J Am Oil Chem Soc
DOI 10.1007/s11746-013-2407-9

REVIEW

Current Knowledge in Soybean Composition

Jelena Medic · Christine Atkinson · Charles R. Hurburgh Jr.

Received: 23 July 2012 / Revised: 29 November 2013 / Accepted: 18 December 2013

Abstract The soybean [*Glycine max* (L.) Merr.] is grown worldwide for its high protein and oil contents. Characterization of soybean seed components lends itself to understanding how soybean production can meet the needs of a growing world population. For this article, literature was reviewed and condensed to create a well-rounded picture of the current understanding of structural, functional, and nutritional properties of soybean components. Natural variation in soybean protein, lipid, and carbohydrate components, as well as the minor constituents phytic acid and isoflavones, are mentioned. Environment- or genetic-induced shifts in natural variation are described with respect to nutrition and functional improvements in soybean.

Keywords Composition · Soybeans · Protein · Oil · Carbohydrates · Phytic acid · Phospholipids · Tocopherols · Isoflavones · Environmental conditions · Breeding

Introduction

The soybean [*Glycine max* (L.) Merr.] is a legume crop native to East Asia, now grown worldwide because of its high protein and oil contents. Its world production reached 263.7 million metric tons in 2010/2011, which is more than double than that in 1992/1993 (Fig. 1). The increase in soybean production can be attributed to increased crop yield and demand to accommodate the food and fuel needs of the growing world population [1]. The largest soybean producer is the USA, with 34 % share in the world's production, followed by Brazil (29 %), Argentina (19 %), China (6 %), India (4 %), Paraguay (3 %), Canada (2 %), and others (4 %) [2].

Asian cultures use soybeans to produce traditional foods, such as soymilk, soy sauce, soy paste, tempeh, miso, tofu, and natto. In Western cultures, soybeans are mainly processed into soybean meal and seed oil. In 2011/2012, 54 % of US produced soybeans were crushed for the domestic oil industry, 4 % was used for seed, feed, and other purposes, whereas the remaining 42 % of soybeans was exported [4]. Processors crush soybeans to make full-fat flakes, which subsequently go through an extraction process with organic solvents to produce oil and defatted flakes. Full-fat flakes can also be used as animal feed components or ground into full-fat flour for use as a food ingredient. Defatted flakes are ground into soybean meal that serves as a high-quality protein source in animal feed or is used for production of texturized vegetable protein, soy concentrate, and soy isolates. Soy protein, concentrates, and isolates are used as value-added food ingredients in infant formulas, meat and meat-like products, baked goods, whipped toppings, frozen desserts, protein drinks, soup bases, etc. About 55 % of produced soybean oil is used as cooking and salad oil, 24 % as baking and frying fats and oils, 4 % as an ingredient in margarines, 7 % for other food and industrial uses, and 11 % as a substrate for biodiesel production [5].

Soybeans contain a variety of biologically active compounds that have been hypothesized to confer significant

J. Medic (✉) · C. R. Hurburgh Jr.
Department of Agricultural and Biosystems Engineering, Iowa State University, Ames, IA 50011, USA
e-mail: jelena.medic@ingredion.com

Present Address:
J. Medic
Ingredion Incorporated, Bridgewater, NJ 08807, USA

C. Atkinson
American Oil Chemists' Society, Urbana, IL 61802, USA

Published online: 20 January 2014

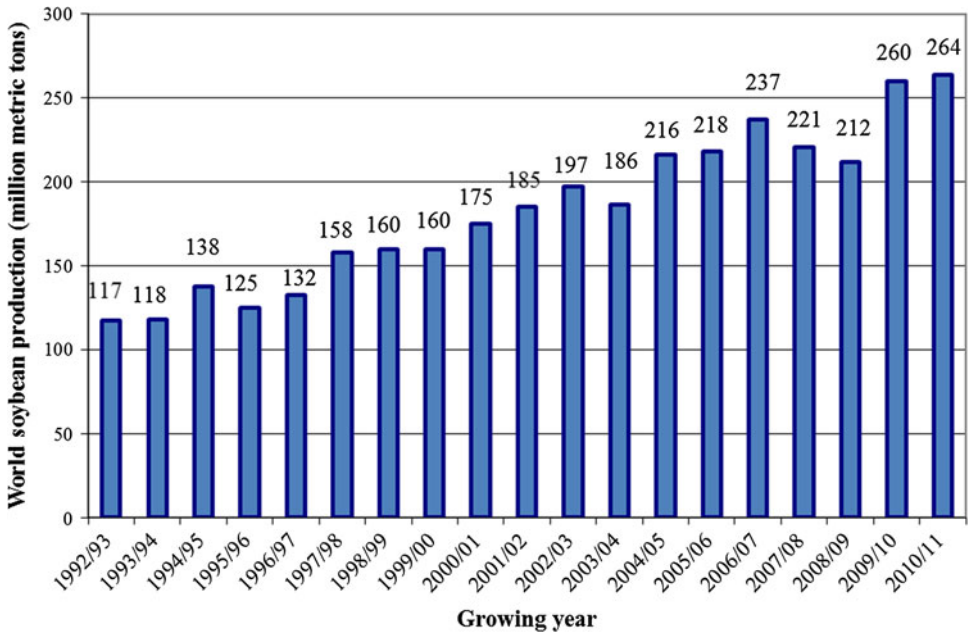

Fig. 1 Historical soybean production [3]

Table 1 Positive health effects of soybean constituents (adapted from Sugano [6])

Constituents	Functions
Proteins	
Storage proteins	Hypocholesterolemic [6]
Trypsin inhibitor	Anticarcinogenic [6, 7]
Lectins	Anticarcinogenic [6, 7]
Lipids	
Linoleic acid	Essential fatty acid, hypocholesterolemic [6]
α-Linolenic acid	α-Linolenic acid essential fatty acid, hypotriglyceridemic, improves cardiovascular function [6]
Tocopherols	Antioxidants
Phytosterols	Hypocholesterolemic [8]
Phospholipids	Hypocholesterolemic [9], reduces fat accumulation in the liver [10], maintain brain functions (memory and learning abilities) [6]
Sphingolipids	Anticarcinogenic [11–15], hypocholesterolemic [16, 17], regulates immune function [18]
Carbohydrates	
Dietary fiber	Antihypertensive [19], improves digestive tract function [6], prevents colon cancer [6], hypotriglyceridemic [19], hypocholesterolemic [19]
Minor constituents	
Phytic acid	Antioxidant, anticarcinogenic [20–22]
Saponins	Regulate lipid metabolism, antioxidant [6]
Isoflavones	Weak estrogenic activity [23], hypocholesterolemic when fed in combination with soy proteins [24, 25], might prevent osteoporosis and certain cancers [25, 26]

health benefits (Table 1). An increasing number of reports confirming these beneficial effects has stimulated food producers to develop new uses for soybeans in food systems and incorporate more soy into the human diet. Thus, it is anticipated that soybeans will shift from being primarily a livestock feed to a more common ingredient in the regular diet of people in Western cultures.

Understanding the factors that influence the chemical composition of soybeans and soybean component structure is crucial from both a processing and a nutritional standpoint. Constant changes in the properties of soybeans require adjustments of processing parameters and reformulation of products, and can lead to altered product quality. This review explains soybean seed constituents in

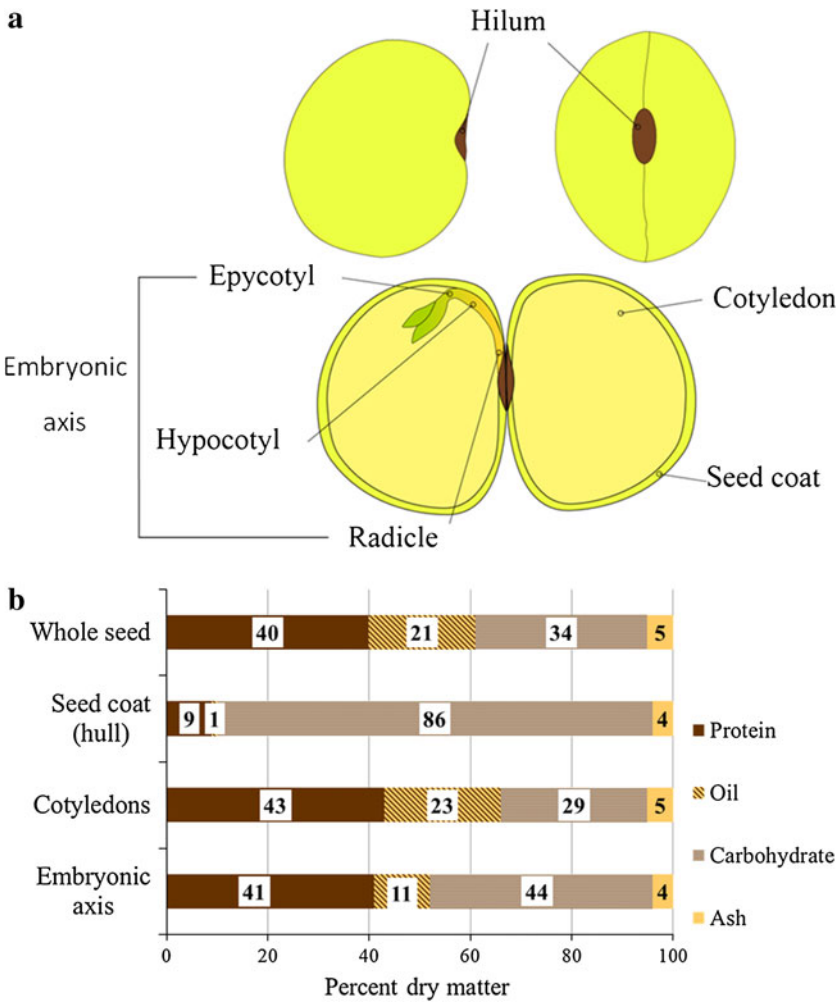

Fig. 2 Soybean seed parts (**a**) and their composition on dry seed basis (**b**) (data source: Kawamura [29])

detail and demonstrates the significant effects of genotype and environment on the structural, compositional, nutritional, and functional characteristics of soybeans.

