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ORIGINAL ARTICLE

Composition of polyamines and amino acids in plant-source foods for human consumption

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Abstract

Dietary polyamines and amino acids (AAs) are crucial for human growth, development, reproduction, and health. However, the scientific literature shows large variations in polyamine and AA concentrations among major staple foods of plant origin, and there is a scarcity of information regarding their complete composition of AAs. To provide a much-needed database, we quantified polyamines, agmatine, and AAs in select plant-source foods. On the dry matter basis, total polyamines were most abundant in corn grains, followed by soybeans, sweet potatoes, pistachio nuts, potatoes, peanuts, wheat flour and white rice in descending order. Glutamine was the most abundant AA in pistachio nuts, wheat flour and white rice, arginine in peanuts, leucine in corn grains, glutamate in soybeans, and asparagine in potatoes and sweet potatoes. Glutamine was the second most abundant AA in corn grains, peanuts, potatoes, and soybeans, arginine in pistachio nuts, proline in wheat flour, and glutamate in sweet potatoes and white rice. Free AAs represented $\leq 3.1\%$ of total AAs in corn grains, peanuts, pistachio nuts, soybeans, wheat flour and white rice, but 34.4% and 28.5% in potatoes and sweet potatoes, respectively. Asparagine accounted for 32.3%, 17.5%, and 19.4% of total free AAs in potatoes, sweet potatoes, and white rice, respectively. The content of histidine, glycine, lysine, tryptophan, methionine, cysteine, and threonine was relatively low in corn grains, potatoes, sweet potatoes, and white rice. All of the analyzed plant-source foods lacked taurine, creatine, carnosine and anserine (antioxidants that are abundant in meats and also present in milk), and contained little 4-hydroxyproline. Proper proportions of plant- and animal-source products are likely most desirable for optimizing human nutrition and health.

Keywords Plant-source foods · Polyamines · Amino acids · Arginine · Methionine · Humans

Abbreviations

AAs	Amino acids
BCAAs	Branched-chain amino acids
DM	Dry matter
HPLC	High-performance liquid chromatography

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Introduction

Polyamines are a group of polycationic amines at neutral pH, including putrescine (1,4-butanediamine), spermidine [*N*-(3-aminopropyl)-1,4-butane-diamine], and spermine (*N*,*N*′-bis-(3-aminopropyl)-1,4-butane-diamine) (Slocum and Flores 1992). They are present in plants as regulators of DNA and protein synthesis, gene expression, and cell proliferation, stabilizers of negatively charged macromolecules and membranes, and anti-oxidative factors (Kusano et al. 2008; Tiburcio and Alcázar 2018; Tiburcio et al. 1993). Consumption of plant-source foods provides individuals with not only dietary amino acids (AAs) and other nutrients but also polyamines. Based on animal studies, there are suggestions that food-derived polyamines may play an important role in the growth, development and health of the small intestine and other tissues of young mammals (including children) (Hunter and Burritt 2012; Larqué et al. 2007; Ralph et al. 1999). These substances may also be beneficial for protecting adults from aging-associated metabolic disorders (Eisenberg et al. 2009; Soda et al. 2009a) and for improving reproductive function (Dai et al. 2015; Kong et al. 2014; Wang et al. 2014). Knowledge about the content of polyamines in plant foods is very useful to estimate their intakes by subjects. At present, there is a paucity of such information regarding major staple plant foods (such as corn, peanut, potato, soybean, sweet potato, wheat flour, and white rice). Additionally, large variations have been reported from a limited number of studies with these foods (Supplemental Tables 1–3). This may be explained, in part, by the different analytical techniques used in various laboratories. Therefore, it is imperative to determine the content of polyamines in different foods under the same experimental conditions.

Besides foods, polyamines in humans and other animals are also derived from syntheses by their constitutive cells and intestinal bacteria (Agostinelli 2016; Blachier et al. 2007). Endogenously generated polyamines are crucial for intracellular polyamine homeostasis, metabolism, and function (Bazer et al. 2018; Blachier et al. 2011). In mammals and microbes, arginine, agmatine, proline, glutamine, glutamate, ornithine, and methionine are substrates for polyamine synthesis via a series of enzymes, including arginase, agmatinase, proline oxidase, ornithine decarboxylase, spermidine synthase, and spermine synthase (Agostinelli et al. 2010; Lenis et al. 2018; Wu 2013). These pathways are regulated by certain amino acids, such as glutamine, aspartate, asparagine, cysteine, lysine, and branched-chain amino acids at the levels of transport, gene expression, and modulation of activities of enzymes in the physiological pathways (Kahana 2009; Pegg and Casero 2011; Perez-Leal and Merali 2012; Wang et al. 2014; Wu 2013). Although there are reports of the content of AAs in major staple plant foods consumed by humans (Supplemental Tables 1–3), the published data are either incomplete (lacking five or more proteinogenic AAs, such as glutamate, glutamine, aspartate, asparagine, and tryptophan) or grossly inconsistent. The large variations of the data may result, in part, from the diverse analytical techniques used by different investigators.

In view of the foregoing, the objective of this study was to determine the content of polyamines and AAs in major staple plant foods consumed by humans. Our high-performance liquid chromatography (HPLC) methods for the analyses of polyamines and AAs are routinely used in our biochemical and nutritional research (Dai et al. 2014a, b).

Materials and methods

Materials

Corn grain, pistachio nuts, potatoes, sweet potatoes, and wheat flour were purchased from the local HEB food store, and soybeans and polished white rice from the local BCS food store (both at College Station, TX, USA). Peanuts were procured from the local Farm Patch food store (Bryan, TX, USA). Dried peanuts, dried pistachio nuts, dried soybeans, wheat flour, and dried white rice at the food stores were packaged in sealed bags, whereas corn grains, potatoes, and sweet potatoes were fresh. HPLC-grade water and methanol were purchased from Fisher Scientific (Houston, TX, USA). Other materials, including HPLC columns and AA standards, were products of Sigma Chemicals (St. Louis, MO, USA).

Chemical analyses

Peanuts and pistachio nuts were shelled (with no shell), whereas potatoes and sweet potatoes were peeled (with no skin). Corn grain, soybeans, wheat flour, polished white rice were used as purchased. Except for wheat flour, each food was finely ground to 0.5 mm in size before use for analysis. Dry matter (DM) content was determined by drying approximately 100 mg samples to a constant mass in a 105 °C oven. Total nitrogen was analyzed in approximately 1.0 g samples using LECO Model FP-528 Analyzer (St. Joseph, MI, USA) (Li et al. 2011), and crude protein (also known as food protein) was calculated as total nitrogen content multiplied by 5.70 for wheat flour (Shoup et al. 1966) or by 6.25 for other foods (Bártová et al. 2015; Hughes 1957; Kaldy and Markakis 1972; Mossé et al. 1988; Wang and Cavins 1989; Venkatachalam and Sathe 2006). The content of carbohydrate was calculated as 100% − (crude protein % + lipids % + minerals %). To assess possible contributions of non-AA nitrogen-containing substances to crude protein, we also measure anserine and carnosine as well as creatine and creatinine using HPLC methods, as previously described (Kai et al. 1983; Wu et al. 2016).

For the determination of polyamines, each food sample (~ 200–500 mg) was homogenized in 2 ml of 1.5 M $HClO_4$. The homogenate was neutralized with 1 ml of 2 M K_2CO_3, followed by addition of 2 ml HPLC-grade water. The whole solution was centrifuged at 600*g* for 10 min, and the supernatant fluid was analyzed for polyamines and agmatine using an HPLC method involving pre-column derivatization with *o*-phthaldialdehyde (Dai et al. 2014b). Polyamines and agmatine in samples were quantified on the basis of known amounts of standards (Sigma Chemicals, St. Louis, MO, USA) using the Millenium-32 Software (Waters, Milford, MA, USA).

