-carotene and lycopene have been shown to increase during maturation.[7] Colorless carotenoids, i.e., phytofluene and phytoene, are the precursors of pigmented carotenoids, present in both immature and mature tomato fruits in low (0.01 mg/100 mg) to high content (2 mg/100 mg).[8] The content of pigmented carotenoids in the tomato fruit is highly affected by genetic factors, growth conditions, and their interactions.[9] Thus, accessions that are adapted to grow under dry conditions were found to have high lycopene and β-carotene content, if subjected to drought conditions.[10] Furthermore, wild tomato relatives have been reported with higher lycopene content than commercial cultivars.[11]

Among the polyamines, putrescine, spermidine, and spermine, which are known to be present in all organisms, have been linked to improved human health who are on the recovery from certain diseases.[12] Polyamines are involved in the cellular metabolic pathways[5] and regulatory function of ion membrane channels.[13] Furthermore, an alteration of the biosynthetic pathway of polyamines in plants has been shown to also alter the biosynthesis of other bioactive compounds, such as carotenoids and vitamin C.[14] Thus, there is an obvious need to increase our understanding of how the content and biosynthesis of various bioactive compounds interrelate, especially in different plant genetic materials cultivated under the same growing conditions.

Tomato is a widely studied crop; nevertheless, despite the fact that Bolivia is a part of the center of origin of tomato,[15] studies on Bolivian tomato accession are scarce. In terms of visible phenotypic characters, a high level of variability has been described for the Bolivian tomatoes,[16] although a recent study revealed a limited genetic diversity in the Bolivian germplasm.[17]

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The aim of the present study was to screen a genetically diverse set of 29 tomato accessions from Bolivia, grown in a greenhouse under the same conditions, for their variation in the contents of some bioactive compounds, i.e., carotenoids, polyamines, and ascorbic acid. Another aim was to increase the understanding of the relationship between the contents of different bioactive compounds in tomato. Furthermore, the relationship between genetic and phenotypic characteristics and the contents of bioactive compounds was evaluated.

MATERIALS AND METHODS

Plant Material, Environmental Conditions, and Collection of Samples. Seeds of 29 tomato accessions (Figure 1 and Table S1) were obtained from the Bolivian National Center of Horticultural Seed Production (CNPSH) and the National Institute of Agricultural and Forestry Innovation (INIAF) in Bolivia. Ten seeds per accession were sown in 4.5 L trays with 40 plugs, filled with nutrient-rich soil (0.08 L per plug) in a greenhouse at the Department of Plant Breeding, Swedish University of Agricultural Sciences (SLU). The greenhouse conditions were as follows: controlled day/night temperature of ±28 °C/22 °C, 16 h of light with HPS (high-pressure sodium) lamps with 100 to 150 μmol/m^2/s or natural light, and 60% relative humidity. When plants developed true leaves, three vigorous plants of each accession were transferred to pots (7.5 L) filled with enriched soil, and distributed in a completely random three-block design in the greenhouse. To maintain standard watering and nutrient balance conditions, an automatic daily ferti-irrigation system was installed. Regular pruning practices were applied to keep only two main branches for each plant. Fruit sampling started when three to four mature fruits per plant were ready for harvesting in each accession. Due to the intrinsic differences in growing patterns among the evaluated accessions, sampling was carried out randomly across the entire tomato plant and in relation to tomato maturation, rather than location within the tomato plant. After harvest, each tomato was evaluated according to color, shape, weight, and firmness, as described below. For bioactive compound analysis, tomatoes of each accession with three replications were chopped, mixed, and later separated into two portions under green light conditions. One portion was designated to evaluate ascorbic acid with 5 g of fresh fruit per sample, and the remaining portion was preserved at −80 °C for further analysis of carotenoids and polyamines.

Figure 1. Tomato (*Solanum lycopersicum*) fruits at the mature stage of 28 accessions representing the core germplasm collection in Bolivia.

Reagents. Three types of bioactive compounds were analyzed: vitamin C, carotenoids, and polyamines. To analyze vitamin C, the following chemicals were used: meta-phosphoric acid, L(+)-ascorbic acid, methanol (Merck, Darmstadt, HE, Germany), dithiothreitol (DTT), and potassium dihydrogen phosphate (Scharlau Sentmenat, Spain). To analyze carotenoids, the following standards were used: lycopene (Extrasynthese, France), total trans-ß-carotene, referred to as β-carotene in this article, the internal standard ß-apo-8-carotenal (Sigma-Aldrich, St. Louis, USA), and 2,6-di*tert*-butyl-4-methylphenol (BHT) (Acros Organics (Geel, Belgium). For extraction of carotenoids and for the HPLC analysis, the following were used: acetone spiked with 0.1% of BHT, ammonium acetate PA, methanol (Merck, Darmstadt, HE, Germany), acetone (Honeywell, Seelze, Germany), and *tert*-butyl methyl ether (MTBE) purchased from Supelco, Burlington MA USA. To analyze polyamines, the standards putrescine (Sigma-Aldrich, St. Louis, MO, USA), spermidine trihydrochloride (Thermo Fisher Acreos Organic, NJ, USA), and spermine tetrahydrochloride (ICN Biomedics Inc., Morrow, OH, USA), and an internal standard 1,7-diaminoheptane (ThermoFisher, Schnelldorf, BY, Germany), were used. The samples were resolved by using acetonitrile (VWR Chemicals, Fontenay-Sous-Bois, France) for HPLC analysis. All dilutions were performed with deionized water purified using a Milli-Q-water system (Thermo Fisher Scientific, Lund, Sweden).

Evaluation of Weight, Color, and Firmness. To evaluate weight, color, and firmness, three to four mature tomatoes were harvested per accession per block in three replicates. Each tomato was weighed using a digital balance, and the average was recorded. The red color (a* value) of the tomatoes was measured with a chromameter (Konica, Minolta CR-400, Osaka, Japan). Thus, each tomato fruit was touched three times on the skin across the equatorial line, and the average value was used for the statistical analysis. Evaluation of firmness in each tomato was performed using a penetrometer (FT 327, Effegi, Italy). Thus, the fruit peeler provided together with the penetrometer was used to remove a small part of the skin of each tomato at the tomato equatorial line, and then, the force needed to penetrate the pulp was determined, pressuring the bulb into the skin until the tomato was perforated. The average of firmness measurements for each accession was used for further analysis.