Soybean Seed Morphology and Composition

The soybean seed is composed of two parts: seed coat (hull) and embryo. The embryo accounts for 90 % of the seed weight [27] and comprises two cotyledons and embryonic axis. Radicle, hypocotyl, and epicotyl form the embryonic axis (Fig. 2a). During germination, the cotyledons serve as food reserves for the growing plant, the radicle becomes the main root, the hypocotyl raises cotyledons and epicotyl above the soil surface, and the epicotyl functions as the stem of the plant [28].

From a commercial perspective, the cotyledons are the most important parts of the seed because they are a storehouse of protein and oil (Fig. 2b). Soy protein and oil are packed into discrete subcellular structures called protein and oil bodies, respectively. Protein and oil bodies are located in the cytoplasm of palisade-like cotyledon cells, with

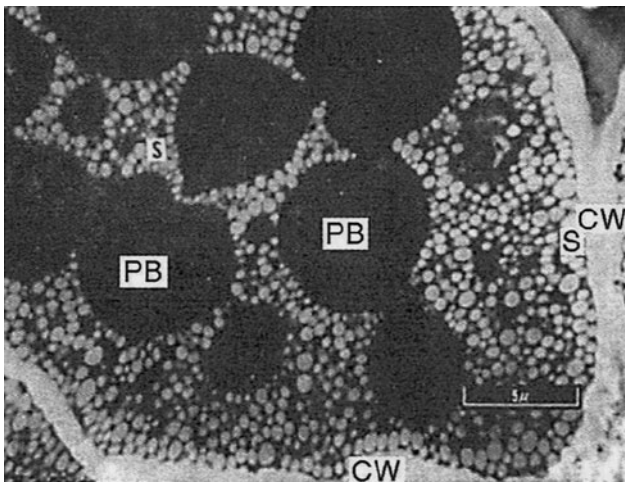

Fig. 3 Electron micrograph of soybean cotyledon cells. *PB* protein bodies, *S* spherosomes, *CW* cell wall [Reprinted from Saio K, Watanabe T (1968) Observation of soybean foods under electron microscope. J Food Sci Technol Japan 15:290–296, Figure 3, with kind permission from Springer Science+Business Media B.V]

spherosomes typically distributed around the protein body (Fig. 3). Protein bodies are large spherical organelles with a

diameter of 2–10 μm, whereas oil bodies are much smaller particles, ranging from 0.2 to 0.5 μm in diameter [27].

Protein

Soybean seeds contain on average 40–41 % protein on a dry weight basis. Seed proteins can be classified in four groups based on their role: metabolic enzymes, structural (including ribosomal and chromosomal), membrane, and storage proteins [30, 31].

Storage Proteins

Storage proteins account for 65–80 % of the total seed protein [24]. The two main seed storage proteins are glycinin and β-conglycinin, which belong to the legumin (11S globulins) and vicilin (7S globulins) families of proteins, respectively. Glycinin and β-conglycinin typically constitute about 40 and 25 % of the total embryo protein, respectively [32], but their content may vary with the genetic background of the soybean and its environmental growing conditions [24, 30]. Their main role is to serve as amino nitrogen sources for the germinating seed [24].

Glycinin is a hexamer with a molecular mass range of 320–375 $\times$ 10^3 g/mol [33, 34]. The hexamer is composed of two trimers connected by hydrophobic, electrostatic, hydrogen, and ionic bonds [33, 35, 36]. Each trimer is made up of three monomeric subunits, and each monomeric subunit is composed of an acidic polypeptide and a basic polypeptide covalently linked by a disulfide bond. The acidic polypeptides have an acidic isoelectric point (pI) and a molecular mass of 30–40 $\times$ 10^3 g/mol, whereas the basic polypeptides have a basic pI and a molecular mass of 18–22 $\times$ 10^3 [37]. Five major monomeric subunits of glycinin are: A1aB2, A1bB1b, A2B1a, A3B4, and A5A4B3, where A and B stand for acidic and basic polypeptides, respectively. A5A4B3 subunit is slightly different from others because it contains an additional acidic polypeptide in its structure [28].

β-Conglycinin is a glycoprotein with a molecular mass of approximately 150–200 $\times$ 10^3 g/mol [37]. It is composed of three subunits: α, α′, and β, with molecular weights of 76, 72, and 53 $\times$ 10^3 g/mol, respectively. The subunits associate through strong hydrophobic and hydrogen bonds [24]. Carbohydrates of mannose and glucosamine type account for 5 % of the β-conglycinin weight [32] and are covalently linked to the peptides of β-conglycinin subunits. Until recently, it was thought that β-conglycinin did not contain intra- and interpeptide disulfide bonds [38]. A recent finding of Wadahama et al. [39] showed that approximately half of the α- and α′-subunits of soybean β-conglycinin were connected by disulfide bonds, either with each other or with an allergenic protein P34.

Glycinin and β-conglycinin exhibit different functional properties in food systems because of their differential structure. Glycinin forms stronger and more resilient gels due to the large number of sulfhydryl groups [40], whereas β-conglycinin has a higher emulsifying capacity and emulsion stability [41]. Glycinin and β-conglycinin are also distinct from a nutritional standpoint: glycinin contains more sulfur-containing amino acids (methionine and cysteine) than β-conglycinin (Table 2). Glycinin monomeric subunits can be separated in two groups based on homology and nutritional value. Group I includes A1aB2, A1bB1b, and A2B1a subunits with 1.7 mol % cysteine and 1.1–1.5 mol % methionine, and Group II includes the remaining two subunits (A3B4, and A5A4B3) with lower content of sulfur-containing amino acids (1.1–1.2 mol % cystein and 0.4–0.8 mol % methionine, respectively) (Table 2). The nutritional value of the β-conglycinin subunits is in the order of $\alpha' > \alpha > \beta$, with β subunit being devoid of methionine and cysteine. This suggests that the content of sulfur-containing amino acids in soybeans could be increased with proper selection of high-glycinin cultivars and alteration in the distribution of acidic and basic polypeptides in glycinin.

Low-Abundance Proteins

In addition to the storage proteins, soybean seeds contain many low-abundance proteins responsible for mobilization of stored nutrients or defense against macro- and microorganisms. Many of these proteins are antimetabolic compounds and may trigger allergenic responses in sensitive humans and animals, such as adverse gastric reactions and atopic eczema [42]. At least 15 proteins of soybeans were found to cause allergies in humans: a spherosome associated protein Gly m Bd 30K (also called P34) [43], proteins Gly m IA and Gly m IB present in the seed hull [44], the α-subunit of β-conglycinin [45], and soybean trypsin inhibitors [46], to name a few. The best-characterized soybean protease inhibitors are the Bowman-Birk trypsin-chymotrypsin inhibitor and the Kunitz trypsin inhibitor. Considerable amounts of the protease inhibitors in soybean seeds ($\sim$6 % of the soybean protein) inhibit pancreatic enzymes in monogastric animals, which results in reduced digestibility of proteins and pancreatic hypertrophy in some animals [30].