For determining peptide-bound plus free AAs (i.e., total AAs) in foods (except for peptide-bound tryptophan), approximately 100 mg samples were hydrolyzed in 10 ml of 6 N HCl at 110 °C for 24 h under N_2 (Dai et al. 2014a). For tryptophan analysis, approximately 100 mg samples were hydrolyzed at 110 °C for 20 h in 10 ml of 4.2 M NaOH plus 0.1 ml of 25% thiodiglycol (an antioxidant), as previously described (Dai et al. 2014a). Glutamine, glutamate, asparagine, and aspartate in food protein were determined using proteases, as we described previously (Haynes et al. 2009; Li et al. 2011). Free AAs were extracted from each food as described previously for the determination of polyamines. All analyses of AAs were performed in triplicates for each sample using HPLC methods involving pre-column derivatization with *o*-phthaldialdehyde (Dai et al. 2014a). Amino acids in samples were quantified on the basis of known amounts of standards (Sigma Chemicals, St. Louis, MO, USA) using the Millenium-32 Software (Waters, Milford, MA, USA). Peptide-bound AAs were calculated as total AAs minus free AAs. The content of true proteins plus peptides was calculated on the basis of the molecular weights of AA residues (i.e., the molecular weight of an intact AA − 18).

Statistical analysis

Values, expressed on the DM basis, are mean ± SEM. Sample size ($n = 6$/food) was chosen on the basis of known variation of AAs among some foods (Li et al. 2011) and statistical power calculation (Fu et al. 2010). Log transformation of variables was performed when variance of data was not homogenous among treatment groups, as assessed by the Levene's test (Fu et al. 2010). Data on AA composition were analyzed by one-way analysis of variance and the Student–Newman–Keuls multiple comparison (Assaad et al. 2014). Probability values ≤ 0.05 were taken to indicate statistical significance.

Results

Content of nutrients in plant-source foods

The content of water in plant-source foods varied greatly from 3.1% in dried peanuts to 81.7% in fresh corn grains (Table 1). Accordingly, the percentages of DM in the foods differed widely, ranging from 18.3% for fresh corn grains to 96.9% for dried peanuts. Thus, the content of nutrients in these foods is expressed on the DM basis to facilitate comparisons of nutritive values among them. Dried peanuts, pistachio nuts, and soybeans contained much more protein and lipids than wheat flour and white rice, as well as fresh corn, potatoes and sweet potatoes. All the foods, except for soybeans, contained < 5.0% minerals (ash), and soybeans contained 5.02% minerals (DM basis). The content of carbohydrates in foods ranged from 17.4% for peanuts to 91.0% for white rice, depending on individual foods.

Content of polyamines and agmatine in plant-source foods

The content of polyamines and their proportions varied greatly among plant-source foods (Table 2). The content of total polyamines (putrescine + spermidine + spermine) was the highest in corn grains, followed by soybeans, sweet potatoes, pistachio nuts, potatoes and peanuts in descending order, with the lowest level in wheat flour and white rice. In corn grains, the content of putrescine was the highest among the polyamines, followed by spermidine and spermine in descending order. In contrast, in potatoes, the content of putrescine was the lowest among the polyamines, followed by spermidine and spermine in ascending order. In sweet potatoes, the content of spermine was the lowest among the

Table 1 The content of nutrients in plant-source foods

Food	Water (% of wet weight)	Dry matter (% of wet weight)	Nutrients in dry matter (% of dry matter)				
			Nitrogen	Crude protein	Crude lipids	Minerals	Carbohydrates
Corn grain	81.7 ± 0.14^{a}	18.3 ± 0.14^{f}	1.62 ± 0.01^{e}	10.1 ± 0.06^{e}	5.18 ± 0.06^{d}	1.35 ± 0.03^{e}	83.4 ± 0.10^{c}
Peanut	3.11 ± 0.02^{f}	96.9 ± 0.02^{a}	4.44 ± 0.02^{b}	27.7 ± 0.15^{b}	52.4 ± 0.27^{a}	2.43 ± 0.03^{d}	17.4 ± 0.41^{f}
Pistachio nut	3.84 ± 0.02^{f}	96.2 ± 0.02^{a}	3.44 ± 0.02^{c}	21.5 ± 0.16^{c}	47.8 ± 0.35^{b}	2.76 ± 0.04^{c}	28.0 ± 0.38^{e}
Potato	79.0 ± 0.03^{b}	21.0 ± 0.03^{e}	1.57 ± 0.01^{e}	9.84 ± 0.04^{e}	2.17 ± 0.05^{e}	4.04 ± 0.09^{b}	84.0 ± 0.11^{c}
Soybean	3.80 ± 0.03^{f}	96.2 ± 0.03^{a}	7.14 ± 0.02^{a}	44.6 ± 0.13^{a}	18.8 ± 0.11^{c}	5.02 ± 0.05^{a}	31.6 ± 0.21^{d}
Sweet potato	77.1 ± 0.03^{c}	22.9 ± 0.03^{d}	1.11 ± 0.01^{g}	6.91 ± 0.03^{g}	0.90 ± 0.02^{f}	4.13 ± 0.04^{b}	88.1 ± 0.06^{b}
Wheat flour	4.90 ± 0.04^{e}	95.1 ± 0.04^{b}	2.35 ± 0.02^{d}	13.4 ± 0.12^{d}	1.48 ± 0.03^{e}	0.75 ± 0.01^{f}	84.4 ± 0.13^{c}
White rice	9.30 ± 0.03^{d}	90.7 ± 0.03^{c}	1.32 ± 0.01^{f}	8.25 ± 0.04^{f}	0.36 ± 0.01^{g}	0.40 ± 0.01^{g}	91.0 ± 0.04^{a}

Values are mean ± SEM, $n = 6$. The content of crude protein (%) was calculated as nitrogen content (%) multiplied by 5.70 for wheat flour or by 6.25 for other foods. The content of carbohydrates in dry matter was calculated by differences [i.e., 100 − (crude protein % + lipids % + minerals %)]

a–h Within a column, means not sharing the same superscript letter differ ($P < 0.05$)

Table 2 The content of polyamines and agmatine as well as the ratio of total amino acids to total polyamines in plant-source foods

Food	Putrescine (nmol/g of dry matter)	Spermidine (nmol/g of dry matter)	Spermine (nmol/g of dry matter)	Total PA (nmol/g of dry matter)	Agmatine (nmol/g of dry matter)	Total AA (µmol/g of dry matter)	Ratio of total AA to total PA (mol/mol)
Corn grain	7240 ± 92^a	1563 ± 48^a	92 ± 4.3^d	8896 ± 112^a	109 ± 3.6^a	847 ± 3.1^e	95 ± 1.4^h
Peanut	49 ± 1.5^f	411 ± 11^c	88 ± 2.6^d	547 ± 12^f	ND	2260 ± 8.1^b	4141 ± 78^c
Pistachio nut	511 ± 6.8^c	631 ± 12^b	425 ± 14^c	1567 ± 22^d	ND	1791 ± 10^c	1144 ± 14^e
Potato	305 ± 1.7^d	407 ± 22^c	576 ± 24^b	1288 ± 27^e	ND	690 ± 1.6^f	537 ± 12^f
Soybean	206 ± 7.9^e	1502 ± 63^a	408 ± 12^c	2116 ± 58^b	113 ± 4.8^a	4020 ± 14^a	1907 ± 54^d
Sweet potato	662 ± 19^b	284 ± 16^d	953 ± 48^a	1899 ± 67^c	ND	590 ± 1.9^h	313 ± 11^g
Wheat flour	21 ± 1.4^g	101 ± 3.1^e	8.1 ± 0.5^e	130 ± 4.8^g	4.9 ± 0.2^b	1210 ± 8.5^d	9353 ± 367^a
White rice	20 ± 0.6^g	57 ± 1.9^f	8.6 ± 0.4^e	86 ± 2.1^h	2.3 ± 0.1^c	660 ± 2.6^g	7656 ± 185^b

Values are mean ± SEM, $n = 6$

Total AA total amino acids (peptide-bound plus free amino acids), *ND* not detected, *PA* polyamines (putrescine + spermidine + spermine)

[a–h]Within a column, means not sharing the same superscript letter differ ($P < 0.05$)

polyamines, with putrescine being intermediate and spermidine being the lowest. In peanuts and soybeans, the content of spermidine was the highest among the polyamines, with spermine being intermediate and putrescine being the lowest. In pistachio nuts, wheat flour and white rice, the content of spermidine was also the highest among the polyamines, with putrescine being intermediate and spermine being the lowest.

An appreciable amount of agmatine was present in corn grain and soybean, but only a negligible amount of this amine was found in wheat flour and white rice (Table 2). Agmatine was not detected in peanuts, pistachio nuts, potatoes, or sweet potatoes. We did not analyze thermospermine or cadaverine in the plant-source foods.