Analysis of Vitamin C. Detection and quantification of ascorbic acid were performed according to the method described by Bergquist et al.[18] with the following modifications: A sample of 5 g of chopped tomatoes was placed in a brown conical flask together with 25 mL of meta-phosphoric acid at 1.5% and homogenized for 60 s in an Ultra

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Table 1. Characteristics of Genetic Background, Size, Shape, Region, Color and Altitude Used as Genetic and Phenotypic Indicators to Evaluate their Effect on Variables of Response and Nest Accessions for ANOVA −2

indicator	criteria	classification of indicator according to criteria
genetic background	clusters of Nei's unbiased genetic distance-based UPGMA cluster analysis.[17] Only 16 accessions were part of this current study	cluster 1:6 accessions, cluster 2:4 accessions, cluster 3:1 accession, cluster 4:1 accession, cluster 5:5 accessions, cluster 6:13 accessions
size	groups based on fruit diameters measured in cm	1 = very small, 2= intermediate
shape	fruit shapes base on UPOV and IPGRI[23]	1 = round, 2 = slightly flattened, 3 = highly rounded.
region	original region of collection in Bolivia	Region 1: Ballivian; Region 2: Nor Yungas; Region 3: Sud Yungas; Region 4: others
color	based on skin color at mature stage	1: red; 2: yellow
altitude	three ranges of altitude in m.a.s.l[a] (for 26 accessions)	1:200 to 890; 2:900 to 1590; 3: 1600−2860

[a]Note: Meters above the sea level.

turrax IKA TP 18/10 (Werke GmbH Co. KG Staufen, Germany) followed by a cold extraction for 60 min in dark conditions at 4 °C. After 10 min of centrifugation in an Eppendorf 5804R (Hamburg, Germany) at 2899*g*, the supernatant was extracted, and an aliquot of 1.7 mL was collected in a 2 mL microtube and frozen at −80 °C for further analysis. After all samples were collected from the three blocks and prepared with the same method as described above, samples were thawed and centrifuged at 12,900*g* for 10 min (Eppendorf 5427 R; Hamburg, Germany). An aliquot of 500 μL of the supernatant was placed in a 2 mL microtube and mixed with an equal part of dithiothreitol solvent (72 mM), and K_2HPO_4 (200 mM) as a buffer to maintain the pH ± 7, centrifuged for 2 min at 8944*g*, at 20 °C. An aliquot of 600 μL of the sample was placed in an amber vial for HPLC analysis. Separately, an ascorbic acid standard stock solution was prepared with a concentration of 50 μg/mL and held at −20 °C until sample analysis. Standards were treated in the same way as for the samples and used to prepare a standard curve to quantify ascorbic acid in the samples. Standards and samples were analyzed in an Agilent Technologies HPLC-Diode Array (DAD) apparatus equipped with a Phenomenex (Torrence, CA, USA) Synergi Polar-RP 80 Å, LC column (4.6 mm × 250 mm, 4 μm). The eluent preparation was a mixture of 20 mM KH_2PO_4 and methanol (4%) with pH adjusted to 2.3. An aliquot of 10 μL of standards or samples was injected into the apparatus in an isocratic mode and run for 14 min with a flow rate of 1 mL/min and a detection wavelength of 248 nm.

Analysis of Carotenoids. A range of solvents have been utilized for the extraction of carotenoids in plants.[19] Based on previous studies,[20] acetone was found to be a suitable and less hazardous extraction solvent of carotenoids as compared to many other solvents, with a high extraction yield of carotenoids, especially when combined with sonication. Here, carotenoids were extracted from lyophilized and milled tomato fruit samples using a standard acetone-based extraction procedure[21] with some modifications. In the present study, a relatively high number of tomato samples (29 accessions with three harvest replicates on each and three technical replicates on the HPLC = 174 samples) were analyzed for carotenoid content and composition. Thus, an extraction methodology allowing samples to be ready for a continuous run on the HPLC (as a continuous run is known to result in most comparable results) was needed. Therefore, an overnight procedure, with loading of a new batch (20 samples) every morning, was required. Thus, a 50 mg sample from each accession was diluted, in a 2 mL microtube, using 1000 μL of 99.6% acetone combined with the antioxidant BHT (0.1%), and 100 μL of the internal standard ß-apo-8-carotenal at 2 μg/mL. Then, the samples were mixed with a vortex (Combi-spin FVL-2400, Biosan, Latvia) for 30 s and then placed in a sonicator-shear bath (Bandelin Son-orex digitec DT 100 H, Bandelin, Germany) for 10 min at room temperature and dark conditions. Thereafter, the samples were sealed and placed horizontally in an orbital shaker (Thermo Forma Scientific Model 430, Ohio, USA) overnight at 5 °C in darkness. Samples were vortexed for 30 s, then centrifuged (Eppendorf 5427 R, Hamburg, Germany) at 4 °C for 10 min at 12,900*g* followed by the placing of the samples in a water bath at 45 °C for 60 min. The supernatant was collected in a 2 mL microtube. A second extraction was performed by adding 500 μL of acetone (99.6%) combined with 0.1% of BHT. Samples were vortexed for 30 s and centrifuged again for 10 min at 12,900*g* at 4 °C. The supernatant of the first and the second extraction was pooled and an aliquot of 600 μL of the supernatant was placed in an amber vial to analyze carotenoids in an HPLC-Diode Array (DAD). To secure complete extraction and ensure that the used antioxidant protected against loss of carotenoids, several pre-experiments were carried out comparing carotenoid yield using different solvents and different extraction times.

An 1100 Series HPLC Agilent Technologies (CA, USA) instrument equipped with a diode array detector (DAD G4212) was used for carotenoid analysis. The carotenoids were separated using a column 100 × 2.1 mm, 2.6 μm Thermo Accucore C30 (Thermo-Fisher) operated at 40 °C with an injection volume of 3 μL. The mobile phases consisted of eluent A: methanol/10 mM NH_4-acetate 92/8, degassed 10 min in a sonicator; and eluent B: MTBE, with the gradient as follows: 0−2 min 0% B, 2−15 min 0−63% B, 15−18 min 63−67% B, 18−19 min 67% B, 19−20 min 67−0% B, 20−26 min 0% B. A constant flow rate of 0.3 mL/min was used. Spectral data of 300−550 nm were collected. A standard solution of lycopene (5.571 ng/μL) was prepared and was then further utilized to locate the retention times of *cis*- and *trans*-lycopene on the HPLC chromatograms. Retention times of the peaks of lutein and *β*-carotene were determined based on previous analyses in the lab and literature data. Furthermore, the standard solution was used to calculate the content of the pigmented carotenoids: lutein, an 'unidentified carotenoid,' *β*-carotene, and *cis*- and *trans*-lycopene in the samples. The content of all the pigmented carotenoids was used to calculate the content of 'total pigmented carotenoids,' while the content of *cis*- and *trans*-lycopene was used to calculate the content of 'total lycopene.' The colorless carotenoids phytofluen and two phytoen picks were identified as one peak at 350 nm and two peaks at 285 nm, respectively. Due to the lack of suitable standard, the amount of these carotenoids was not calculated, but the area under the peaks in the chromatogram was used for correlation analyses to further understand the variation of the colorless carotenoids in tomato and their relation to other compounds evaluated.

Polyamine Analysis. Samples were lyophilized at −105 °C in a CoolSafe TM SCANVAC apparatus (ScanLaf A/S; Lynge, Denmark) until the dry weight was constant. Dry samples were milled in an ultra centrifugal mill with trapezoid sieve holes of 0.5 mm pore size and speed of 2016*g* (ZM 200 RETSCH GmBH; Haan, Germany), and the milled samples were preserved at −80 °C. One day before the extraction of polyamines, 50 mg of each accession sample was weighed. Standards and polyamines extraction were carried out according to our previous publication,[22] with minor modifications explained as follows:

The internal standard 1,7-diaminoheptane concentration was reduced to 7.5 μg/mL and after the hydrochloric acid extraction, 200 μL of supernatant was mixed with 300 μL of saturated $NaHCO_3$, 100 μL of dH_2O, and 600 μL of dansyl chloride (20 mM). Liquid−liquid extraction and HPLC-DAD-MS conditions were same as reported before.[22] Dry samples were dissolved in 200 μL of pure acetonitrile and analyzed in an HPLC-DAD-MS 1260 infinity system (Agilent Technologies, CA, USA).