Lectins (hemagglutinins) are a class of proteins with a strong ability to agglutinate red blood cells and intestinal mucosa cells through strong interactions with cell surface carbohydrates. Soybean lectins are also considered antinutritional factors because they inhibit animal growth by interfering with the absorption of nutrients [47]. The concentration of lectins in soybean seed ranges between 1 and 2 % on seed dry mass [48]. The activity of lectins and

Table 2 Amino acid composition of monomeric subunits of glycinin and β-conglycinin

Amino acids	Glycinin										β-conglycinin					
	$A_{1a}B_{1b}$		$A_{1b}B_2$		A_2B_{1a}		A_3B_4		$A_5A_4B_3$		A		α′		B	
	No.[a]	mol %	No.	mol %	No.	mol %	No.	mol %	No.	mol %	No.	mol %	No.	mol %	No.	mol %
Ala	27	5.7	28	6.1	31	6.6	18	3.7	22	4.1	23	4.0	23	4.2	22	5.3
Arg	27	5.7	29	6.3	29	6.2	33	6.7	36	6.7	38	6.6	43	7.9	29	7.0
Asn	37	7.8	36	7.8	40	8.6	33	6.7	33	6.1	37	6.4	37	6.8	33	7.9
Asp	17	3.6	16	3.5	18	3.9	24	4.9	30	5.6	28	4.9	27	8.0	21	5.0
Cys	8	1.7	8	1.7	8	1.7	6	1.2	6	1.1	1	0.2	1	0.2	0	0
Gln	48	10.1	49	0.6	51	10.9	45	9.1	48	8.9	52	9.0	45	8.3	33	7.9
Glu	41	8.6	38	8.2	37	7.9	42	8.5	55	10.2	79	13.7	77	14.2	37	8.9
Gly	35	7.4	31	6.7	34	7.3	40	8.1	37	6.9	29	5.0	24	4.4	18	4.3
His	8	1.7	6	1.3	4	0.9	15	3.0	15	2.8	20	3.5	6	1.1	8	1.9
Ile	26	5.5	24	5.2	23	4.9	17	3.5	21	3.9	28	4.9	30	5.5	26	6.3
Leu	33	6.9	31	6.7	33	7.1	34	6.9	37	6.9	41	7.1	45	8.3	42	10.1
Lys	24	5.0	18	3.9	18	3.9	18	3.7	27	5.0	38	6.6	31	5.7	21	5.0
Met	6	1.3	5	1.1	7	1.5	4	0.8	2	0.4	4	0.7	1	0.2	0	0.0
Phe	20	4.2	26	5.6	19	4.1	15	3.0	14	2.6	29	5.0	27	5.0	28	6.7
Pro	29	6.1	29	6.3	26	5.6	37	7.5	37	6.9	33	5.7	38	7.0	21	5.0
Ser	32	6.7	32	6.9	30	6.4	38	7.7	43	8.0	40	6.9	39	7.2	31	7.5
Thr	20	4.2	18	3.9	18	3.9	20	4.1	20	3.7	14	2.4	11	2.0	10	2.4
Trp	4	0.8	3	0.6	4	0.9	4	0.8	6	1.1	2	0.3	1	0.2	0	0.0
Tyr	11	2.3	10	2.2	11	2.4	15	3.0	15	2.8	13	2.3	13	2.4	12	2.9
Val	23	4.8	25	5.4	26	5.6	34	6.9	35	6.5	28	4.9	24	4.4	24	5.8
Total	476		462		467		492		539		577		543		416	

Adapted from Utsumi [41]

Republished with permission of Taylor and Francis Group LLC Books, Utsumi et al. [41], permission conveyed through Copyright Clearance Center, Inc

[a] Number of amino acid residues per subunit

protease inhibitors is reduced by the heat treatment of soybeans, but 10–20 % of the residual trypsin inhibitor activity remains [7]. There are an increasing number of reports demonstrating a protective role of the Bowman-Birk trypsin inhibitor and lectins against several cancers (as reviewed by Friedman and Brandon [7]). This brings new light to these antimetabolic proteins as potential anticarcinogen agents.

Lipoxygenase enzymes are not considered anti-nutritional factors but are associated with undesirable flavors ("greeny" and "beany") of soybean foods. They catalyze oxidation of fatty acids with *cis*,*cis*-1,4-pentadiene structure (typically linoleic and α-linolenic acids) to hydroperoxides, which are subsequently decomposed to secondary products (e.g. hexanal) responsible for off-flavors [49].

Genetic Improvement of Soybean Proteins

The primary goals for genetic improvement of soybean proteins have been to increase seed protein content, improve the amino acid composition, reduce the amounts of food allergens, and develop specialty soybean lines for the food industry that contain proteins with specific functional properties.

The efforts to develop high-protein soybean cultivars have been impeded by a consistent negative relationship between the agronomic yield and the protein content of seeds. Soybean lines with up to 57.9 % protein on the seed dry weight basis can be found in the USDA soybean germplasm collection [50–53], but the high-protein lines are characterized by smaller numbers of seeds per plant, which precludes achieving both high yield and high content of protein in seeds [54, 55]. Consequently, they are not profitable to grow and thus, of little commercial value. More recently, breeders have managed to produce commercial higher-than-average-protein cultivars with substantially improved seed yield. Prolina was one of the first cultivars containing high protein content (44.8 % on the dry seed mass) and a moderate seed yield loss (87 %) yield compared to a control cultivar [56]. Lines R05-1415 and

R05-1771 were characterized with 46.3–46.9 % protein content (seed dry mass) and 6–9 % lower seed yield than the high-yielding conventional cultivar 50002T [57]. N6202 germplasm line produced seeds with 45.7 % protein content (dry seed mass), respectively, and 90 % yield compared to the control cultivar NC-Roy [58]. Soybean germplasm lines TN03-350 and TN04–5321 achieved elevated protein content (43.1–43.9 % protein content) without sacrificing the seed yield [59]. In addition to protein content, the line TN04–5321 also had an increased amount of sulfur amino acids (3.3 % content of protein dry mass) in the seed [59]. These findings suggest that the negative correlation between the seed yield and the protein content might be overcome in the future.

From an animal nutrition perspective, protein quality (amino acid composition of protein) is more important than total protein content in soybeans. Animal feed needs to have a balanced amino acid composition to meet the animal's requirements for essential amino acids. The low concentration of sulfur-containing amino acids (methionine and cysteine) and threonine limits the soybean protein's nutritive value in poultry and swine feed. Consequently, feed manufacturers often add synthetic methionine as a supplement. If soybean protein is added to meet the limiting amino acid needs, there is an excess of non-limiting amino acids in the rations. Excess amino acids are deaminated with the nitrogen excreted as urea at an energy cost to animals [60].

Increasing the protein content of soybeans does not necessarily improve the nutritional quality of protein stored in the soybean seed. Yaklich [61] found that increasing the protein content of soybean seeds led to elevated levels of storage proteins glycinin and β-conglycinin, but did not increase the content of sulfur-containing amino acids (dry seed basis). This was also confirmed in a survey of the Iowa State University Grain Quality database, containing 1805 soybean samples collected during 1993–2010 (Fig. 4). Contents of most limiting amino acids (for swine: lysine, threonine, and tryptophan and for poultry: methionine, lysine, cysteine, and threonine [62]) calculated on a seed dry mass were positively correlated with the protein content of soybeans (Fig. 4a). When amino acids were expressed as percentages of the total soybean protein, however, the percentages of the five most limiting amino acids decreased with increased protein content (Fig. 4b), mainly at the expense of glutamic amino acid (Fig. 4c). This means that protein in low-protein soybean lines was more concentrated in essential amino acids than that of high-protein cultivars.

The review of Krishnan [63] explains in great detail approaches which have been undertaken to increase the contents of sulfur-containing amino acids in soybeans; these include traditional plant breeding methods, expression of heterologous seed proteins rich in sulfur amino acids, expression of synthetic genes with well-balanced amino acid composition, elevating levels of endogenous sulfur-rich proteins (soybean albumin fraction), and modification of soybean storage proteins (glycinin and β-conglycinin). The latter approach of altering the glycinin/β-conglycinin ratio not only changes the nutritional value of soybeans, but also results in modified protein functional properties that may be valuable in certain food systems. For example, soybean lines with high glycinin/β-conglycinin ratio and altered glycinin subunit composition produce firmer tofu, as evidenced by increased breaking stress of tofu with increasing glycinin/β-conglycinin ratio in soybean seeds (Table 3). Recent work of Oltmans-Deardorff et al. [64] and Jenkinson and Fehr [65] showed that soybean lines with higher β-conglycinin/glycinin content can be produced without sacrificing protein and oil content of the seed and the agronomic yield. The soybean lines reported by Oltmans-Deardorff [64] had increased amounts of α′ and β subunits of β-conglycinin at the expense of the α unit. Functional properties and nutritional profiles of these lines should be evaluated to determine their added value. The literature suggests that soybean cultivars enriched in α' subunit might have beneficial effects in lowering plasma lipids and regulation of low-density lipoprotein receptors [64].