Content of total AAs (peptide-bound plus free AAs) in plant-source foods

Expressed on a DM basis, the percentages of total AAs (peptide-bound plus free AAs) in plant-source foods varied greatly with foods (Table 3). Among all the analyzed foods, soybeans had the highest content of total AAs and all individual AAs, followed by peanuts and pistachio nuts. The abundances of individual AAs in plant-source foods varied greatly, with the five most abundant AAs in the foods being listed in Table 4. Except for sweet potatoes, all the foods contained a high content of glutamate plus glutamine. In all the analyzed foods, tryptophan was the least abundant AA (e.g., only 0.75 mg/g of DM in corn grains and 1.1 mg/g of DM in white rice), with histidine being the fourth least abundant (e.g., only 2.7 mg/g of DM in corn grains and 2.2 mg/g of DM in white rice). Interestingly, cysteine or methionine was either the second or third least abundant AA in food, depending on its type. For example, cysteine and methionine were the second and third least abundant AAs, respectively, in corn grains, pistachio nuts, potatoes and white rice, but the order of their abundances was reversed in peanuts, soybeans, sweet potatoes, and wheat flour.

The content of branched-chain AAs (BCAAs) in plant-source foods was relatively high in comparison with many of the other AAs. Of note, leucine was the most abundant AA in corn grains. The content of BCAAs (leucine + isoleucine + valine) in the total AAs of the analyzed foods was as follows: 20.4%, corn grains; 14.2%, peanuts; 17.4%, pistachio nuts; 14.2%, potatoes; 17.0%, soybeans; 17.1%, sweet potatoes; 13.5%, wheat flour; and 19.1%, white rice. The content of total glutamate plus glutamine in foods was either similar to, lower than, or greater than the content of total BCAAs, depending on individual foods. The content of total glutamate plus glutamine in the DM of the analyzed foods (i.e., % of DM) was as follows: 1.9%, corn grains; 5.8%, peanuts; 4.5%, pistachio nuts; 1.7%, potatoes; 9.6%, soybeans; 0.77%, sweet potatoes; 4.8%, wheat flour; and 1.5%, white rice. Of particular note, glutamine alone represented 18.0% and 29.0% of total AAs in potatoes and wheat flour, respectively. Glutamine was the most abundant AA in wheat flour and the second most abundant AA in potatoes. In contrast, glutamate was the most abundant AA in soybeans, accounting for 10.1% of total AAs.

The content of total aspartate plus asparagine was not particularly high in non-tuber foods, but asparagine was the most abundant AA in potatoes and sweet potatoes. The content of total aspartate plus asparagine in the DM of the analyzed foods (i.e., % of DM) was as follows: 0.86%, corn grains; 3.4%, peanuts; 2.0%, pistachio nuts; 2.3%, potatoes; 6.2%, soybeans; 1.5%, sweet potatoes; 0.81%, wheat flour; and 0.89%, white rice. It is noteworthy that asparagine represented 21.2% and 16.2% of total AAs in potatoes and sweet potatoes, respectively.

Table 3 The content of total amino acids (peptide-bound plus free amino acids) in plant-source foods

AA	Corn grain	Peanut	Pistachio nut	Potato	Soybean	Sweet potato	Wheat flour	White rice
Asp	4.74 ± 0.04^{d}	14.2 ± 0.11^{b}	9.89 ± 0.14^{c}	4.05 ± 0.03^{e}	37.3 ± 0.17^{a}	3.34 ± 0.03^{f}	3.58 ± 0.03^{f}	4.27 ± 0.03^{e}
Asn	3.88 ± 0.03^{f}	19.7 ± 0.15^{b}	10.2 ± 0.15^{d}	19.2 ± 0.12^{b}	24.6 ± 0.11^{a}	12.0 ± 0.10^{c}	4.47 ± 0.03^{e}	4.60 ± 0.03^{e}
Glu	7.13 ± 0.06^{d}	28.6 ± 0.19^{b}	18.4 ± 0.20^{c}	1.01 ± 0.01^{e}	52.6 ± 0.38^{a}	5.46 ± 0.03^{e}	2.80 ± 0.02^{f}	7.38 ± 0.12^{d}
Gln	11.8 ± 0.11^{f}	29.0 ± 0.19^{c}	26.9 ± 0.29^{d}	16.3 ± 0.23^{e}	43.0 ± 0.31^{b}	2.20 ± 0.01^{h}	45.5 ± 0.37^{a}	7.96 ± 0.13^{g}
Ser	5.05 ± 0.04^{d}	14.4 ± 0.16^{b}	14.0 ± 0.15^{b}	3.55 ± 0.03^{g}	30.2 ± 0.32^{a}	4.54 ± 0.04^{e}	6.90 ± 0.06^{c}	4.09 ± 0.03^{f}
His	2.68 ± 0.03^{e}	6.98 ± 0.05^{b}	5.30 ± 0.04^{c}	1.70 ± 0.02^{g}	12.7 ± 0.10^{a}	1.18 ± 0.04^{h}	3.54 ± 0.04^{d}	2.20 ± 0.03^{f}
Gly	4.43 ± 0.05^{e}	19.0 ± 0.25^{b}	11.7 ± 0.22^{c}	2.74 ± 0.03^{h}	24.0 ± 0.17^{a}	3.52 ± 0.03^{g}	6.31 ± 0.04^{d}	3.95 ± 0.06^{f}
Thr	3.58 ± 0.04^{e}	8.12 ± 0.05^{b}	7.14 ± 0.04^{c}	3.19 ± 0.03^{f}	20.9 ± 0.24^{a}	3.74 ± 0.03^{e}	4.09 ± 0.04^{d}	3.02 ± 0.04^{f}
Arg	4.34 ± 0.04^{f}	35.5 ± 0.23^{b}	23.8 ± 0.35^{c}	5.15 ± 0.03^{e}	37.2 ± 0.32^{a}	3.08 ± 0.03^{g}	7.20 ± 0.05^{d}	7.28 ± 0.05^{d}
Ala	7.97 ± 0.05^{d}	12.4 ± 0.18^{b}	11.3 ± 0.26^{c}	2.82 ± 0.02^{g}	22.9 ± 0.22^{a}	4.80 ± 0.03^{f}	5.42 ± 0.04^{e}	4.58 ± 0.04^{f}
Tyr	4.80 ± 0.04^{d}	11.0 ± 0.22^{b}	5.32 ± 0.05^{c}	2.34 ± 0.03^{g}	18.4 ± 0.19^{a}	2.99 ± 0.05^{f}	3.86 ± 0.04^{e}	2.37 ± 0.04^{g}
Met	2.26 ± 0.03^{e}	3.43 ± 0.04^{c}	3.80 ± 0.05^{b}	1.53 ± 0.03^{g}	6.43 ± 0.04^{a}	1.22 ± 0.02^{h}	2.48 ± 0.03^{d}	2.02 ± 0.05^{f}
Val	5.07 ± 0.05^{e}	12.7 ± 0.18^{c}	13.2 ± 0.20^{b}	4.98 ± 0.04^{e}	24.6 ± 0.15^{a}	4.46 ± 0.03^{f}	6.24 ± 0.04^{d}	5.19 ± 0.08^{e}
Phe	5.18 ± 0.05^{e}	14.8 ± 0.15^{b}	11.5 ± 0.21^{c}	3.92 ± 0.03^{h}	25.6 ± 0.20^{a}	4.83 ± 0.04^{f}	7.53 ± 0.04^{d}	4.39 ± 0.06^{g}
Ile	3.85 ± 0.03^{e}	10.8 ± 0.16^{b}	10.2 ± 0.11^{c}	3.19 ± 0.03^{f}	23.9 ± 0.21^{a}	3.31 ± 0.04^{f}	4.92 ± 0.04^{d}	3.74 ± 0.06^{e}
Leu	12.8 ± 0.16^{d}	18.1 ± 0.14^{b}	16.9 ± 0.12^{c}	4.72 ± 0.04^{g}	40.0 ± 0.28^{a}	4.88 ± 0.03^{g}	10.0 ± 0.15^{e}	7.26 ± 0.06^{f}
Lys	2.85 ± 0.03^{f}	9.98 ± 0.12^{c}	11.9 ± 0.22^{b}	5.13 ± 0.02^{d}	32.6 ± 0.24^{a}	3.61 ± 0.05^{e}	3.64 ± 0.04^{e}	2.33 ± 0.05^{g}
Cys	2.17 ± 0.03^{e}	4.15 ± 0.05^{b}	3.56 ± 0.07^{c}	1.14 ± 0.02^{g}	7.67 ± 0.04^{a}	1.63 ± 0.03^{f}	3.04 ± 0.04^{d}	1.66 ± 0.05^{f}
Pro	11.3 ± 0.31^{e}	16.5 ± 0.14^{c}	12.9 ± 0.35^{d}	3.02 ± 0.05^{g}	28.4 ± 0.22^{a}	2.64 ± 0.03^{g}	23.2 ± 0.35^{b}	5.41 ± 0.05^{f}
Hyp	0.04 ± 0.001^{e}	0.79 ± 0.01^{a}	0.59 ± 0.01^{b}	0.08 ± 0.001^{d}	0.78 ± 0.01^{a}	0.05 ± 0.001^{e}	0.43 ± 0.01^{c}	0.04 ± 0.001^{e}
Trp	0.75 ± 0.02^{f}	2.72 ± 0.06^{b}	2.62 ± 0.03^{b}	1.01 ± 0.02^{e}	7.02 ± 0.04^{a}	0.48 ± 0.01^{g}	1.70 ± 0.04^{c}	1.12 ± 0.05^{d}
Total	106.7 ± 0.39^{e}	292.9 ± 1.1^{b}	231.1 ± 1.3^{c}	90.8 ± 0.22^{f}	520.6 ± 1.8^{a}	73.9 ± 0.37^{h}	156.9 ± 1.1^{d}	84.9 ± 0.34^{g}