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ACS Food Sci. Technol. 2024, 4, 1082−1093

Table 2. ANOVA for Bioactive and Nutritional Compound Contents Extracted from the Fruits of 29 Bolivian Tomato Accessions[a]

source of variation	putrescine (SS)	spermidine (SS)	spermine (SS)	total polyamines (SS)	lutein (SS)
accession	4.2×10^{04}**	2.4×10^{03} (NS)	1.9×10^{02} (NS)	5.6×10^{04}*	1.2×10^{01} (NS)
replication	5.7×10^{02}	1.6×10^{02}	3.7×10^{01}*	1.1×10^{03}	1.1×10^{00}
residuals	2.5×10^{04}	2.7×10^{03}	1.8×10^{02}	4.9×10^{04}	2.1×10^{01}
	'unidentified carotenoid' (SS)	β-carotene (SS)	total lycopene (SS)	total pigmented carotenoids (SS)	
accession	7.6×10^{01}***	2.0×10^{03}***	3.2×10^{05}***	4.6×10^{05}***	
replication	1.5×10^{00}	3.5×10^{00}	3.3×10^{03}	6.1×10^{02}	
residuals	2.8×10^{01}	3.2×10^{02}	4.3×10^{04}	4.5×10^{04}	
	vitamin C (SS)	a-value (SS)	weight (SS)	firmness (SS)	
accession	1.8×10^{08}***	9.2×10^{03}***	2.7×10^{04}***	2.8×10^{00}***	
replication	2.7×10^{06}	4.7×10^{01}	9.2×10^{01}	1.0×10^{-01}	
residuals	5.8×10^{07}	8.9×10^{02}	4.5×10^{03}	1.3×10^{00}	

[a]Note: Significance levels were represented as follows: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

Statistical Analysis. Analysis of variance (ANOVA) was performed to determine the variance within and among accessions. A Tukey post hoc test was performed and $p \leq 0.05$ was used as a significance level to verify the differences among accessions. To detect relationships between carotenoids, polyamines, vitamin C, weight, color, and firmness, principal component analysis (PCA) was conducted. A second ANOVA was performed to evaluate variance at a nested level using six different indicators (Table 1) i.e., size, shape, original region of collection, color, and altitude, characteristics explained in Table 1.

The nested analysis enabled a partial explanation of the effect of the above-mentioned indicators on the accessions. Correlation among response variables was analyzed to determine the relationships between them. Statistical analysis was carried out using the Integrated Development free software R-Studio version 4.1.2 with the packages emmeans, factoextra, tidyverse, and corrplot. Data sets were subjected to a linear regression model-based analysis of variance (ANOVA) that included either accession or accession and block effects. Accessions were considered statistically significantly different if $p \leq 0.05$. Differences between estimated marginal means were evaluated using the algorithm compact letter displays (CLDs) with a significance level of $p \leq 0.05$.

RESULTS

Variation in Contents of Bioactive Compounds. Large differences were found in the contents of bioactive compounds among the 29 accessions analyzed. The lutein content varied from 1.43 to 3.38 μg/g DW for carotenoids; 2.15 to 7.06 μg/g DW for 'unidentified carotenoid'; 0.75 to 15.7 μg/g DW for β-carotene; 2.50 to 254 μg/g DW for total pigmented carotenoids; and 0.58 to 229 μg/g DW for total lycopene. For polyamines, the concentrations varied between accessions; putrescine from 73.5 to 181 μg/g DW; spermidine from 26.7 to 54.4 μg/g DW; spermine from 4.85 to 12.0 μg/g DW; and total polyamines from 122 to 225 μg/g DW. Concentrations of vitamin C varied between 1797 and 7500 μg/g DW.

Relationships Among Accessions and the Variation of Bioactive Compounds. The analyses of variance (ANOVA) revealed that the differences in the content of bioactive compounds among the accessions were statistically significant for all analyzed parameters, with the exception of spermidine, spermine, and lutein (Table 2).

The first principal component (PC1), accounting for 38% of the variation, grouped the tomato accessions based on their vitamin C content (negative PC1 value) versus a*-value, weight, and firmness (positive PC1 values) of the tomato fruits (Figure 2A). A negative correlation between these parameters was also obtained through a Pearson correlation analysis

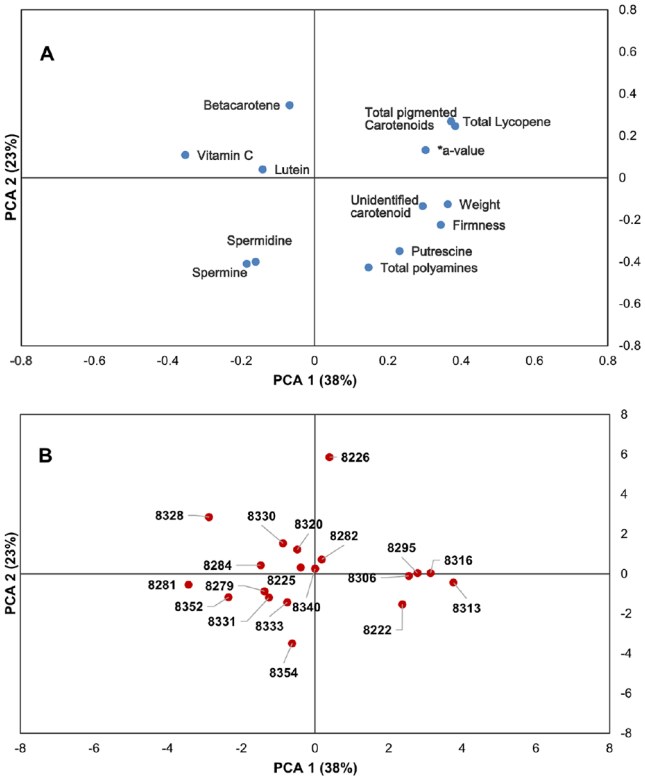

Figure 2. Score (A) and loading (B) plots generated through PCA analysis of content of various bioactive compounds (putrescine, spermidine, spermine, total polyamines, lutein, 'unidentified carotenoid,' total pigmented carotenoids, and total lycopene), nutritional compounds (vitamin C) and quality traits (a*-value, weight, and firmness) in 19 tomato accessions. Note: only the numerals in the accession names are shown for simplicity.