Well-known soybean cultivars with reduced amounts of allergens are Kunitz (lacks Kunitz's soybean trypsin inhibitor) [67] and Kyu-kei 305 (lacks 28 K protein, α- and β-subunit of β-conglycinin) [66]. Kyu-kei 305 is the cultivar with the least amount of allergens and was developed by back-crossing of the wild soybean line lacking β-conglycinin with the conventional soybean line Fukuyutaka [66]. Transgenic suppression and conventional breeding have been used to reduce the amount of a major allergenic protein in the soybean seed, P34 protein. The transgenic line had suppressed accumulation of the P34 protein without any negative effect on other agronomic traits [68]. Only two out of 60,000 lines from the USDA Germplasm Collection were found to have reduced amounts of P34 protein in seeds [69]. Bileyeu et al. [70] recently developed a molecular marker that will facilitate development of new cultivars with reduced amount of P34 allergen. Development of soybean lines with reduced amount of lectins has received limited research interest. George et al. [48] published a recent research study demonstrating that the lectin content of soybean seed can be reduced using mutation breeding. In comparison with the parent line, the mutant soybean lines produced seeds with comparable weight and protein content while the lectin content was reduced 1.5–17 times [48]. In an attempt to eliminate off-flavors and increase acceptability of soybean foods in Western cultures, agronomists developed lipoxygenase-free cultivars.

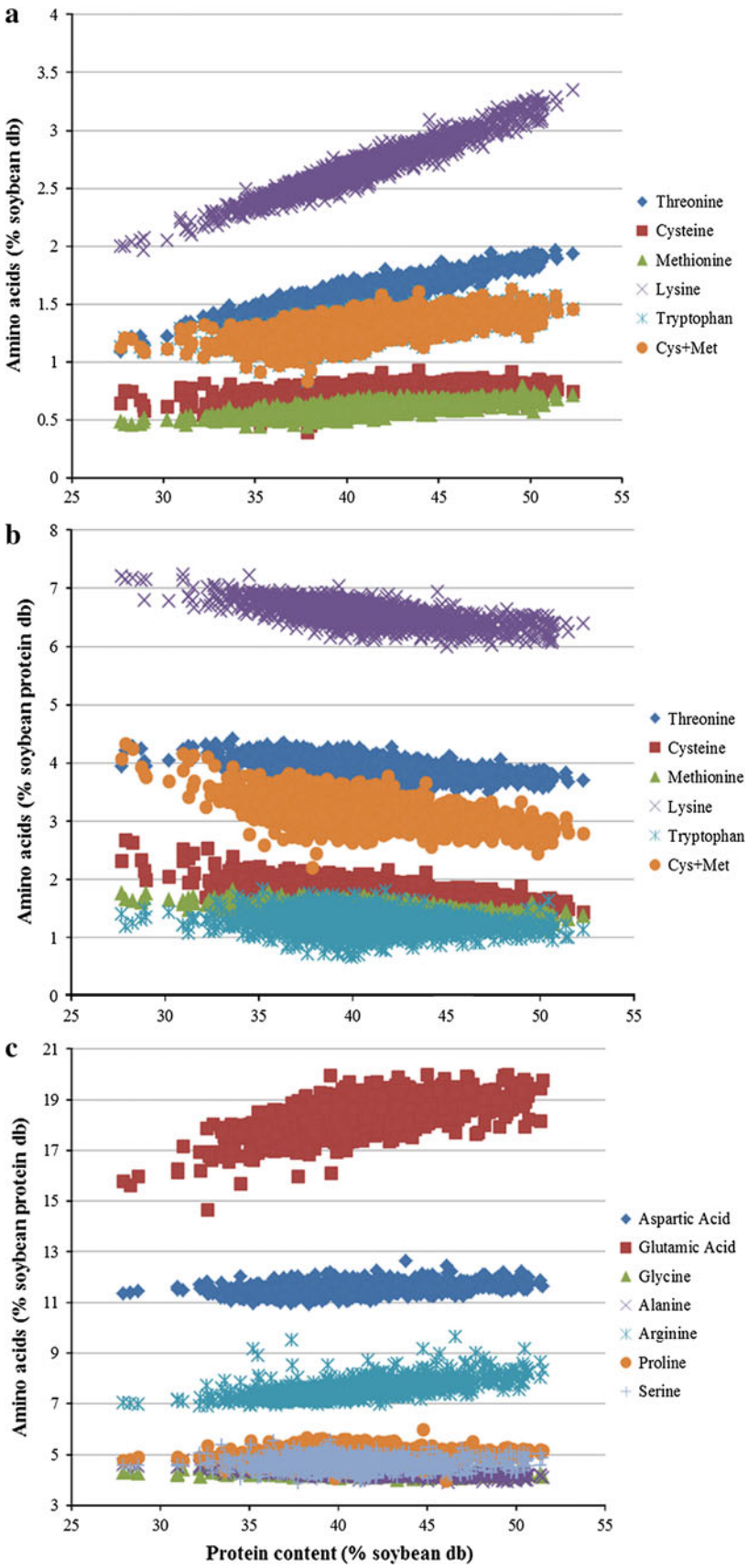

Fig. 4 Amino acid composition of whole soybeans (**a**) and protein (**b**, **c**) of soybeans with varying protein contents. (n = 1,805 soybean samples, 1993–2010 crop years), *db* dry basis

Table 3 Breaking stress of tofu gel made from soybeans with differential glycinin/β-conglycinin ratios and glycinin subunit compositions (adapted from Fukushima [66])

Glycinin/β-conglycinin ratio	Glycinin subunit			Breaking stress of tofu gel (Pa)
	Group I[a]	$A_5A_4B_3$	A_3B_4	
1.94	✔	✔	✔	9,989
1.63	✔	✔	–	8,955
1.38	✔	–	✔	9,891
1.32	✔	–	✔	10,171
1.08	–	✔	–	6,791
0.82	✔	–	–	7,162
0.49	–	✔	–	4,835
0.33	–	–	✔	5,381
0.14	–	–	–	3,002

[a] Group I includes $A_{1a}B_{1b}$, $A_{1b}B_2$, and A_2B_{1a} glycinin subunits

The sensory characteristics of tofu and soymilk did improve with the use of lipoxygenase-free cultivars, but those of bread, meat patties, and beverage products did not [49]. Off-flavors originating from auto-oxidation of oil were still present [24]. As a result, lipoxygenase-free cultivars have not been used extensively [49].

Lipids

The USDA soybean germplasm collection contains accessions with 8.1–24.0 % lipid (oil) content on the dry seed basis [50–53]. Soybean seed lipids function as energy storage for the plant, constituents of membranes, signaling molecules, defense against pathogens, etc. Storage lipids are deposited mainly in the form of triacylglycerols in oil bodies. A triacylglycerol molecule is composed of three fatty acids esterified to a glycerol backbone. The most abundant fatty acid in triacylglycerols of commodity soybeans is linoleic acid (18:2), followed by oleic (18:1), palmitic (16:0), linolenic (18:3), and stearic (18:0) acids (Table 4).

The distribution of fatty acids within a single triacylglycerol and among different triacylglycerols is not random because of the specificity of plant lipases [72]. According to Liu [28], "saturated (palmitic and stearic acid) and long-chain (with more than 18 carbons) fatty acids are distributed proportionately and randomly between the positions 1 and 3 on triglycerides, oleic and linolenic acid in all three positions, and the rest of available positions are filled with linoleic acid" (Fig. 5).

Fatty acid composition and distribution determine oil quality, nutritional value, flavor, oxidative stability, melting point, crystallization form, etc. [73]. Soybean oil has a high nutritional value because it is a rich source of unsaturated fatty acids, such as oleic, linoleic, and linolenic

Table 4 Fatty acid composition of selected soybean lines (adapted from Wilson et al. [71])

Line	Fatty acid (% crude oil)				
	Palmitic (16:0)	Stearic (18:0)	Oleic (18:1)	Linoleic (18:2)	Linolenic (18:3)
Normal	12	4	21	55	9
Low linolenic	5–12	3–4	19–48	36–57	3–6
High linolenic	11–15	3–4	11–14	52–55	15–19
High oleic	8–9	3–4	60–79	3–26	2–6
Low palmitic	4–8	3–4	22–39	44–61	5–9
High palmitic	15–18	3–4	16–26	48–55	7–8
High stearic	7–11	9–28	18–25	38–51	5–9

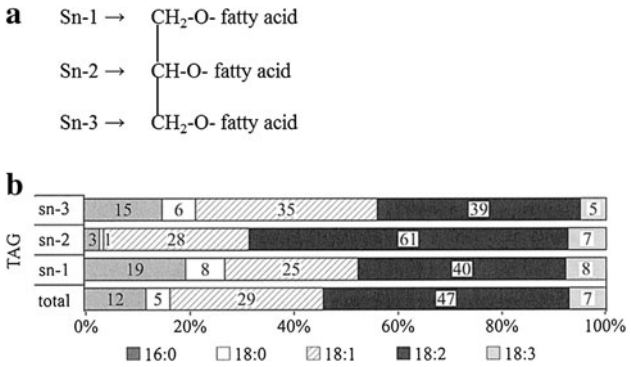

Fig. 5 Stereospecific distribution of fatty acids in triacylglycerols of commodity soybeans (reprinted with permission of AOCS Press from Gerde and White [49])

acids with one, two, and three double bonds, respectively. Unsaturated fatty acids exhibit several positive effects on human health, such as prevention of atherosclerosis, reduction of total and low-density lipoprotein (LDL) cholesterol and triacylglycerol levels in plasma, and suppression of inflammatory processes [74]. Linoleic and linolenic acids are also essential fatty acids that mammals cannot synthesize and, thus, need to be obtained from their diets.