Values, expressed as mg/g of dry matter, are mean ± SEM, $n=6$. The molecular weights of intact amino acids were used to calculate the amount of peptide-bound plus free amino acids in the acid or alkaline hydrolysates of foods. This calculation always overestimates the true content of protein and peptides in foods

Hyp 4-hydroxyproline

[a–h]Within a row, means not sharing the same superscript letter differs ($P<0.05$)

Table 4 Most abundant amino acids in plant-source foods (based on mg of amino acid/g of dry matter in food)

Order of abundance	Corn grain	Peanut	Pistachio nut	Potato	Soybean	Sweet potato	Wheat flour	White rice
Most abundant amino acids (peptide plus free amino acids) in foods								
First	Leucine	Arginine	Glutamine	Asparagine	Glutamate	Asparagine	Glutamine	Glutamine
Second	Glutamine	Glutamine	Arginine	Glutamine	Glutamine	Glutamate	Proline	Glutamate
Third	Proline	Glutamate	Glutamate	Arginine	Leucine	Leucine	Leucine	Arginine
Fourth	Alanine	Asparagine	Leucine	Lysine	Aspartate	Phe	Phe	Leucine
Fifth	Glutamate	Leucine	Serine	Valine	Arginine	Alanine	Arginine	Proline
Most abundant free amino acids in foods								
First	Glutamine	Glycine	Glycine	Asparagine	Arginine	Asparagine	Aspartate	Asparagine
Second	Glutamate	Glutamate	Glutamate	Glutamine	Glutamate	Glutamate	Asparagine	Glutamate
Third	Proline	Alanine	Alanine	Arginine	Asparagine	Serine	Glutamate	Proline
Fourth	Serine	Phe	Arginine	Aspartate	Aspartate	Aspartate	Glutamine	Leucine
Fifth	Leu, Ala	Asparagine	Aspartate	Valine	Histidine	Threonine	Arginine	Arginine
Most abundant peptide-bound amino acids in foods								
First	Leucine	Arginine	Glutamine	Asparagine	Glutamate	Asparagine	Glutamine	Glutamine
Second	Glutamine	Glutamine	Arginine	Glutamine	Glutamine	Leucine	Proline	Glutamate
Third	Proline	Glutamate	Glutamate	Lysine	Leucine	Phe	Leucine	Arginine
Fourth	Alanine	Asparagine	Leucine	Leucine	Aspartate	Alanine	Phe	Leucine
Fifth	Glutamate	Leucine	Serine	Valine	Arginine	Valine	Arginine	Proline

The percentage of arginine in total AAs was relatively high in peanuts (12.1%) and pistachio nuts (10.3%), intermediate in soybeans (7.2%), white rice (8.6%), and potatoes (5.7%), but was relatively low in corn grains (4.1%), sweet potatoes (4.2%), and wheat flour (4.6%). In corn grains and wheat flour, the content of total arginine was lower than that of proline, but the opposite was observed for all other foods. A very small amount of 4-hydroxyproline was present in peanuts, pistachio nuts, soybeans, and wheat flour, but this amino acid was barely detectable in corn grains, potatoes, sweet potatoes, and white rice (Table 3).

The ratios of total AAs to total polyamines in plant foods (mol/mol) were the greatest ($P < 0.05$) in wheat flour and the lowest ($P < 0.05$) in corn grains, with the values being 9337:1 and 95:1, respectively (Table 2). Thus, compared with total AAs, the amount of total polyamines in these foods was relatively small.

Content of free AAs in plant-source foods

On the DM basis, potatoes and sweet potatoes contained 3.1% and 2.1% of free AAs, respectively, whereas corn grains, peanuts, pistachio nuts, soybeans, wheat flour and white rice were comprised of < 0.5% of free AAs (Table 5). Except for asparagine, glutamine, arginine, aspartate, and valine in potatoes, as well as asparagine, glutamate, serine, aspartate, threonine, alanine, phenylalanine, proline and valine in sweet potatoes, the content of free AAs in plant-source foods was very low or negligible. The percentages of free AAs in the total AAs (peptide-bound plus free AAs) of the analyzed foods were as follows: 3.1%, corn grains; 1.4%, peanuts; 2.1%, pistachio nuts; 34.4%, potatoes; 0.81%, soybeans; 28.5%, sweet potatoes; 0.82%, wheat flour; and 0.57%, white rice. The five predominant free AAs in the foods are listed in Table 4. The most abundant free AA in the analyzed foods was: glutamine in corn grains; glycine in peanuts and pistachio nuts; asparagine in potatoes, sweet potatoes and white rice; arginine in soybeans; and aspartate