(Figure 3). The second principal component (PC2), explaining 23% of the variation, grouped the tomato accessions based on their β-carotene (positive PC2) versus their polyamine content (negative PC2 value; Figure 2A). The accessions BOL-8295-HT, BOL-8306-HT, BOL-8222-HT, BOL-8316-HT, and BOL-8313-HT were found with positive PC1 values, thereby indicating that these accessions hold a high a* value, weight, and firmness and a low content of vitamin C, in contrast to the accessions BOL-8281-HT, BOL-8352-HT, BOL-8284-HT, BOL-8279-HT, and BOL-8331-HT with negative PC1 values (Figure 2B). The accession BOL-8226-HT had a large positive

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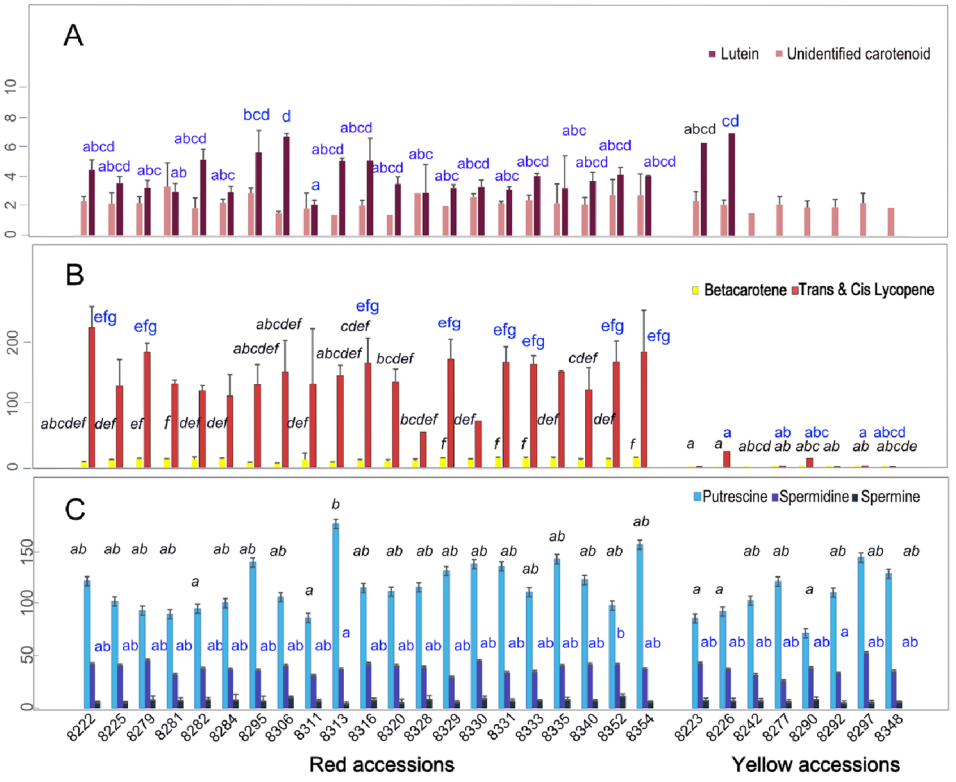

Figure 3. Carotenoids (lutein, 'unidentified carotenoid,' β-carotene, trans, and *cis*-lycopene) and polyamines (putrescine, spermidine, and spermine) contents (μg/g DW) at the mature stage of 29 tomato accessions from the Bolivian germplasm collection. Tukey post-hoc test was used to detect significant differences between accessions ($p < 0.05$). Accessions sharing the same letter for each variable were not statistically different in that variable.

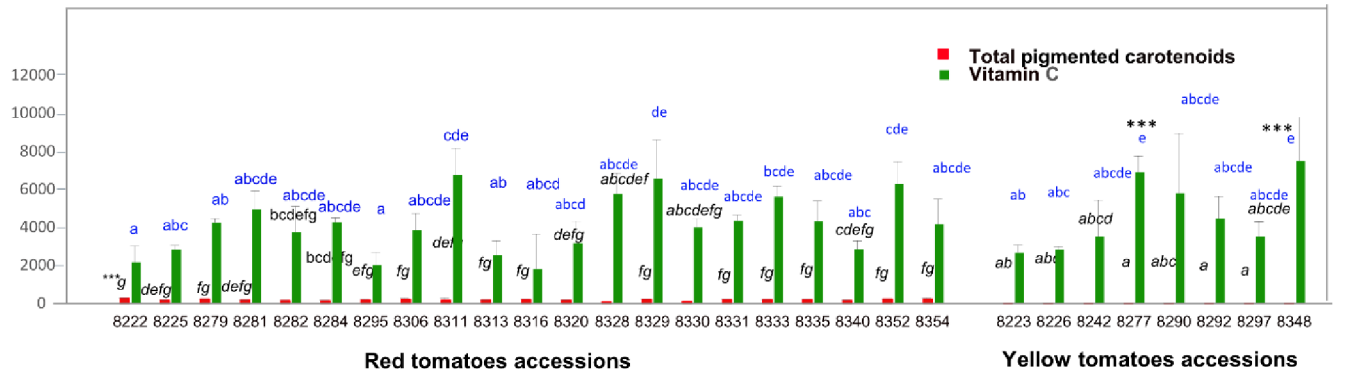

Figure 4. Content of total pigmented carotenoids and vitamin C (μg/g of DW) across 29 tomato accessions. Accessions on the left produce red fruits, while accessions on the right produce yellow fruits. Tukey post-hoc test was used to detect significant differences between accessions ($p < 0.05$). Accessions sharing the same letter for each variable were not statistically different in that variable.

PC2 value, indicating that it had a high content of carotenoids, while BOL-8354-HT showed a negative PC2 value, indicating that it had a high content of polyamines (Figure 2B).

By comparing mean values using the Tukey post-hoc test, some differences among accessions were revealed in relation to their contents of various bioactive compounds (Figure 3). Thus, the fruits of accessions BOL-8226-HT, BOL-8295-HT, and BOL-8306-HT had a significantly higher 'unidentified carotenoid' content compared to accession BOL-8311-HT (Figure 3A). Accessions BOL-8223-HT and BOL-8226-HT showed significantly low levels of β-carotene compared to other accessions (Figure 3B).

Low levels of total pigmented carotenoids were found in BOL-8223-HT, BOL-8277-HT, BOL-8290-HT, BOL-8292-HT, and BOL-8297-HT, which were significantly different from that of several other accessions (Figure 3B). For polyamine contents, only putrescine content in accession BOL-8313-HT was statistically different (higher) compared to that of the other accessions (Figure 5C).

Spermidine and spermine contents did not show statistically significant differences among accessions (Figure 5C).

Effect of Tomato Fruit Color on Bioactive Compounds. Accessions with yellow fruits (BOL-8223-HT, BOL-8226-HT, BOL-8242-HT, BOL-8277-HT, BOL-8290-HT, BOL-8292-HT, BOL-8297-HT, and BOL-8348-HT) showed low contents of total pigmented carotenoids (2.5−18.9 g/g DW), although statistically significantly different only when compared to one of the tomato accessions with red fruits