On the other hand, the number of double bonds is directly related to oil stability. Because of its high linolenic acid content, soybean oil is relatively unstable and prone to oxidation and off-flavor development. Thus, soybean oil is often hydrogenated to reduce the number of unsaturated double bonds. The process of hydrogenation, however, introduces trans fatty acids, which have been shown to raise LDL and decrease HDL serum cholesterol levels, increasing the risk of coronary heart disease [75].

Soybean seed membrane lipids are mainly composed of phospholipids (~3 % of total soybean lipids or 0.74 % on dry-seed weight) [76], which are similar to triacylglycerols except that the fatty acid on the *sn*-3 position of glycerol moiety is replaced by a phosphate group. This phosphate group is frequently linked to polar choline,

ethanolamine, and inositol groups. The amphiphilic nature of phospholipids containing a polar phosphate group and a non-polar acyl tail is important in membrane structure and function. Phospholipids are removed from crude soybean oil during the degumming stage of oil refining process. The removed fraction, rich in phospholipids, is commonly called soybean lecithin and used commercially as an emulsifier. The major phospholipids in soybean lecithin are phosphatidylcholine (55.3 %), phosphatidylethanolamine (26.3 %), and phosphatidylinositol (18.4 %) [76].

Besides phospholipids, soybean seeds contain sphingolipids as minor membrane constituents, glycosylceramide being the most abundant one [49]. These non-glyceride lipid components contain a ceramide backbone with a sugar or phosphorylcholine attached to it. Ceramides consist of a fatty acid attached to a long-chain amino alcohol (sphingosine) *via* an amide bond. Both phospholipids and sphingolipids are bioactive components of soybeans: the intake of sphingolipids has been shown to inhibit the development of colorectal and skin cancer [11–15], decrease plasma and liver cholesterol levels [16, 17], and regulate immune cell function [18], whereas the intake of phospholipids results in the reduction of serum cholesterol levels [9] and fat accumulation in the liver [10]. Phosphatidylcholine contains choline, a nutrient required for proper neural development and liver function [77].

Phytosterols are another class of bioactive lipid components in soybean seeds that have been studied extensively because of their serum LDL cholesterol-lowering effect [8]. They are 28- or 29-carbon alcohols and resemble cholesterol in terms of both structure and function (regulators of plant cell membrane fluidity and permeability) [78]. Their concentration varies between 300 and 600 ppm on a dry seed basis [10]. The most abundant phytosterols in soybeans are campesterol, stigmasterol, and β-sitosterol [49]. Phytosterols are recovered as co-products of the soybean oil refining process and are used in the production of commercial extracts for the health and nutrition industry.

Tocopherols serve as natural plant defenses to protect biological membranes against oxidative deterioration of polyunsaturated fatty acids [79]. They inhibit lipid peroxidation by scavenging active oxygen species and peroxyl radicals and thereby preventing their reaction with lipids [80]. They also act as chain terminators in lipid autooxidation reactions [80].

Tocopherols consist of a polar chromanol head and a hydrophobic phytil tail [81]. Soybean seeds contain four types of tocopherols, α-, β-, γ-, and δ-, which defer in the number and position of methyl groups on the chromanol head [49]. α-Tocopherol has the most potent antioxidant activity *in vivo*; β-, γ-, and δ-tocopherols have 60, 90, and 98–99 %, respectively, less vitamin E activity than α-tocopherol [80, 81]. In *in vitro* systems, however, the potency of tocopherol homologs varies significantly with experimental conditions (e.g. temperature and light) (as reviewed by Gerde and White [49]). The concentration of tocopherols in soybean seeds typically ranges from 198 to 278 ppm on a dry basis (Table 5). The amount of individual tocopherols in the seed decreases in the following order: γ-, δ-, α-, and *β*-tocopherol (Table 5). Crude soybean oil contains between 1,205 and 2,195 ppm tocopherols (Table 5) that contribute to the oxidative stability of oil, but a considerable amount is removed during the refining process [49].

Tocopherols are predominantly deposited in the embryonic axis, followed by the cotyledons and seed coat [85, 86]. Accumulation of tocopherols is proportionate with the oil accumulation during the seed's maturation, with the most active synthesis in the first 30–47 days after flowering [87]. The relative proportion of individual tocopherols also changes with the development of soybean seeds [83]. There is a positive correlation between the level of oil unsaturation and total tocopherols in soybean seeds; thus, soybean varieties containing low concentrations of linolenic acid contain lower content of tocopherols [84].

Genetic Improvement of Soybean Oil Composition

Nutritional and functional properties of soybean oil can be modified by conventional seed breeding and genetic engineering. Using these techniques, many soybean lines with altered fatty acid compositions have been developed to target different end uses (Table 4). Soybean lines with low linolenic acid content (2–6 %) have been developed for the oilseed industry to produce oils with improved oxidative stability without the need of hydrogenation [88]. These lines are targeted for cooking oil, shortening, and frying fat markets. To meet current consumer demand for low-saturated-fat foods and need for oils with acceptable oxidative stability, high-oleic acid soybean lines have been produced.

Table 5 Tocopherol composition of soybean seeds and crude soybean oil

Tocopherol	Soybean seed[a] (ppm of dry matter)		Soybean crude oil[b] (ppm)	
	Mean	Range	Mean	Range
α-Tocopherol	26	11–53	84	41–158
β-Tocopherol	–	13	13	2–30
γ-Tocopherol	162	145–191	1,066	750–1,559
δ-Tocopherol	49	25–73	419	254–775
Total	241	198–278	1,577	1,205–2,195

[a] Guzman and Murphy [82], Kumar et al. [83]

[b] Dolde et al. [84]

In contrast, oils with high concentrations of saturated fatty acids are desirable in the margarine industry [89], and those with elevated levels of linolenic acid are more useful in paint and varnish applications [90].

Traditional breeding and genetic engineering approaches, undertaken to develop soybean lines with improved fatty acid profiles and altered tocopherol content and composition, have been explained in a great detail in reviews by Yamada et al. [91], Clemente and Cahoon [92], Fehr [93], and Cahoon [90]. Low-linolenic acid soybean lines have been mainly developed by traditional breeding techniques (mutagenesis) [93]. Soybean lines containing as low as $\approx$1 % linolenic acid in seed oil have been produced without affecting the seed yield and composition of major seed components [93]. More recently, Flores et al. [94] produced ultra-low-linolenic acid soybean lines using RNA interference to suppress the expression of three *FAD 3* genes. *FAD 3* genes encode ω-3 fatty acid desaturase, which adds a third double bond into linoleic acid to produce linolenic acid. The transgenic soybean lines contained between 1.0 and 3.1 % linolenic acid [94]. Conversely, increasing expression of *FAD 3* genes can lead to increased accumulation of linolenic acid in seed [92].

Use of traditional breeding techniques led to the development of cultivars containing 30–70 % oleic acid in the seed oil [50–53, 95–98]. This trait, unfortunately, was linked to a reduced seed yield and was not stable across different environments (higher oleic acid content was obtained in warmer climates) [99–101]. Spear et al. [102] gave a summary of genetic modification efforts to down-regulate the expression of the *FAD2* family of genes. *FAD2* genes encode ω-6 desaturase enzyme responsible for the conversion of oleic acid to linoleic acid [103]. This approach resulted in the development of transgenic soybean lines containing $\geq$80 % oleic acid in seed oil [92, 102]. The DuPont Company used genetic engineering to insert a copy of the *FAD2-1* gene that silenced the naturally occurring gene in the plant [93]. This event suppressed the synthesis of linoleic acid in the seed and elevated oleic acid content (84.6 % in seed oil) without any negative effect on agronomic traits. Commercialization of the cultivar was terminated because a gene for ampicillin resistance was used as the selectable marker for transformation [93]. The soybean line developed by Buhr et al. [104] contained more than 85 % oleic acid in the seed oil with no negative effect on the yield, and oil and protein content of the seed [105]. The line was stable across different environments [105]. Soybean lines containing transgene *DP-305423-1* were reported to have an average oleic acid content of 82.1 % (% seed oil) and 4.5 % lower seed yield, 2.4 % more protein, and 1.2 % less oil than lines containing normal concentration of oleic acid [102, 106].

Enhanced levels of stearic acid in mutant soybean lines have been associated with the reduced activity of the Δ-9-stearoyl-acyl carrier protein desaturase (SACPD) enzyme, especially the isoform C that is highly expressed only in the seed [107]. A, B, and C isoforms of the SACPD enzyme introduce a double bond at C9 position of stearic acid to produce oleic acid. Mutant lines FAM94-41, A6, RG7, RG8 carried SACPD-C mutation [107, 108] and contained between 9 and 26 % stearic acid in the seed oil [107, 109]. Most of the earlier studies showed reduced seed yield and germination potential of soybean lines with an elevated stearic acid content [93]. A recent study published by Ruddle et al. [110] found that only SACPD-B mutants exhibited lower seed yield, germination potential, and seed size, while SACPD-C mutants had similar agronomic performance as the wild-type lines.