Table 5 The content of free amino acids in plant-source foods

AA	Corn grain	Peanut	Pistachio nut	Potato	Soybean	Sweet potato	Wheat flour	White rice
Asp	151 ± 3.3^{d}	128 ± 3.8^{d}	269 ± 4.3^{c}	2017 ± 24^{a}	240 ± 3.9^{c}	1803 ± 10^{b}	256 ± 7.3^{c}	21.0 ± 0.72^{e}
Asn	114 ± 3.2^{f}	154 ± 3.3^{e}	112 ± 2.4^{f}	10095 ± 126^{a}	435 ± 5.8^{c}	3686 ± 32^{b}	237 ± 6.4^{d}	93.7 ± 0.84^{g}
Glu	410 ± 4.8^{d}	572 ± 18^{c}	833 ± 11^{b}	112 ± 2.3^{f}	601 ± 5.6^{c}	2250 ± 26^{a}	165 ± 3.6^{e}	65.7 ± 1.7^{g}
Gln	429 ± 6.9^{c}	8.30 ± 0.24^{g}	39.5 ± 1.6^{e}	7957 ± 46^{a}	15.2 ± 0.34^{f}	603 ± 7.4^{b}	88.2 ± 0.95^{d}	10.3 ± 0.43^{g}
Ser	233 ± 4.2^{c}	96.0 ± 3.1^{d}	95.8 ± 3.3^{d}	679 ± 9.0^{b}	62.7 ± 1.0^{e}	1946 ± 29^{a}	42.7 ± 0.71^{f}	34.2 ± 0.70^{g}
His	40.2 ± 0.75^{d}	35.8 ± 0.48^{d}	36.6 ± 1.5^{d}	965 ± 23^{a}	217 ± 4.5^{b}	183 ± 2.1^{c}	14.8 ± 0.28^{e}	8.20 ± 0.26^{f}
Gly	193 ± 4.1^{c}	1082 ± 33^{a}	1019 ± 33^{a}	108 ± 2.2^{d}	48.5 ± 0.82^{e}	401 ± 5.5^{b}	24.7 ± 0.44^{f}	7.02 ± 0.13^{g}
Thr	197 ± 3.8^{c}	89.7 ± 1.2^{e}	129 ± 3.4^{d}	399 ± 4.2^{b}	24.3 ± 0.36^{f}	1485 ± 20^{a}	16.8 ± 0.43^{g}	10.3 ± 0.42^{h}
Arg	37.8 ± 1.4^{g}	781 ± 16^{c}	722 ± 14^{d}	2058 ± 30^{a}	1819 ± 20^{b}	467 ± 8.6^{e}	84.6 ± 0.81^{f}	35.5 ± 0.76^{g}
Ala	224 ± 4.3^{d}	344 ± 4.7^{c}	746 ± 8.4^{b}	243 ± 3.8^{d}	146 ± 2.9^{e}	1342 ± 18^{a}	70.4 ± 0.83^{f}	33.8 ± 0.65^{g}
Tyr	146 ± 3.4^{b}	80.5 ± 1.4^{c}	78.3 ± 1.6^{c}	619 ± 8.2^{a}	38.7 ± 0.80^{d}	632 ± 6.4^{a}	20.6 ± 0.51^{e}	15.2 ± 0.60^{f}
Met	35.7 ± 0.65^{c}	34.0 ± 0.57^{c}	35.5 ± 0.80^{c}	483 ± 7.5^{a}	34.2 ± 0.52^{c}	274 ± 5.9^{b}	11.2 ± 0.38^{d}	5.85 ± 0.14^{e}
Val	162 ± 2.8^{c}	108 ± 2.4^{d}	91.1 ± 1.3^{d}	1463 ± 30^{a}	39.1 ± 0.76^{e}	1103 ± 28^{b}	26.1 ± 0.44^{f}	19.8 ± 0.53^{g}
Phe	72.5 ± 0.76^{e}	164 ± 2.7^{c}	103 ± 2.4^{d}	824 ± 17^{b}	56.2 ± 0.58^{f}	1319 ± 18^{a}	15.9 ± 0.38^{g}	7.47 ± 0.24^{h}
Ile	119 ± 3.7^{c}	88.0 ± 1.1^{d}	77.9 ± 1.5^{d}	731 ± 10^{a}	32.3 ± 0.49^{e}	671 ± 8.6^{b}	14.3 ± 0.51^{f}	8.28 ± 0.20^{g}
Leu	225 ± 6.0^{c}	136 ± 2.3^{d}	116 ± 3.1^{e}	514 ± 5.9^{b}	50.7 ± 0.60^{f}	813 ± 5.7^{a}	52.6 ± 0.73^{f}	40.5 ± 0.62^{g}
Lys	84.3 ± 1.1^{c}	83.8 ± 1.3^{c}	82.5 ± 1.6^{c}	492 ± 6.7^{a}	86.2 ± 0.48^{c}	297 ± 3.2^{b}	28.8 ± 0.69^{d}	6.37 ± 0.34^{e}
Cys	32.6 ± 0.80^{d}	28.5 ± 0.62^{de}	26.0 ± 0.37^{e}	387 ± 5.5^{a}	40.2 ± 0.57^{c}	220 ± 5.1^{b}	14.7 ± 0.51^{f}	5.48 ± 0.18^{g}
Pro	280 ± 3.8^{c}	60.7 ± 1.6^{f}	56.4 ± 0.89^{f}	689 ± 9.2^{b}	109 ± 1.9^{d}	1246 ± 13^{a}	78.3 ± 1.1^{e}	43.8 ± 0.70^{g}
Trp	20.2 ± 0.41^{e}	24.0 ± 0.29^{d}	23.0 ± 0.41^{d}	322 ± 4.8^{a}	34.6 ± 0.42^{c}	193 ± 3.4^{b}	5.73 ± 0.05^{f}	4.61 ± 0.07^{g}
Cit	28.5 ± 0.41^{a}	12.9 ± 0.44^{d}	17.6 ± 0.66^{c}	18.7 ± 0.35^{c}	22.3 ± 0.42^{b}	12.7 ± 0.52^{d}	2.30 ± 0.05^{e}	1.68 ± 0.04^{e}
β-Ala	9.92 ± 0.35^{f}	16.7 ± 0.63^{d}	23.3 ± 1.2^{c}	46.0 ± 1.9^{b}	69.3 ± 2.2^{a}	12.2 ± 0.5^{e}	3.99 ± 0.23^{g}	2.38 ± 0.03^{h}
Orn	19.2 ± 0.46^{c}	8.10 ± 0.16^{ef}	11.8 ± 0.50^{d}	91.8 ± 1.2^{a}	9.08 ± 0.30^{e}	21.7 ± 0.62^{b}	6.79 ± 0.07^{f}	0.83 ± 0.04^{g}
Total	3266 ± 13^{e}	4137 ± 42^{d}	4745 ± 57^{c}	31247 ± 261^{b}	4231 ± 37^{d}	21092 ± 144^{a}	1282 ± 17^{f}	482 ± 2.9^{g}

Values, expressed as µg/g of dry matter, are mean ± SEM, $n = 6$. The molecular weights of intact amino acids were used to calculate the amount of free amino acids in foods

Cit citrulline, *β-Ala* β-alanine, *Orn* ornithine

$^{a\text{–}h}$Within a row, means not sharing the same superscript letter differs ($P < 0.05$)

in wheat flour. Note that free glycine accounted for 26.2% and 21.5% of total free AAs in peanuts and pistachio nuts, respectively, whereas asparagine represented 32.3%, 17.5% and 19.4% of total free AAs in potatoes, sweet potatoes and white rice, respectively.

A small amount of free citrulline, β-alanine and ornithine was present in all the analyzed foods (Table 5). In contrast, taurine, carnosine, anserine, creatine and free 4-hydroxyproline were not detected in corn grains, peanuts, pistachio nuts, potatoes, soybeans, sweet potatoes, wheat flour, or white rice. This is a distinct difference between plant- and animal-source foods.

Content of peptide-bound AAs in plant-source foods

Except for potatoes and sweet potatoes, the content and the order of abundance of peptide (protein, polypeptide and oligopeptide)-bound AAs in plant-source foods were generally similar to the patterns of their total AAs (peptide-bound plus free AAs) (Tables 3, 6). Among all the analyzed foods, the content of peptide-bound AAs (DM basis) was the greatest in soybeans, followed by peanuts, pistachio nuts, wheat flour, corn grains, white rice, potatoes, and sweet potatoes in descending order. In both potatoes and sweet potatoes, asparagine was the most abundant peptide-bound AA (Table 4). Glutamine, lysine, leucine and valine were the second, third, fourth and fifth most abundant peptide-bound AAs, respectively, in potatoes. In sweet potatoes, leucine was the second most abundant peptide-bound AA, followed by phenylalanine, alanine and valine in descending order.

Because one molecule of water is lost from each AA when one peptide bond is formed in proteins and polypeptides, the amounts of total peptide-bound AAs as calculated based on the molecular weights of AA residues were about 15% lower than those as calculated based on the molecular weights of intact AAs. For example, the ratios of total peptide-bound