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Table 3. ANOVA for Effects of Genetic Background, Size, Shape, Region, Color, and Altitude Upon Bioactive and Nutritional Compounds, Weight and Firmness of Bolivian Tomato Germplasm[a]

quality traits	source	genetic background (SS)	size (SS)	shape (SS)	region (SS)	color (SS)	altitude (SS)
bioactive compounds							
polyamines							
putrescine	group	5.5×10^{03}	5.1×10^{03}**	1.6×10^{03}	1.2×10^{04}**	2.1×10^{03}•	1.6×10^{02}
	replication	1.7×10^{03}	1.2×10^{03}	1.1×10^{03}	8.5×10^{02}	1.3×10^{03}	1.6×10^{03}
	EIB (G*A)	8.4×10^{03}	3.7×10^{04}*	4.1×10^{04}**	3.1×10^{04}*	4.0×10^{04}**	4.1×10^{04}**
	residuals	1.5×10^{04}	2.6×10^{04}	2.6×10^{04}	2.6×10^{04}	2.6×10^{04}	2.5×10^{04}
spermidine	group	2.2×10^{02}	4.7×10^{01}	2.6×10^{02}	2.7×10^{02}	1.9×10^{01}	3.0×10^{01}
	replication	2.0×10^{02}	1.7×10^{02}	1.5×10^{02}	1.7×10^{02}	1.9×10^{02}	2.7×10^{02}•
	EIB (G*A)	3.0×10^{02}	2.4×10^{03}	2.2×10^{03}	2.2×10^{03}	2.4×10^{03}	1.7×10^{03}
	residuals	1.7×10^{03}	2.8×10^{03}	2.8×10^{03}	2.8×10^{03}	2.8×10^{03}	2.2×10^{03}
spermine	group	2.0×10^{01}	6.2×10^{00}	3.9×10^{00}	9.9×10^{00}	1.3×10^{01}•	4.4×10^{00}
	replication	5.9×10^{01}**	3.3×10^{01}*	3.0×10^{01}*	3.5×10^{01}*	3.3×10^{01}*	3.0×10^{01}*
	EIB (G*A)	2.9×10^{01}	1.8×10^{02}•	1.9×10^{02}*	1.8×10^{02}•	1.8×10^{02}•	1.8×10^{02}*
	residuals	7.8×10^{01}	1.8×10^{02}	1.8×10^{02}	1.8×10^{02}	1.8×10^{02}	1.5×10^{02}
total polyamines	group	6.4×10^{03}	1.5×10^{04}***	6.0×10^{02}	1.2×10^{04}*	8.4×10^{03}**	1.7×10^{02}
	replication	7.0×10^{02}	6.6×10^{02}	9.4×10^{02}	7.8×10^{02}	1.0×10^{03}	1.5×10^{03}
	EIB (G*A)	1.4×10^{04}	4.2×10^{04}	5.6×10^{04}*	4.5×10^{04}	4.8×10^{04}	5.2×10^{04}*
	residuals	2.6×10^{04}	5.2×10^{04}	5.2×10^{04}	5.2×10^{04}	5.2×10^{04}	4.5×10^{04}
carotenoids							
lutein	group	4.0×10^{00}	6.1×10^{-01}	4.7×10^{-01}	5.9×10^{-01}	5.1×10^{-01}	1.9×10^{-01}
	replication	5.5×10^{-01}	1.1×10^{00}	1.3×10^{00}	1.2×10^{00}	1.3×10^{00}	1.9×10^{00}
	EIB (G*A)	1.6×10^{00}	1.1×10^{01}	1.1×10^{01}	1.1×10^{01}	1.1×10^{01}	1.0×10^{01}
	residuals	1.1×10^{01}	2.1×10^{01}	2.1×10^{01}	2.1×10^{01}	2.1×10^{01}	2.0×10^{01}
'unidentified carotenoid'	group	2.7×10^{01}*	2.2×10^{01}***	5.6×10^{00}*	8.8×10^{00}*	1.4×10^{01}***	3.7×10^{-01}
	replication	2.0×10^{00}	1.7×10^{00}	1.5×10^{00}	1.8×10^{00}	2.7×10^{00}	2.0×10^{00}
	EIB (G*A)	1.5×10^{01}	5.3×10^{01}**	7.0×10^{01}***	6.7×10^{01}***	6.0×10^{01}***	7.2×10^{01}***
	residuals	2.5×10^{01}	2.8×10^{01}	2.8×10^{01}	2.8×10^{01}	2.8×10^{01}	2.7×10^{01}
β-carotene	group	4.2×10^{02}***	1.5×10^{01}	7.6×10^{01}**	5.8×10^{02}***	1.6×10^{03}	1.1×10^{01}
	replication	3.4×10^{01}**	3.1×10^{00}	2.8×10^{00}	3.3×10^{00}	3.6×10^{00}	8.7×10^{-01}
	EIB (G*A)	5.1×10^{02}***	2.0×10^{03}***	1.9×10^{03}***	1.4×10^{03}***	4.0×10^{02}*	1.7×10^{03}***
	residuals	6.3×10^{01}	3.2×10^{02}	3.2×10^{02}	3.2×10^{02}	3.2×10^{02}	3.2×10^{02}
total cartenoids	group	1.2×10^{04}**	6.2×10^{04}***	6.1×10^{03}	3.8×10^{04}***	4.0×10^{05}***	1.4×10^{04}*
	replication	4.3×10^{03}*	5.7×10^{03}	5.2×10^{03}	3.2×10^{03}	2.5×10^{03}	9.5×10^{03}*
	EIB (G*A)	1.9×10^{05}***	4.0×10^{05}***	4.5×10^{05}***	4.2×10^{05}***	6.2×10^{04}*	3.5×10^{05}***
	residuals	7.2×10^{03}	4.5×10^{04}	4.5×10^{04}	4.5×10^{04}	4.5×10^{04}	4.5×10^{04}
total lycopene	group	4.3×10^{03}	4.1×10^{04}***	7.0×10^{03}•	2.8×10^{04}***	2.6×10^{05}***	1.4×10^{04}**
	replication	1.8×10^{03}	6.5×10^{03}•	8.1×10^{03}*	7.0×10^{03}•	4.8×10^{03}	4.9×10^{03}
	EIB (G*A)	1.6×10^{05}***	2.7×10^{05}***	3.1×10^{05}***	2.9×10^{05}***	5.3×10^{04}•	2.6×10^{05}***
	residuals	9.8×10^{03}	4.3×10^{04}	4.3×10^{04}	4.3×10^{04}	4.3×10^{04}	4.3×10^{04}
nutritional compounds							
vitamins							
vitamin C	group	2.8×10^{02}***	3.0×10^{02}***	2.4×10^{02}***	3.0×10^{02}***	1.6×10^{01}	6.2×10^{01}*
	replication	2.2×10^{01}	2.0×10^{01}	2.8×10^{01}	2.3×10^{01}	3.3×10^{01}	2.8×10^{01}
	EIB (G*A)	1.8×10^{02}**	7.9×10^{02}***	8.5×10^{02}***	7.9×10^{02}***	1.1×10^{03}***	8.7×10^{02}***
	residuals	1.2×10^{02}	3.6×10^{02}	3.6×10^{02}	3.6×10^{02}	3.6×10^{02}	3.3×10^{02}
external quality traits							
a*-value	group	4.3×10^{02}**	2.6×10^{03}***	3.3×10^{02}***	8.3×10^{02}***	8.1×10^{03}	1.1×10^{02}•
	replication	3.9×10^{01}	7.1×10^{01}	7.9×10^{01}	1.1×10^{02}•	8.1×10^{01}	1.4×10^{02}*
	EIB (G*A)	4.9×10^{03}***	6.6×10^{03}***	8.8×10^{03}***	8.3×10^{03}***	1.1×10^{03}*	7.6×10^{03}***
	residuals	4.1×10^{02}	8.9×10^{02}	8.9×10^{02}	8.9×10^{02}	8.9×10^{02}	8.7×10^{02}
weight	group	5.6×10^{03}***	2.2×10^{04}***	5.1×10^{03}***	5.4×10^{03}***	1.5×10^{03}***	8.2×10^{02}*
	replication	1.7×10^{02}	1.7×10^{02}	3.9×10^{02}	2.4×10^{02}	5.5×10^{02}•	7.7×10^{02}*
	EIB (G*A)	1.0×10^{04}***	4.7×10^{03}*	2.2×10^{04}***	2.2×10^{04}***	2.5×10^{04}***	2.4×10^{04}***
	residuals	3.6×10^{03}	4.5×10^{03}	4.5×10^{03}	4.5×10^{03}	4.5×10^{03}	4.4×10^{03}
firmness	group	4.9×10^{-01}***	2.3×10^{00}***	5.0×10^{-01}***	5.7×10^{-01}***	1.3×10^{-01}*	1.8×10^{-02}
	replication	6.3×10^{-02}	9.7×10^{-02}	7.6×10^{-02}	7.2×10^{-02}	7.7×10^{-02}	7.1×10^{-02}
	EIB (G*A)	1.0×10^{00}***	5.1×10^{-01}	2.4×10^{00}***	2.3×10^{00}***	2.7×10^{00}***	2.6×10^{00}***
	residuals	3.3×10^{-01}	1.3×10^{00}	1.3×10^{00}	1.3×10^{00}	1.3×10^{00}	1.3×10^{00}