Elevated palmitic acid contents in soybean seeds have been achieved by the chemical mutagenesis of genes expressing 3-ketoacyl-ACP synthase II [111]. This enzyme is responsible for the synthesis of stearic acid from palmitate. Mutant lines contained up to 42.7 % palmitic acid in seed oil, but have never been commercially produced because of the decreased yield and oil content of the seed, a low germination potential, and a smaller seed size compared to the conventional lines [93]. Reduction of the palmitic acid content in the soybean seed has been accomplished by the mutagenesis of genes encoding 16:0-acyl carrier protein (ACP) thioesterase enzyme, which is responsible for the synthesis of free palmitate that subsequently becomes incorporated in triacylglycerols [112]. A soybean line containing 4.4 % palmitic acid in seed oil has been commercialized [113]. Recently, a *GmFATB1a* gene has been used to develop a marker that will be used in the development of new low-palmitate soybean lines [112].

Carbohydrates

Carbohydrates are the third abundant component in soybean seeds and account for ca. 35 % of the dry seed weight. They are present in a high concentration in the soybean seed coat (86 % of the seed coat's dry weight) but can also be found in parenchyma cells of the embryo. A portion of seed carbohydrates is removed with the hulls, but soybean meal can still contain up to 40 % total carbohydrates [114, 115]. Approximately half of the total carbohydrates in soybeans are structural carbohydrates, whereas the other half are nonstructural carbohydrates [115]. Structural carbohydrates are cell-wall polysaccharides (cellulose, hemicellulose, and pectins), whereas non-structural carbohydrates include starch and different mono-, di-, and oligosaccharides.

Structural Carbohydrates

Mammals lack enzymes required to hydrolyze cell-wall polysaccharides, and these complex carbohydrates cannot

Table 6 Carbohydrate composition and dietary fiber content of soybeans

Seed carbohydrates	Percentage seed dry weight (%)	References
Dietary fiber		
Enzymatic–gravimetric methods	19.7–24.4	[122, 123]
Enzymatic-chromatographic methods	22.1–31.9	[131, 132]
Crude fiber	4–8	[69, 127, 128]
Neutral-detergent fiber	11.3–24.9	[133, 134]
Starch	0.2–1	[135, 136]
Verbascose	Trace	[137, 138]
Stachyose	1.2–6.9	[137, 139–142]
Raffinose	0.1–1.4	[137, 139–141]
Sucrose	1.1–7.4	[135, 137–139]
Maltose	0.3–0.5	[138]
Glucose	0.03–2.4	[137, 140, 141, 143]
Fructose	0.03–2.5	[137, 140, 141, 143]

be digested in the small intestine. Together with lignin (nonpolysaccharide) and enzyme-resistant starch and oligosaccharides, cell-wall polysaccharides are constituents of dietary fiber, a nondigestible portion of food/feed. The dietary fiber content of soybean seeds varies with the cultivar and the methods used to measure it (Table 6). The total dietary fiber content in foods is commonly measured using enzymatic–gravimetric dietary fiber analyses to determine their nutritive value (e.g. AOAC 985.29 [116], AOAC 991.43 [117], AACC 32-05 [118], AACC 32-06 [119], AACC 32-07 [120], and AACC 32-21 [121] methods). Redondo-Cuenca et al. [122] reported a 24.4 % total dietary fiber content in raw seeds of a commercial soybean line, whereas raw black soybeans were found to contain 19.7 % total dietary fiber [123] on a dry seed basis using AOAC 991.42 and 993.19 and AOAC 985.29 methods, respectively. The dietary fiber content of soybeans obtained in these two studies is comparable to those of other legumes reported by Tosh and Yada [124]. For soybean trading purposes, the content of fiber in soybean seeds is determined using the crude fiber analysis (e.g. AACC 32-30 [125], AOAC 978.10 [126]) and range between 4 and 8 % seed dry weight [127, 128]. It has been reported, however, that crude fiber analysis recovers (captures) only 20 % of hemicellulose and 50–80 % of cellulose on average [129]. Thus, crude fiber values underestimate levels of cell-wall polysaccharides. Other methods that determine fiber contents of soybeans (such as acid-detergent fiber (ADF) and neutral detergent fiber (NDF) methods) are also of limited value because they fail to measure pectins, a soluble fraction of fiber (which underestimates the fiber content), and include heat-damaged proteins in the residue (which overestimates the fiber content) [130].

Most cell-wall polysaccharides are removed from soybeans in the dehulling process. Thus, hulls are a rich source of dietary fiber (83 % total dietary fiber) [144] that might be useful in certain food applications. They can also be blended back with soybean meal in animal feed rations if soybean meal crude fiber content does not exceed the animal's fiber requirements. Cell-wall polysaccharides in hulls cannot be utilized efficiently by nonruminant animals and thus, are more favorably used in ruminant feeds where they contribute some calories to the diet. Ruminal microflora synthesize and secrete $\beta 1 \rightarrow 4$ cellulase enzymes that are able to hydrolyze plant cell-wall constituents.

Nonstructural Carbohydrates

Soybeans usually contain between 11 and 25 % soluble carbohydrates, which include 15–20 different sugar species [138, 145]. The most abundant soluble sugars are sucrose, raffinose and stachyose (Table 6). Sucrose imparts a pleasant sweet taste to soybean foods (e.g. natto and tofu) and is a desirable component in soybean seeds [146]. Galactooligosaccharides (raffinose, stachyose, and verbascose) are considered antinutritional factors because their consumption is associated with flatulence and digestive disturbance in humans and nonruminant animals [147, 148]. Raffinose, stachyose, and verbascose contain one, two, and three galactose molecules, respectively, attached to sucrose *via* $\alpha 1 \rightarrow 6$ glycosidic bond. Mammals do not synthesize α-galactosidase enzyme required to hydrolyze galactooligosaccharides to D-galactose and sucrose in the small intestine. Consequently, galactooligosaccharides pass to the lower intestine where they serve as substrates for bacterial fermentation that generates carbon-dioxide, methane, and other flatulence-producing gases [141]. The primary physiological role of galactooligosacharides is thought to be to serve as storage or transport carbohydrates in mature seeds, vegetative organs, and leaves [149]. Raffinose and stachyose are accumulated in the late phase of soybean seed maturation, mainly after 50 days after flowering [150]. Conversely, content of the monosaccharides glucose and fructose are high in early stages of soybean development but decline to negligible levels at maturity [151–153].

Starch is a storage polysaccharide composed of D-glucose monomeric units. It is synthesized in a granular form in the cotyledon cells of soybeans (Fig. 6). Developing soybean seeds accumulate starch until 30–40 days after flowering [152], and then the starch content sharply declines to <1 % dry seed basis at maturity (Table 6).

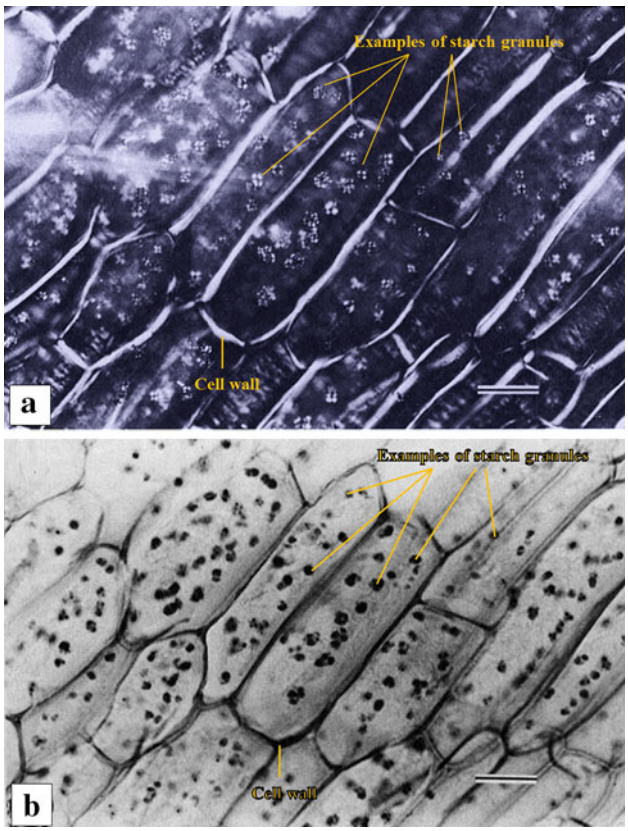

Fig. 6 Polarized-light (**a**) and bright-light (**b**) micrographs of starch granules in soybean cotyledon cells. Reprinted from Wilson et al. [135]

Two principal components of starch are amylose and amylopectin, amylose being less susceptible to enzyme hydrolysis. Amylose is a linear polymer of glucose linked mainly by α-(1 → 4) bonds, whereas amylopectin is a highly branched polymer composed of relatively short chains of α-(1 → 4) linked D-glucose units interconnected by α-(1 → 6) glycosidic bonds. Stevenson et al. [154] found that starches from immature soybean seeds collected 20 days prior to harvest contained relatively low absolute amylose contents (11.8–16.2 % of the starch db) and short average branch-chain length of amylopectin (20.4–20.9 glucose units), which is a favorable starch structure for the rapid enzyme hydrolysis. The findings of Stevenson et al. [154], Wilson et al. [135], and Saldivar et al. [136] suggest that starch serves as a transient reserve material in soybeans that is rapidly hydrolyzed to glucose in later stages of maturity to provide energy for the developing seed.