Table 6 The content of peptide-bound amino acids in plant-source foods

AA	Corn grain	Peanut	Pistachio nut	Potato	Soybean	Sweet potato	Wheat flour	White rice
Asp	4.59 ± 0.04^{d}	14.0 ± 0.11^{b}	9.62 ± 0.15^{c}	2.04 ± 0.03^{g}	37.1 ± 0.17^{a}	1.53 ± 0.02^{h}	3.33 ± 0.03^{f}	4.25 ± 0.03^{e}
Asn	3.77 ± 0.03^{g}	19.6 ± 0.15^{b}	10.1 ± 0.15^{c}	9.15 ± 0.13^{d}	24.1 ± 0.11^{a}	8.28 ± 0.12^{e}	4.23 ± 0.04^{f}	4.51 ± 0.03^{f}
Glu	6.72 ± 0.06^{e}	28.0 ± 0.19^{b}	17.6 ± 0.20^{c}	0.89 ± 0.02^{h}	52.0 ± 0.39^{a}	3.21 ± 0.04^{f}	2.64 ± 0.03^{g}	7.32 ± 0.12^{d}
Gln	11.4 ± 0.10^{e}	28.9 ± 0.19^{c}	26.9 ± 0.29^{d}	8.36 ± 0.27^{f}	43.0 ± 0.31^{b}	1.59 ± 0.01^{g}	45.4 ± 0.37^{a}	7.95 ± 0.13^{f}
Ser	4.82 ± 0.04^{d}	14.3 ± 0.16^{b}	13.9 ± 0.15^{b}	2.88 ± 0.02^{f}	30.0 ± 0.33^{a}	2.60 ± 0.05^{f}	6.86 ± 0.06^{c}	4.05 ± 0.03^{e}
His	$2.64 \pm \pm 0.03^{e}$	6.94 ± 0.05^{b}	5.27 ± 0.04^{c}	0.74 ± 0.04^{h}	12.5 ± 0.10^{a}	0.99 ± 0.04^{g}	3.53 ± 0.04^{d}	2.19 ± 0.03^{f}
Gly	4.24 ± 0.05^{e}	17.9 ± 0.24^{b}	10.7 ± 0.20^{c}	2.63 ± 0.03^{g}	24.0 ± 0.17^{a}	3.12 ± 0.03^{f}	6.28 ± 0.04^{d}	3.95 ± 0.06^{e}
Thr	3.38 ± 0.04^{e}	8.04 ± 0.05^{b}	7.01 ± 0.04^{c}	2.79 ± 0.03^{f}	20.9 ± 0.24^{a}	2.26 ± 0.03^{g}	4.07 ± 0.04^{d}	3.01 ± 0.04^{f}
Arg	$4.30 \pm \pm 0.04^{d}$	34.7 ± 0.23^{a}	23.1 ± 0.36^{b}	3.10 ± 0.03^{e}	35.4 ± 0.32^{a}	2.61 ± 0.03^{e}	7.12 ± 0.05^{c}	7.25 ± 0.05^{c}
Ala	7.74 ± 0.05^{d}	12.1 ± 0.18^{b}	10.6 ± 0.27^{c}	2.58 ± 0.02^{h}	22.7 ± 0.23^{a}	3.46 ± 0.04^{g}	5.35 ± 0.04^{e}	4.55 ± 0.04^{f}
Tyr	4.66 ± 0.04^{d}	10.9 ± 0.22^{b}	5.24 ± 0.05^{c}	1.73 ± 0.03^{g}	18.4 ± 0.19^{a}	2.36 ± 0.05^{f}	3.84 ± 0.04^{e}	2.36 ± 0.04^{f}
Met	2.23 ± 0.03^{e}	3.39 ± 0.04^{c}	3.76 ± 0.05^{b}	1.05 ± 0.03^{g}	6.39 ± 0.04^{a}	0.95 ± 0.04^{g}	2.47 ± 0.03^{d}	2.02 ± 0.05^{f}
Val	4.90 ± 0.05^{e}	12.6 ± 0.18^{c}	13.1 ± 0.20^{b}	3.58 ± 0.07^{f}	24.6 ± 0.15^{a}	3.36 ± 0.05^{f}	6.22 ± 0.04^{d}	5.17 ± 0.08^{e}
Phe	5.11 ± 0.05^{e}	14.7 ± 0.15^{b}	11.4 ± 0.22^{c}	3.10 ± 0.03^{h}	25.6 ± 0.20^{a}	3.51 ± 0.05^{g}	7.51 ± 0.04^{d}	4.39 ± 0.06^{f}
Ile	3.73 ± 0.04^{e}	10.7 ± 0.16^{b}	10.1 ± 0.11^{c}	2.46 ± 0.03^{f}	23.9 ± 0.21^{a}	2.64 ± 0.04^{f}	4.91 ± 0.04^{d}	3.73 ± 0.06^{e}
Leu	12.5 ± 0.16^{d}	18.0 ± 0.13^{b}	16.7 ± 0.12^{c}	4.21 ± 0.04^{g}	39.9 ± 0.28^{a}	4.07 ± 0.03^{g}	9.95 ± 0.15^{e}	7.22 ± 0.06^{f}
Lys	2.77 ± 0.03^{f}	9.90 ± 0.12^{c}	11.8 ± 0.22^{b}	4.64 ± 0.02^{d}	32.6 ± 0.24^{a}	3.32 ± 0.04^{e}	3.62 ± 0.06^{e}	2.32 ± 0.05^{g}
Cys	2.14 ± 0.03^{e}	4.12 ± 0.05^{b}	3.54 ± 0.07^{c}	0.75 ± 0.02^{h}	7.73 ± 0.09^{a}	1.41 ± 0.03^{g}	3.02 ± 0.04^{d}	1.62 ± 0.05^{f}
Pro	11.0 ± 0.31^{e}	16.4 ± 0.14^{c}	12.8 ± 0.35^{d}	2.33 ± 0.05^{g}	28.3 ± 0.22^{a}	1.40 ± 0.03^{h}	23.2 ± 0.35^{b}	5.36 ± 0.05^{f}
Hyp	0.04 ± 0.001^{e}	0.79 ± 0.01^{a}	0.59 ± 0.01^{b}	0.08 ± 0.001^{d}	0.78 ± 0.01^{a}	0.05 ± 0.001^{e}	0.43 ± 0.01^{c}	0.04 ± 0.001^{f}
Trp	0.73 ± 0.01^{e}	2.70 ± 0.06^{b}	2.60 ± 0.03^{b}	0.69 ± 0.01^{e}	6.99 ± 0.04^{a}	0.29 ± 0.02^{g}	1.70 ± 0.04^{c}	1.12 ± 0.05^{d}
Total[1]	103.5 ± 0.37^{e}	288.8 ± 1.1^{b}	226.4 ± 1.3^{c}	59.8 ± 0.30^{g}	516.5 ± 1.7^{a}	53.0 ± 0.34^{h}	155.6 ± 1.1^{d}	84.4 ± 0.34^{f}
Total[2]	88.5 ± 0.32^{e}	248.3 ± 0.92^{b}	194.7 ± 1.1^{c}	51.3 ± 0.26^{g}	444.0 ± 1.5^{a}	45.3 ± 0.29^{h}	133.8 ± 1.0^{d}	72.5 ± 0.29^{f}

Values, expressed as mg/g of dry matter, are mean ± SEM, $n = 6$

Hyp 4-hydroxyproline

[1]The molecular weights of intact amino acids were used to calculate the amount of peptide-bound amino acids in the acid or alkaline hydrolysates of foods. This calculation always overestimates the true content of protein and peptides in foods

[2]The molecular weights of amino acid residues were used to calculate the amount of peptide-bound amino acids in the acid or alkaline hydrolysates of foods. Total peptide-bound amino acids represent true proteins plus peptides in foods

[a–h]Within a row, means not sharing the same superscript letter differs ($P < 0.05$)

AAs calculated based on the molecular weights of AA residues to total peptide-bound AAs calculated based on the molecular weights of intact AAs were: 0.855, corn grains; 0.860, peanuts; 0.860, pistachio nuts; 0.858, potatoes; 0.860, soybeans; 0.855, sweet potatoes; 0.860, wheat flour; and 0.859, white rice. The content of total peptide-bound AAs calculated based on the molecular weights of AA residues represents the content of true proteins plus peptides in foods. The ratios of true proteins plus peptides to crude protein varied among foods and were: 0.876, corn grains; 0.896, peanuts; 0.906, pistachio nuts; 0.521, potatoes; 0.996, soybeans; 0.656, sweet potatoes; 0.998, wheat flour; and 0.879, white rice. The content of true protein plus peptides in soybeans and wheat flour was almost the same as that of crude protein, but the differences were substantial for potatoes and sweet potatoes.