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ACS Food Sci. Technol. 2024, 4, 1082−1093

Table 3. continued

[a]Note: Accessions were divided into groups according to their common backgrounds: (a) Genetic background-based grouping of 16 accessions into six groups based on their genetic relationship 17 (b) Region: 1 = Ballivian, 2 = Nor Yungas, 3 = Sud Yungas, 4 = others. (c) Altitude: 1= 200 to 890, 2 = 900 to 1590, 3 = 1600 to 2860 m.a.s.l. (26 accessions). (d) Size: 1 = very small; 2= intermediate. (e) Shape: 1 = round, 2 = slightly flattened, 3 = highly rounded. (f) Color: 1 = red, 2 = yellow. EIB(G*A) corresponds to 'the effect of interaction between common background (group) and accessions'. Note: Significance levels were represented as follows: ***$p < 0.001$; ** $p < 0.01$; *$p < 0.05$; •$p < 0.1$.

(BOL-8222-HT with 254 g/g DW; Figure 4). Two of the yellow-fruited accessions, BOL-8277-HT and BOL-8348-HT showed significantly higher content (17.26 and 18.75 g/g DW, respectively), of vitamin C than the accessions with red fruits. This accession also had higher vitamin C content compared to the other accessions with yellow fruits (Figure 4).

Effect of Indicators on Content of Bioactive Compounds. ANOVA at a nested level showed a significant relationship between the six used indicators for the content and composition of carotenoids, although their effects on lutein content were limited. β-carotene and total lycopene contents were mainly correlated to the tomato shape and altitude of collection, respectively. The indicators had a highly significant effect on the vitamin C content and on parameters, such as a*-value, weight, and firmness (with the exception of the tomato fruit color for vitamin C, and altitude of collection for a*-value and firmness). The content and composition of polyamines were less affected by the indicators as only tomato fruit size, fruit color, and region of collection had significant effects on the putrescine content (Table 3). Tomatoes from genotype groups 5 and 6 showed low levels of β-carotene, total pigmented carotenoids, and vitamin C, while tomatoes of genotype group 1 showed high levels of the same bioactive compounds. High levels of lycopene were found in tomatoes collected from the Ballivian region, while high levels of putrescine were found in tomatoes collected from the Sud Yungas region and high levels of vitamin C were found in tomatoes collected at altitudes between 1600 and 2860 m.a.s.l. Furthermore, large tomato fruits had high contents of putrescine, polyamines, 'unidentified carotenoid,' total lycopene, and total pigmented carotenoids, while small tomatoes and rounded tomatoes had high levels of vitamin C. Yellow tomato fruits contained significantly higher amounts of 'unidentified carotenoid' than red tomato fruits, while red tomatoes had higher β-carotene, total pigmented carotenoids, and total lycopene contents compared to yellow tomatoes.

Correlation Among Content of Different Bioactive Compounds. The Pearson correlation analyses (Figure 5) resulted in a significantly positive correlation between lutein and β-carotene ($r = 0.33$) while the 'unidentified carotenoid' was positively correlated with firmness ($r = 0.42$) and negatively correlated with vitamin C ($r = -0.46$). Additionally, β-carotene showed a strong positive correlation with total pigmented carotenoids ($r = 0.83$), total lycopene ($r = 0.78$), phytofluene ($r = 0.39$), and a negative correlate ion with phytoene-2 ($r = 0.34$). Furthermore, content of total pigmented carotenoids and total lycopene correlated significantly ($r = 0.99$), and they were also correlated with phytoene-1 (r= 0.58, 0.51), and phytofluene ($r = 0.69$, 067), respectively. Putrescine was the most abundant polyamine compared with spermidine and spermine in all studied accessions, affecting the total amount of polyamines directly. Therefore, putrescine and total polyamines were positively correlated ($r = 0.95$). Putrescine was also positively correlated with firmness ($r = 0.30$) and negatively correlated with spermine ($r = -0.24$).

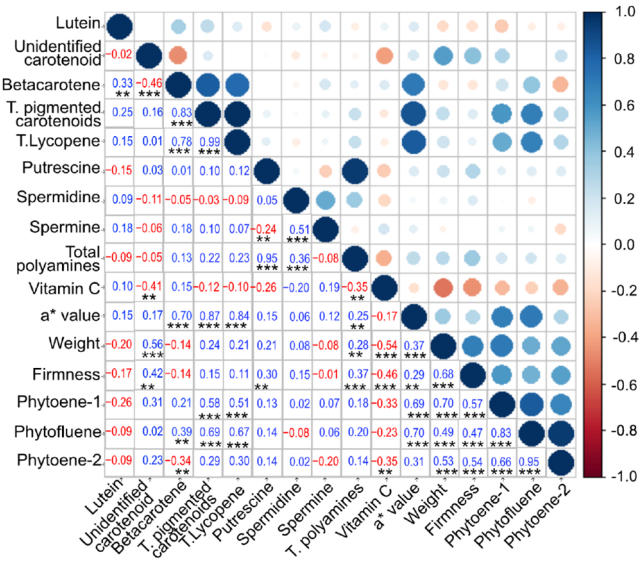

Figure 5. Linear correlation between bioactive and nutritional compounds and quality traits of tomato fruits: carotenoids (lutein, 'unidentified carotenoid,' β-carotene, total pigmented carotenoids, and total lycopene); polyamines (putrescine, spermidine, spermine, and total polyamines); vitamins (vitamin C); quality traits (color index a*-value, weight, and firmness). Blue circles represent positive correlations, and red circles represent negative correlations. The number, size and color intensity of the circles reflect the strength of the correlations. ** and *** indicate significance at $p < 0.05$ and $p < 0.001$, respectively.