Genetic Improvement of Carbohydrate Composition in Soybeans

Soybean breeders increased the digestibility and total metabolizable energy of soybeans by developing lines with reduced levels of nondigestible oligosaccharides in the seed. In these mutant lines, the nondigestible carbohydrate (raffinose + stachyose) content decreased to 4.7–21.0 μmol/g seed dry base as compared with 94.7 μmol/g in commercial soybean lines [155]. When fed to poultry, soybean meals produced from lines with low content of nondigestible oligosaccharides contained 7–9 % more metabolizable energy [156], comparable digestibility of amino acids, and a higher concentration of essential amino acids [157] than conventional lines. Baker et al. [157] demonstrated that less soybean meal was needed in diets formulated for broiler chicks if low-oligosaccharide soybean meal was used instead of the conventional meal. Soy flour derived from processing of soybeans low in oligosaccharides produced less flatulence in humans than that from conventional soybeans [158]. However, the yield loss and marketing costs of specialty soybeans outweighed the gain from quality.

Minor Constituents

Phytic Acid

Phytic acid (myo-inositol-1,2,3,4,5,6-hexaphosphoric acid) is the main storage form of phosphorus in legumes and cereals. It accounts for 65–80 % of the total soybean seed phosphorous [159] and ranges from 1.0 to 2.3 % on a dry seed basis [160]. Phytic acid accumulates throughout the whole seed maturation period [161] and is concentrated mostly in the protein bodies of soybean cotyledons [160].

Unlike inorganic phosphorous, phytic acid phosphorus is not available to humans and nonruminant animals (e.g. swine and poultry) because they do not synthesize the phytase enzyme in their digestive system [162]. Thus, it is a major source of phosphorous in manure and an environmental pollutant [163]. Feed producers usually supplement feed rations with inorganic phosphorus to provide an adequate amount of phosphorus for animal health, which further increases phosphorous excretion in the manure [164].

Phytic acid can be found in the form of mixed phytate and phytin salts in soybean seeds. Charged phytin salts chelate metal cations, such as the nutritionally important minerals zinc, calcium, magnesium, and iron, and render them unavailable to humans and nonruminant livestock [165, 166]. Thus, phytic acid is considered as an antinutritional factor in foods/feeds. Phytic acid also has a strong ability to associate with soybean storage proteins and affect their functional properties (e.g. isoelectric point and solubility) [167–169]. On the other hand, there is an increasing number of reports suggesting that phytate may have a positive effect on animal and human health and act as an anticarcinogen and an antioxidant by complexing iron and decreasing free radical generation and peroxidation of membranes [20–22].

Several efforts have been made to develop low phytic acid soybean lines to ameliorate environmental problems with phosphorus excretion in animal manure. Soybean mutants LR33 [155] and M153 [170] showed 50 % and ≥75 % reduction in phytate content, respectively, with an accompanying increase in the inorganic phosphorus content. Both mutant lines, however, showed low seeding rates and reduced yield, which made them of limited commercial value in breeding [162]. More recently, Yuan et al. [171] reported two soybean lines Gm-lpa-TW-1 and Gm-lpa-ZC-2 with reduced phytate content (66.6 and 46.3 % reduction, respectively), increased inorganic phosphorus (6 and 1.4 times, respectively), and unchanged total phosphorous seed content compared to the parent lines. These seeds showed a good seedling emergence in all environments except subtropical and no yield loss compared to a commercial cultivar.

Isoflavones

Isoflavones, a class of phytoestrogens, have phenolic structures similar to estrogen 17β-estradiol, which gives them the ability to bind estrogen receptors and exhibit weak estrogenic activity [23]. Many studies have demonstrated a cardioprotective role of soybean isoflavones fed in combination with soy proteins, mainly by decreasing serum LDL cholesterol levels and increasing the oxidative stability of LDL cholesterol [24, 25]. Isoflavones fed without soy protein did not show the cholesterol lowering effects [24]. Soybean isoflavones have also been suggested to have a protective role against several cancers and osteoporosis [25, 26], but the evidence for a link between isoflavone consumption and these diseases still remains unclear and controversial [26].

Twelve isomers of isoflavones have been reported, including aglycons (daidzein, genistein, and glycitein), their conjugated glycosides (daidzin, genistin, and glycitin), malonyl glucosides (6″-*O*-malonyl daidzin, 6″-*O*-malonyl genistin, and 6″-*O*-malonyl glycitin), and acetyl glucosides (6″-*O*-acetyl daidzin, 6″-*O*-acetyl genistin, and 6″-*O*-acetyl glycitin). Soybeans are a rich source of isoflavones (0.2–4.2 mg/g seed dry weight) [172, 173], and the content of individual isoflavones varies with the genotype, growing location, and crop year [173, 174]. Isoflavone accumulation in soybean seeds takes place between 35 and 60 days after flowering, with daidzin and malonyl daidzin concentrations increasing gradually during the entire maturation period and genistin and malonyl genistin mostly in the last stages of development [175]. Mature soybeans do not have a uniform distribution of isoflavones within a seed: the hypocotyl contains the largest concentration of isoflavones (4–6 times higher than cotyledons), followed by cotyledons and the seed coat, respectively [175, 176].

A significant portion of isoflavones is lost during soybean processing: 44 % in tofu processing, 53 % during alkaline extraction in soy isolate production, and 12 and 49 % during soaking and heat processing steps of tempeh production, respectively [177]. Thus, the isoflavone content of soybean foods varies significantly, from 1 μg/g in soy sauce to 540 μg/g in tempeh [178]. Soybean oil contains only traces of isoflavones because these highly polar compounds are removed during oil refining process [179].

Geographic Variation in Seed Composition

Seed composition of soybean cultivars varies significantly with different geographic regions. Chinese and Brazilian soybean cultivars in most reported studies had higher protein contents than the US soybeans [62, 134]. Cultivars from Argentina were characterized with the lowest protein content [62, 133]. Chinese cultivars contained the lowest amount of oil compared to those from other regions [133, 134]. The fiber content of soybeans was not significantly affected by the geographic region [133, 134]. US soybeans had superior protein quality compared to Brazilian and Chinese, as indicated by the highest concentration of total essential amino acids (sum of all essential amino acids) in the protein dry mass [62, 133, 134]. A study conducted with 105 food-grade soybean genotypes showed that US cultivars had on average 41.3 % protein and 19.9 % oil content on the seed dry mass, whereas seeds of Japanese and South Korean cultivars contained on average 44.5 % protein and 18.1 % oil [180]. The fact that the Asian cultivars had higher protein but lower oil content than the US cultivars authors attributed to different genetic backgrounds of the genotypes in these two regions [180].

Variability in the soybean composition exists not only among countries, but also among regions within the United States. Surveys of US soybeans in the years 1986, 1987, and 1988 showed consistent state and regional differences in protein and oil content; soybeans from northern and western soybean-growing states (North Dakota, South Dakota, Minnesota, Iowa, Wisconsin) contained 1.5–2 % less protein and 0.2–0.5 % more oil than soybeans from southern states (Texas, Arkansas, Louisiana, Mississippi, Tennessee, Kentucky, Alabama, Georgia, South Carolina and North Carolina) [181]. A reported consistent negative relationship between oil and protein contents of the soybean [182–184] is less evident with warmer temperatures at more southern latitudes [181, 185]. These regional differences could be attributed to both genetic and environmental factors [185]. Piper and Boote [185] found that northern US cultivars had a higher genetic potential to produce high oil contents than did southern cultivars. These inherent compositional differences were further augmented by the

differential climates of these two US regions. Soybeans grown in warmer climates, such as southern US states, contained lower linoleic and linolenic and higher oleic acid contents [186]. The study of Zhe et al. [187] indicated that unsaturated fatty acids of the soybean seed grown in Wisconsin were more sensitive to environmental effects than saturated fatty acids.

Similarly, the isoflavone content in the seed varied not only among cultivars, but within a cultivar grown in different locations and years [188]. Significant interaction between environment and genotype makes breeding for this trait difficult [188]. Growing location has a significant effect on soybean protein composition, in particular β-conglycinin content of seed protein in soybean lines grown for its high β-conglycinin content [189].