Discussion

Plants are important sources of nutrients in human diets (Ewart 1967; Clarke et al. 1976; Goldflus et al. 2006; Rizzo and Baroni 2018; Wu et al. 2014). About 150 plant species have been cultivated by humans for food in modern history, with about 20 of them being consumed as food by a majority of the world's population (Abiose and Ikujenlola 2014; Badenhop and Hackler 1971; Han and Liu 2010; Young and Pellett 1994). Thus, adequate knowledge about the composition of polyamines, as well as free and protein-bound AAs, is essential to promote human consumption of foods of plant origin. However, despite some studies of cereal grains, legumes, tubers, and nuts, data on their content of polyamines and AAs are incomplete and highly inconsistent (Tables 7 and 8; Supplemental Tables 1–3). This is possibly because

Table 7 Published data on the content of polyamines and agmatine in plant-source foods

Food	Bardócz et al. (1993)	Kalač et al. (2005)	Okamoto et al. (1997)	Nishibori et al. (2007)	Nishimura et al. (2006)	Farriol et al. (2004)	Hou et al. (this study)
Putrescine (nmol/g wet weight)							
Corn grain	–	–	–	–	198–842	111	1325
Peanut, dried	–	–	–	18	–	–	48
Pistachio nut, dried	–	–	–	207	–	–	503
Potato	110	–	200	82	96–255	2.6	69
Soybean, dried	46	351	470	194	400–650	–	198
Sweet potato	–	–	–	43	15	–	226
Wheat flour	–	–	17	32	34	–	20
White rice[a]	–	–	< 10	2	14	1.3	18
Spermidine (nmol/g wet weight)							
Corn grain	–	–	–	–	298	17	286
Peanut, dried	–	–	–	110	–	–	407
Pistachio nut, dried	–	–	–	77	–	–	621
Potato	77	–	93	50	86	7	92
Soybean, dried	329	1241	1430	728	1090	–	1445
Sweet potato	–	–	–	31	20	–	97
Wheat flour	–	–	66	34	56	–	96
White rice	–	–	27	3	12	0.62	52
Spermine (nmol/g wet weight)							
Corn grain	–	–	ND	–	6	ND	17
Peanut, dried	–	–	–	88	–	–	87
Pistachio nut, dried	–	–	–	66	–	–	419
Potato	15	–	ND	14	17	1.2	130
Soybean, dried	159	36–95	340	181	290	–	393
Sweet potato	–	–	–	4	29	–	326
Wheat flour	–	–	26	7	ND	–	8
White rice	–	–	< 20	3	ND	2	8

Values are means

ND not detected, the sign "–" absence of data

[a]Polished white rice

Table 8 Published data on amino acid (AA) composition in potatoes and sweet potatoes

AA	Potatoes					Sweet potatoes				
	Hughes (1957)[a]	Kaldy and Markakis (1972)[a]	Bártová et al. (2015)[a]	Hou et al. (this study)		Yeoh and Truong (1996)[b]	Ooman et al. (1961)[a]	Purcell and Walter (1982)[a]	Hou et al. (this study)	
				(2019)[a]	(2019)[b]				(2019)[a]	(2019)[b]
Asp	13.0[c]	18.6–29.0[c]	17.0–33.0[c]	4.22	4.46	14.6–27.1[c]	28.0[c]	20.2[c]	4.84	4.51
Asn	–	–	–	20.0	21.2	–	–	–	17.4	16.2
Glu	11.3[d]	13.2–17.0[d]	12.2–15.1[d]	1.05	1.11	13.9–21.1[d]	8.02[d]	7.41[d]	7.91	7.40
Gln	–	–	–	17.0	18.0	–	–	–	3.19	2.97
Ser	5.8	3.5–4.9	2.78–4.92	3.70	3.91	6.7–7.4	3.94	3.83	6.58	6.14
His	2.4	2.1–2.4	4.03–5.83	1.77	1.88	1.5–1.9	0.72	2.75	1.71	1.59
Gly	4.9	2.5–3.6	3.60–5.22	2.85	3.02	3.6–6.3	2.94	4.19	5.10	4.76
Thr	5.7	3.4–4.9	2.16–3.32	3.32	3.51	4.8–5.9	3.14	4.50	5.42	5.06
Arg	5.5	4.8–5.1	12.0–17.9	5.36	5.67	3.1–4.7	5.08	4.28	4.46	4.17
Ala	4.7	2.3–3.6	2.88–5.24	2.94	3.11	6.0–7.4	4.70	6.24	6.96	6.50
Tyr	6.1	3.4–4.2	1.80–2.47	2.44	2.58	3.2–4.1	2.37	5.81	4.33	4.05
Met	2.8	1.4–1.8	0.97–1.26	1.59	1.68	1.6–2.2	1.02	2.69	1.77	1.65
Val	8.0	5.4–6.0	3.44–4.84	5.19	5.48	4.6–5.3	4.30	6.83	6.46	6.03
Phe	6.2	3.9–5.2	3.08–4.52	4.08	4.32	4.8–5.9	3.49	7.32	7.00	6.53
Ile	6.8	3.6–4.8	2.42–3.09	3.32	3.52	3.1–3.5	3.84	4.57	4.80	4.48
Leu	11.1	4.8–7.9	3.25–4.95	4.92	5.20	6.2–7.8	4.85	7.47	7.07	6.60
Lys	8.3	5.3–7.0	7.18–10.5	5.34	5.65	3.3–5.6	2.62	6.60	5.23	4.89
Cys	1.6	1.1–1.5	0.92–1.57	1.19	1.25	0.1–0.2	–	–	2.36	2.20
Pro	5.1	3.0–4.8	–	3.15	3.33	3.7–4.9	3.09	3.99	3.83	3.57
Hyp	–	–	–	0.083	0.088	–	–	–	0.070	0.064
Trp	1.8	1.3–1.7	–	1.05	1.11	0.5–1.0	1.66	0.44	0.70	0.65

[a]Values are expressed as g AA/16 g nitrogen (100 g food protein) to facilitate comparisons among different studies. Amounts of AAs (peptide-bound plus free AAs) were calculated on the basis of their intact molecular weights

[b]Values are expressed as g AA/100 g of total AAs. Amounts of AAs (peptide-bound plus free AAs) were calculated on the basis of their intact molecular weights

[c]Aspartate plus asparagine

[d]Glutamate plus glutamine

Hyp 4-hydroxyproline. The sign "–" denotes the absence of data

different analytical techniques were used among the different laboratories. Natural differences in the content of polyamines and AAs among plant-source foods reflect differences in the metabolism of polyamines and AAs among different plant species and even among the different varieties of the same plant species (Bártová et al. 2015; Chung et al. 2013; Keeney 1970; Kaldy and Markakis 1972; Khoi et al. 1987; Shoup et al. 1966; Young 1980). Given the exceedingly large variations in reported values for the same kind of food, accurate data are necessary for nutritionists and medical professionals to make quantitative recommendation for the consumption of foods by humans. To our knowledge, this is the first study to determine putrescine, spermidine, spermine, agmatine, and all proteinogenic AAs in corn grains, peanuts, pistachio nuts, potatoes, soybeans, sweet potatoes, wheat flour, and white rice as common staple plant-source foods in most regions of the world.

There are no recommendations for dietary intake of polyamines by humans. Dietary polyamines are readily absorbed by enterocytes of the small intestine into the portal blood circulation (Bardócz et al. 1995) and can contribute directly to the total pool of polyamines in the body (Hunter and Burritt 2012; Soda et al. 2009b). Importantly, dietary polyamines may play an important role in human health (Kalač 2014). For example, because polyamines are essential to intestinal cell growth and to the repair of gastrointestinal damage (Blachier et al. 2007), foods (e.g., corn flour, soybean-derived tofu, sweet potatoes and potatoes) relatively rich in polyamines are expected to be beneficial for subjects with stomach or gut injuries. In addition, because polyamines promote conceptus survival, growth and development (Kong et al. 2014; Lenis et al. 2018; Wang et al. 2014), the polyamine-rich foods may also improve pregnancy outcomes in women and other mammals (Lefèvre et al. 2011; Sooranna et al.

1998). Furthermore, because polyamines can regulate the metabolism of microorganisms (Kalač 2014), dietary polyamines may modulate the population and metabolic activity of the intestinal microbiota. Based on the average consumption of various foods by the United States (USDA 2018) and Chinese (Wu et al. 2014; FAO 2017) adults, we estimated their daily intakes of polyamines (Supplemental Table 4). The amounts of polyamine intakes from plant-source foods by adults were similar between these two countries, and were 54%, 38%, and 57% of those from both plant- and animal-source foods reported for United States, European and Japanese adults (Zoumas-Morse et al. 2007; Supplemental Table 5). Differences in regional dietary habitats within a country may occur to account for regional differences in dietary intakes of polyamines by individuals. Future research is warranted to estimate the amounts of polyamines needed daily by healthy adults and how much of the requirements for polyamines can be met from the consumption of plant-source foods.