Spermidine was positively correlated with spermine ($r = 0.51$) and total polyamines ($r = 0.37$). Total polyamines were negatively correlated with vitamin C ($r = -0.35$) and positively correlated with a*-value ($r = 0.25$) and firmness (0.37). Furthermore, the a*-value was positively correlated with weight, firmness, phytoene-1, and phytofluene with r = 0.37, 0.29, 0.69, and 0.70, respectively. Weight and firmness showed a highly significant positive correlation ($r = 0.68$) and correlated with phytoene-1 ($r = 0.70$, 0.57), phytoene-2 ($r = 0.53$, 0.54), and phytofluene ($r = 0.49$, 0.47).

DISCUSSION

The present study clearly showed the large variation in the content of different types of bioactive compounds in the mature fruit of Bolivian tomato genotypes. Most of the analyzed compounds varied around 2-fold among the accessions, while a 20-fold, 100-fold, and 500-fold variation was noted for β-carotene, total lycopene, and total pigmented carotenoids among the genotypes, respectively. Despite the large variation in the studied compounds, only a few of the genotypes were differentiated with significantly higher amounts of certain compounds compared to the rest of the genotypes. In addition, there was no covariation for different types of compounds (carotenoids, polyamines, and vitamin C) although there was a covariation of compounds of the same

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ACS Food Sci. Technol. 2024, 4, 1082−1093

types, i.e., carotenoids or polyamines. There were some effects of the indicators (genotype group and location of origin) on the contents of the different compounds (mainly carotenoids and vitamin C).

Variation in Contents of Bioactive Compounds and Domestication Relationship. The present study showed a high level of variation for all carotenoids except lutein among the genotypes evaluated here, which corresponds with results from previous studies that have shown high variation in especially lycopene and β-carotene among tomato genotypes.[9,24] Thus, in a wide array of cultivated tomatoes, the total lycopene content was reported to be from almost 0 μg/g DW and up to around 140 μg/g DW[25] as compared to 0.58−229 μg/g DW in the present study. However, studies on wild relatives to tomatoes have shown a 10-fold higher amount of the carotenoid compounds (ca. 20 μg/g DW for lutein, ca. 140 μg/g DW for β-carotene, and ca. 2000 μg/g DW for total lycopene)[26] as compared to levels reported here. The levels of vitamin C were generally found high in the present study (1796−7500), as previous studies have reported levels of around 100 μg/g DW[25] in cultivated tomatoes and 1000 μg/g DW[25] in wild tomatoes.[27] Previous reports on variation in content of polyamines among genotypes are in principal lacking. However, the contents of polyamines reported here were generally lower than those reported in a previous study[22] where a few hybrid accessions and genotypes from a breeding program were analyzed, while the genotypes analyzed here can be categorized as more 'wild.' Level of bioactive compounds presented in various studies might be affected by selected genotypes of investigation, cultivation conditions of the tomatoes, sampling places on the tomato plant, and extraction methods of the compounds. Here, a wide array of tomato genotypes have been evaluated, and they have all been grown under controlled conditions in a greenhouse to minimize the environmental effects on the accumulation of bioactive compounds. The diverging plant material together with the cultivation conditions, though, minimized the opportunities for sampling all tomatoes at the same location on the plant, hence, a random sampling all over the plant was utilized. Despite this, clear genotypic differences in the content of bioactive compounds were noted in the material. Thus, the present study clearly emphasizes the importance of the genetic background of genotypes for the content of various bioactive compounds in tomato, and that such information can be used in breeding to increase the nutritional potential of the tomatoes. The present study, together with previous findings,[28] indicate a specific potential of the uses of wild tomato genotypes and relatives in the breeding for highly nutritious tomatoes, as such genotypes often have high contents of carotenoids,[29] and other bioactive compounds. Domestication normally leads to selected individuals with desirable quality characteristics, such as larger size, heavier weight, and resistance to diseases, and this is generally termed the domestication syndrome. In the present study, none of the investigated accessions had an elongated shape or large size, which is the standard for many modern cultivars.[30] The tomato fruits evaluated in the present study were very small, small, or intermediate, indicating that the accessions were of non-commercial type, as tomato domestication has resulted in increased weight and size of tomato fruits.[31] The differences in bioactive compounds found between wild and cultivated tomatoes in this study can be represented by the high vitamin C content in accessions BOL-8348-HT and BOL-8277-HT; high lycopene content in accessions BOL-8279-HT, BOL-8352-HT and BOL-8354-HT; and high β-carotene content in BOL-8281-HT and BOL-8354-HT, all of which are wild accessions with small fruits, compared to those with intermediate size fruits, which had lower levels of these compounds. Conversely, the intermediate size accession BOL-8313-HT showed higher levels of putrescine and spermidine compared with small sized tomatoes BOL-8223-HT, BOL-8226-HT, and BOL-8290-HT although none of them showed exceptional carotenoids and vitamin C contents. Therefore, some of the wild accessions presented in this study are superior in bioactive compound contents compared with intermediate size tomatoes, despite the fact that some of the newer accessions underwent a domestication process before being collected from the Bolivian territory.

Indicators of Genetic and Environmental Effects on the Levels of Bioactive Compounds. The present study used indicators to understand the possible effects of genetic background and environment on the contents of bioactive and nutritional compounds and external quality traits, such as weight and firmness. In a previous study, simple sequence repeat markers were used to cluster the tomato genotypes evaluated here, representing similarities and differences in their genetic background. The present study found a correlation between this clustering and the content of vitamin C in the tomato genotypes, indicating the effects of genetic variation in Bolivian tomatoes on the vitamin C content. However, several of the accessions in cluster 1, e.g., BOL-8281-HT and BOL-8328-HT were collected in semitropical areas, while accessions BOL-8222-HT and BOL-8226-HT in clusters 5 and 6 were collected in a valley or were part of a breeding program (Table S1), indicating a possible effect of the environment on vitamin C content. Previous studies have shown that the vitamin C content in tomatoes is impacted by genetics, environmental conditions, and their interactions.[9]

Landraces of different tomato species from the Andean region, e.g., *S. lycopersicum* have in previous studies been found to have higher contents of ascorbic acid than that of *S. habrochaites*.[32] Furthermore, it is well-known that ecological divergence and geographical isolation, or environmental conditions, such as soil characteristics have played an essential role in the diversification of the Andean tomato species.[33,34] Geography and ecological patterns have been shown to impact tomato dispersal patterns and hybridization processes.[35] Ecological descriptors and climate diversity that have been associated with the diversification of tomatoes include altitude, humidity, and temperature of the places where they are grown.[34] Tomatoes that originate from diverse environments with different altitudinal and longitudinal conditions,[36] could serve as a potential sources of genotypes to deal with biotic and abiotic stresses.[37]

Previous studies have shown that the contents of bioactive and nutritional compounds are influenced by the environment, e.g., tomatoes grown under a higher temperature with unlimited radiation have been found to have higher vitamin C contents than the same tomatoes grown under a lower temperature.[38] The findings from this study, where tomatoes originating from higher altitudes produced an increased level of vitamin C in their fruits, might thus be the result of adaptation to the increased radiation at higher altitudes. The lycopene contents of tomatoes have been found to be affected by cultivation conditions, with negligible amounts at temperatures below 12 °C or over 30 °C.[39] Despite the fact that differences

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ACS Food Sci. Technol. 2024, 4, 1082−1093

were found among the accessions in vitamin C content in the fruits, no clear pattern of differences in vitamin C content was found between tomato fruits with yellow and red skins. These findings are in line with reports from previous studies, where yellow tomatoes had lower β-carotene contents than red tomatoes, while the vitamin C content did not differ.[40] However, two of the accessions with yellow fruits in the present study showed a higher vitamin C content than all other tomato accessions studied, including both red and yellow tomatoes.

Relationship Among Investigated Parameters. The most obvious relationship among the investigated parameters was the high intercorrelation observed among different evaluated carotenoid compounds and the positive correlation between several of them and the a*-value, as shown by both PCA and Pearson correlation analyses. Lycopene is known as the major carotenoid in tomatoes,[41] which was also shown in the present study, although several of the carotenoids are precursors to each other. Thus, the colorless carotenoids, phytoene and phytofluene are precursors to lycopene, which in turn is a precursor to β-carotene.[41,42] Such an interconnection clearly explains the covariation in amounts of the colorless carotenoids, the total lycopene content, and the total pigmented carotenoids content. Carotenoids are natural pigments that give tomatoes a variety of colors,[42,43] which explains the correlation between the amount of several of the colorless and pigmented carotenoids with the a*-value, also agreeing with previous results.[44] As for color measurements, the present study only collected the a*-value. Parameters such as hue and chroma could be of interest as well in relation to the bioactive compounds evaluated here, and for further studies, the recommendation is to collect these as well.

In the present study, fruit weight and firmness correlated positively, as larger tomatoes were more firm. A negative correlation was found with vitamin C for both fruit weight and firmness, which, as discussed above, can be the result of the fact that the smaller tomatoes are more 'wild' and thereby more nutritious. Also, a positive correlation was found among the content of colorless carotenoids and fruit weight and firmness, which might be the result of the larger fruits also being more red, as was verified by a positive correlation to the a*-value.

In the present investigation, a carotenoid peak of comparable magnitude to that of several other identified pigmented carotenoids was seen in the carotenoid chromatogram. Here, we refer to that peak as an 'unidentified carotenoid.' Based on the placing of the spectral data of the chromatogram, it can potentially be lycoxanthin. Lycoxanthin is a carotenoid that has been identified by others as present in tomatoes.[45,46] However, the levels reported are often smaller than those for the 'unidentified carotenoid' in the present study. Thus, a further identification of this peak is necessary by using NMR or MS/MS, which was not possible in the present study. Here, the amount of the 'unidentified carotenoid' was positively correlated with fruit weight (e.g., in genotypes such as BOL-8295-HT and BOL-8306-HT), which also had a lower vitamin C content. Previous studies reported that lycoxanthin is sensitive to the presence of vitamin C, because of co-oxidation reactions,[47] which might explain the negative correlation between 'unidentified carotenoid' and vitamin C contents of the fruits observed in the present study.

The present study showed higher levels of spermine in the fruits of accession BOL-8352-HT than in the rest of the accessions. This accession also had higher β-carotene and lycopene contents. Previous studies have shown an increase in lycopene contents in tomato fruits of engineered tomato plants that overexpress polyamines or spermidine.[48] Lycopene is a potent antioxidant,[49] and lycopene and polyamines in our foods have been suggested to play an important role in preventing myocardial infarction risk.[50] Among the polyamines, spermidine has been associated with longevity.[12] In general, tomatoes are a source of health-promoting compounds, such as lycopene, β-carotene, vitamin C,[4] and polyamines.[5]

The content and composition of most bioactive compounds in mature tomatoes showed large variation among accessions, although there was no significant variation in the contents of certain compounds, such as lutein, spermidine, and spermine. In the present study, tomato accessions that significantly differed from the other accessions in 'unidentified carotenoid,' β-carotene, total pigmented carotenoids, putrescine, and vitamin C contents were clearly differentiated. Among the bioactive compounds evaluated, the vitamin C content was affected by more variables than the other bioactive compounds. Vitamin C content was negatively correlated with a*-value, weight, firmness, and phytoene-2 of the tomato fruits. The altitude of the original location sites influenced the vitamin C content similar to the effect of the accessions' genetic backgrounds and fruit shapes. Furthermore, two yellow tomato accessions showed the highest levels of vitamin C among all of the accessions. The carotenoid contents of tomato fruits were mainly affected by the fruit colors, although fruit size has some effects. The levels of β-carotene content were mainly associated with fruit shapes, while the lycopene content was affected by germplasm's altitude of origin. In general, there was a lack of covariation among different evaluated bioactive compounds, although a positive covariation of compounds of the same type was found for several of them, and a negative correlation was found between β-carotene and polyamine contents, phytoene-2 and phytofluene.

The present study suggests that tomato genotypes with high levels of various bioactive compounds are available. Tomato genotypes with high specific bioactive content to be utilized in tomato breeding programs or the production of certain products could be identified through screening of available germplasm. In the case of vitamin C, the yellow fruit color could serve as a phenotypic marker to identify genotypes with high vitamin C content, as genotypes with small yellow fruits tend to have high vitamin C content. Additionally, growing tomatoes at altitudes with high levels of radiation can contribute to increased levels of vitamin C. Overall, our results provide new insights into polyamine, carotenoid, and vitamin C contents of Bolivian tomato genetic resources, implying a direct influence of ecological divergence and genetic backgrounds on the levels of various bioactive compounds in tomato fruits.

■ ASSOCIATED CONTENT

Supporting Information

The Supporting Information is available free of charge at https://pubs.acs.org/doi/10.1021/acsfoodscitech.3c00622.

Table S1: Description of twentynine tomato accessions from Bolivian germplasm (XLSX)

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Notes

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ABBREVIATIONS

Acronym	Meaning
a*value	Color component a* defined along the axis of red−green
ANOVA	Analysis of variance
BHT	2,6-di*tert*-butyl-4-methylphenol
CLDs	The algorithm compact letter−displays
CNPSH	Bolivian National Center of Horticultural Seed Production
CrtISO	Prolycopene isomerase
DAD	Diode array detection
DTT	Dithiothreitol
EIB(G*A).	EIB(G*A) corresponds to "the effect of interaction between common background (group) and accessions
g	g force
HPLC	High performance liquid chromatography
HPS	High pressure sodium
INIAF	National Institute of Agricultural and Forestry Innovation—Bolivia
IPGRI	The International Plant Genetic Resources Institute
K_2HPO_4	Potassium phosphate dibasic
L	Liters
LC	Liquid chromatography
m.a.s.l	Meters above the see level
mL	Milliliter
mM	Millimolar
MS	Mass spectrometry
MTBE	Tert-butyl methyl ether
ng	Nanogram
nm	Nanometer
°C	Degree Celsius
p≤	p Significance levels
PC	Principal component
PCA	Principal component analysis
r	Correlation coefficient
R-Studio	R foundation for statistical computing
SLU	Swedish University of Agricultural Sciences
SS	Sum of squares
UPGMA	Unweighted pair group method with arithmetic mean
UPOV	International Union for the Protection of New Varieties of Plants
ZCS	Zeta-carotene desaturase
μg/g DW	Microgram per gram of dry weight
μL	Microliter
$\mu mol/m^2/s$	Number of micromol photons in ″parabolic aluminized reflector″

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