Historically, the content of nitrogen (N) in food protein is considered to be 16% and, therefore, the content of crude protein in foods except for wheat flour is calculated as N % × 6.25 (Bártová et al. 2015; Hughes 1957; Kaldy and Markakis 1972; McDermott and Pace 1957; Mossé et al. 1988; Patrick et al. 1974; Wang and Cavins 1989; Venkatachalam and Sathe 2006; Wu 2018). This conversion factor of 6.25 is appropriate for soybeans. Consistent with the report of Shoup et al. (1966), we found that the conversion factor of 5.70 can be used to accurately estimate the content of true protein in wheat flour, because this food contains a very high content of nitrogen-rich glutamine (Table 3). Corn grains contain high percentages of glutamine (a nitrogen-rich AA), as well as alanine and proline with a relatively high content of nitrogen (Table 4). Of note, peanuts, pistachio nuts, potatoes, sweet potatoes, and white rice contain nitrogen-rich AAs, such as arginine, asparagine or glutamine; therefore, the conversion factor of 6.25 is not applicable to these five foods. Based on the results of the present study, we suggest that different conversion factors be used to estimate the content of true protein plus peptides in different foods: 5.46, corn grains; 5.59, peanuts; 5.66, pistachio nuts; 3.27, potatoes; 6.22, soybeans; 4.08, sweet potatoes; 5.69, wheat flour; and 5.49, white rice. For highly digestible foods, such as those analyzed in the present study, the total content of individual AAs, rather than protein content, is most relevant to human nutrition.

Although the glutamate family of AAs plays an important role in intestinal, immunological, neurological, renal, and circulatory systems (Wu 2013), little is known about the composition of glutamate, glutamine, aspartate and asparagine [nutritionally and physiologically important AAs (Hou et al. 2015; Hou and Wu 2017; Wu et al. 2013)] in human foods. To our knowledge, this is the first report of the ratios of glutamate to glutamine and of aspartate to asparagine in pistachio nuts, potatoes, sweet potatoes, wheat flour, soybeans, and white rice. Of particular note, peanuts, pistachio nuts and soybeans contained a relatively high content of peptide-bound AAs (e.g., glutamate, glutamine, and proline) and free AAs (glutamate and glutamine) that are precursors for the synthesis of polyamines in humans (Table 2). Interestingly, soybean is particularly rich in glutamate and glutamine, supplying 52.6 and 43.0 mg glutamate and glutamine per g of DM, respectively. It is also noteworthy that wheat flour and potatoes contained an exceedingly high content of glutamine (45.5 mg/g of DM) and asparagine (16.3 mg/g of DM), respectively. Furthermore, arginine was the most abundant AA in peanuts (35.5 mg/g of DM). Glutamate also confers a unique taste flavor through activating specific receptors (e.g., taste receptors type 1, member 1 and member 3, as well as metabotropic glutamate receptors) in the surface of the tongue, small intestine and other parts of the digestive tract (San Gabriel and Uneyama 2013). While peptide-bound glutamine is known to be a major AA in wheat protein (Shoup et al. 1966), we identified for the first time a high abundance of free glutamine in potatoes, peanuts and pistachio nuts (Table 6). Given the importance of glutamate, glutamine and arginine in intestinal function (Fan et al. 2019; Haynes et al. 2009; Tan et al. 2010), consumption of wheat flour, potatoes, soybeans (without anti-nutritive factors) and peanuts may be beneficial for repairing intestinal epithelial damage, improving intestinal function, and treating diarrhea.

The Food and Agriculture Organization of the United Nations/World Health Organization (2007) and U.S. Institute of Medicine (2005) have recommended dietary requirements of humans for AAs that are not synthesized by mammalian cells. However, these official organizations have not recommended dietary requirements of infants, children or adults for AAs that are synthesized by mammalian cells. Most of the plant-source foods tested in this study had low concentrations of lysine, methionine, cysteine, tryptophan, threonine, and glycine. In contrast, animal proteins contain a high content of these so-called nutritionally essential AAs (Hou and Wu 2018). To meet the Institute of Medicine-recommended dietary allowance of methionine plus cysteine by the 70-kg adult human (19 mg/kg body weight per day; IOM 2005), daily intake of meat, wheat flour, or rice would be 45, 241, or 361 g DM, respectively. Of note, starch is rich in plant foods but glycogen is limited in animal products (Wu 2018). Consumption of high amounts of wheat flour and rice to meet protein requirement may disturb metabolic profiles in individuals due to their high intakes of digestible carbohydrates. The excessive starch can be converted into fat in the body, thereby possibly contributing to the development of obesity, dyslipidemia, and other metabolic disorders (Jobgen et al. 2006). Thus, a proper mix of plant- and animal-source proteins can ensure adequate amounts and proportions of all proteinogenic AAs in human diets.

While there are thoughts that plant-source foods can provide all AAs and substances that can be obtained from animal products (Wu et al. 2014), results of the present work indicated that this was not true for taurine, creatine, carnosine and anserine. These four compounds have important regulatory or anti-oxidative functions in humans (Wu 2013), occur abundantly in meat (Wu et al. 2016) and are present in milk (Ducci et al. 2006) but are absent from all of the tested plant-source foods. In humans and other animals, taurine is synthesized from methionine and cysteine; creatine is formed from methionine, arginine and glycine; and both carnosine and anserine are generated from histidine and β-alanine (Wu 2013). As noted previously, methionine, glycine, histidine, and β-alanine are among the least abundant AAs in plant foods. Furthermore, 4-hydroxyproline, which is a potent anti-oxidative AA in the small and large intestines of mammals (Ji et al. 2018; Wu et al. 2019), is highly abundant in meat (Li and Wu 2018) but is barely detectable or negligible in plant-source foods (Table 3). It is unknown whether consumption of plant foods as the sole source of dietary protein can meet the physiological needs for the synthesis of not only polyamines but also taurine, creatine, carnosine and anserine in humans without compromising their metabolic profiles or health. This again points to the necessity of careful consideration of both plant- and animal-source foods for optimal human health (Wu 2016).

In humans and other animals, polyamines are synthesized from AAs, and this biosynthetic process can be augmented by certain AAs such as glutamine and asparagine through an increase in ornithine decarboxylase expression (Wu 2009). Thus, foods that are rich in AAs can generally provide high amounts of substrates for polyamine synthesis in nearly all cell types. In this regard, among all of the analyzed foods of plant origin, soybeans and pistachio nuts may be the best dietary sources of both polyamines and AAs. In addition, agmatine, which is present in some plants (Slocum and Flores 1992), is a substrate for polyamine synthesis in humans and other animals (e.g., sheep) through the tissue-specific agmatinase pathway (Wang et al. 2014). Given the negligible content or absence of agmatine in the analyzed foods, this amine is unlikely to be a significant source of polyamines in humans. It is unknown whether a high intake of dietary AAs will result in a high rate of polyamine synthesis in healthy humans and in subjects with various diseased conditions. This issue should be addressed in future studies involving the use of stable or radioactive isotopes.

In conclusion, among the plant-source foods analyzed, total polyamines were most abundant in fresh corn grains, followed by soybeans and sweet potatoes, but are least abundant in wheat flour and rice. The ratios among putrescine, spermidine and spermine varied among foods. Putrescine was the predominant polyamine in corn grains, spermine in sweet potatoes, and spermidine in other foods. Glutamine was the most abundant AA in pistachio nuts, wheat flour and white rice; and was the second most abundant AA in corn grains, peanuts, potatoes, and soybeans. Arginine was the most abundant AA in peanuts and was the second most abundant AA in pistachio nuts. Asparagine was the most abundant AA in potatoes and sweet potatoes, and the fourth most abundant AA in peanuts. Glutamate was the most abundant AA in soybeans and the second most abundant AA in sweet potatoes and white rice. The high abundances of the glutamate family of AAs in the foods are of enormous importance in human metabolism. The content of total histidine, glycine, lysine, tryptophan, methionine, cysteine, and threonine was relatively low in corn grains, potatoes, sweet potatoes, and white rice. Because plant foods lacked taurine, creatine, carnosine and anserine, proper proportions of plant- and animal-source products are likely most desirable for optimizing human nutrition and health.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethics statement This study involved plant-source foods. No approval of animal use protocols is required.

Informed consent No informed consent is required for this study.

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