Year-to-Year Variation in Seed Composition

Composition of the soybean seed also varies with growing seasons (years). The data Iowa State University Grain Quality Laboratory collected for US-grown soybeans demonstrates that, on average, the protein and oil contents of soybeans slightly changed over the previous 25 years; the protein content decreased and the oil content increased about 1 percentage point (Fig. 7), mainly because US soybean production shifted to the northwestern parts of the country [190], known to produce soybeans with lower protein content. However, year-to-year variation in the seed composition was significant because of the differential weather conditions in various growing years (Fig. 7). The average year-to-year difference in protein and oil contents of soybeans was 0.8 (0.1–1.8 range) (Fig. 7a) and 0.5 (0.0–1.6 range) (Fig. 7b) percentage points, respectively. Yaklich [61] studied 19 normal and high-protein seed soybean lines and found that the average protein and oil content varied from 47.2 to 48.6 and 16.9 to 18.3 % dry matter, respectively, in a five year period (1994–1998).

A study conducted with eight American and three Japanese soybean varieties grown in Iowa in three consecutive years showed that isoflavone content was more affected by the crop year than by the location and genetics [135]. Soybeans grown in 1989 contained 1.9–2.8 times higher isoflavone contents than those in 1990 and 1991 [173]. Content and composition of phytosterols in soybeans did not change significantly with crop years [191].

Relationship Between Soybean Composition and Environmental Factors

A soybean plant is exposed to various environmental factors during its growth. Temperature, availability of water and mineral nutrients [192–194], cultural practices [195], soil type [196], planting dates [197–199], and weed and insect attacks [196] during seed development have significant impacts on the seed yield and composition. These factors vary significantly across geographic regions and crop years. This review article will focus only on the most important environmental factors: growing temperature and water availability.

Effect of Growing Temperature on Seed Composition

Several studies reported a significant positive correlation between growing temperature and oil content of soybean seeds. Howell and Cartter [200] found that soybean plants grown at 29 °C produced seeds with 2–3 % higher oil content than those grown at 22 °C. Several other authors also reported a 5.2–8.5 g kg^{-1} increase per degree Celsius in oil concentration with increased growth temperature [201–204]. Protein content was not affected by growth temperature in these studies. Delayed planting of soybeans in late May and June led to slightly reduced oil content of the seed produced in Indiana, which was mainly attributed to the decreased average daily temperature during the seed filling period [197].

In a greenhouse study, Wolf et al. [205] found that the oil content of soybeans increased 37 % and sucrose decreased 56 % with the increase in the growing temperature from 18/13 to 33/28 °C (day/night temperature), protein and stachyose contents were stable up to 30/25 °C, and then protein increased 19 % and stachyose decreased ca. 29 % at 33/28 °C. Glucose, fructose, and raffinose contents were not affected by the growing temperature. The amino acid composition of soybean protein remained relatively unchanged, with an exception of methionine, whose relative content increased 3.5 times with the increased growing temperature. Fatty acid composition was significantly affected: linoleic and linolenic acid decreased significantly (from 55.8 to 40.3 % and from 16.4 to 5.0 %, respectively), and oleic acid increased (from 13.1 to 38.7 %) as the temperature increased. Palmitic and stearic acids were unaffected by the change in growing temperature in this study [205]. A more recent work of Ren et al. [206] showed that seed development under a high temperature regime (37/30 °C) significantly increased contents of oil and oleic, palmitic, and stearic acids in the seed, whereas the concentrations of linoleic and linolenic acid decreased compared to the control temperature regime (27/18 °C). These findings were also corroborated by Carrera et al. [207] who reported increased concentrations of total oil and oleic acid in the seed, whereas linolenic acid decreased with elevated growing temperatures. Changes in the concentration of unsaturated fatty acids in the seed oil might be attributed to a reduction in the activity of

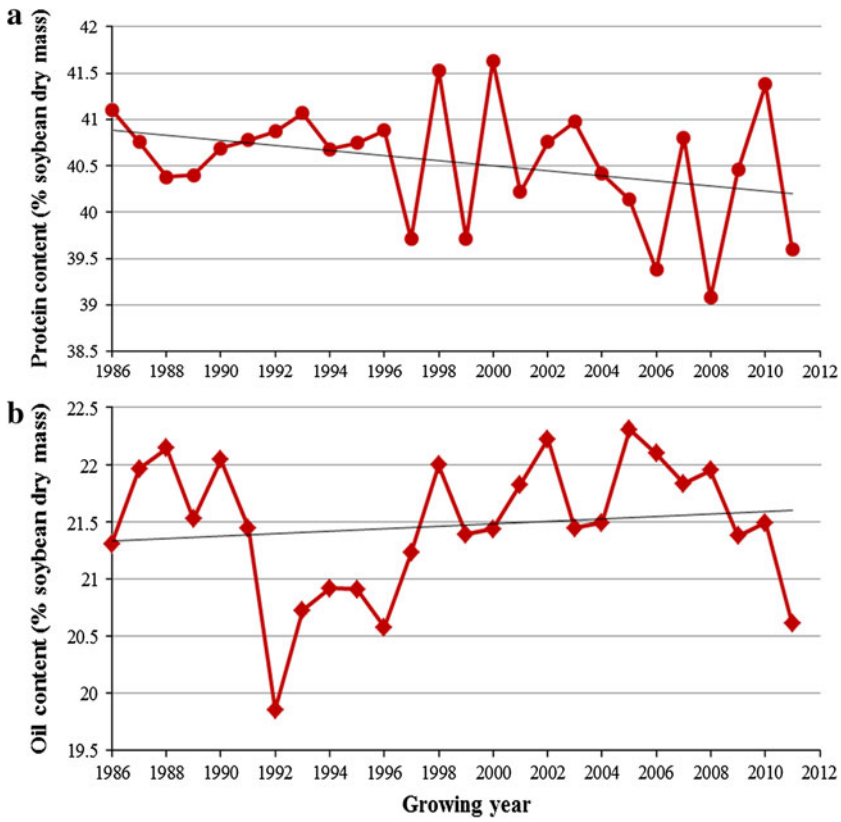

Fig. 7 Estimated protein (**a**) and oil (**b**) contents of US grown soybeans in the period 1986–2010. Total number of surveyed soybean samples was 37,762 with an average of 1,452 samples per year

desaturase enzymes in soybean seeds with elevated growing temperatures, which are involved in the synthesis of these fatty acids [208].

Of minor soybean constituents, isoflavones were very sensitive to growing temperature, and their content in soybeans declined with higher growing temperatures [207, 209–212]. Lozovaya et al. [210] reported 3.4 mg total isoflavones/g seed dry weight in soybeans grown at a low temperature regime (13/23 °C, day/night) and 1.3 mg/g seed dry weight in soybeans at a high temperature regime (23/33 °C, day/night). Tsukamoto et al. [212] reported a 13.6–18.2 times decrease in isoflavone content of the seed when growing temperature increased from 25/10 °C (day/night) to 38/28 °C (day/night). Content of phytosterols increased 2 times in soybean oil when soybean growth temperature increased from 20/10 to 35/25 °C [215]. Composition of isoflavones and phytosterols also changed with growing temperature [210, 213]. The relationship between the tocopherol content of soybean seed and plant growing temperature still remains unclear: Dolde et al. [84] reported an approximately 4 times decrease in the amount of tocopherol at 20/10 °C (day/night) temperature compared to 35/25 °C, whereas Almonor et al. [87] reported a 1.5 times increase in the tocopherol content of the seeds with an increase in the average growing temperature from 15.5 to 27.5 °C. Britz and Kremer [214], on the other hand, found no change in the total tocopherol content of soybean seeds, but the relative proportion of α-tocopherol increased two times at a 28 °C average growing temperature compared to 23 °C. Carrera et al. [207] also reported that temperate to cooler temperatures (16–20 °C) favored accumulation of δ-tocopherol in the seed, while the concentration of α-tocopherol increased with growing temperature.

Effect of Soil Moisture on Seed Composition

It is well known that water deficit during the seed set period reduces seed number, whereas water deficit during later stages of seed development shortens seed filling duration and thereby reduces soybean size [215, 216]. The relationship between water stress and soybean seed composition, however, still remains controversial. Dornbos and Mullen [217], Kumar et al. [218], and Rotundo and Westgate [216, 219], reported 2–23 % increased protein contents, whereas Carrera et al. [220], Specht et al. [221], Rose [222], and Boydak et al. [223] reported about 3 % decreased protein contents with soil moisture deficit. Carrera et al. [220] attributed differences among the reported results to the timing and intensity of the drought stress during seed development. Results of Bellaloui and Mengistu [199] suggest that the plant's response to soil moisture deficit might be dependent on the cultivar; the soybean cultivar Dwight grown in the mid-south US displayed, on

average, 2 % higher protein concentrations under irrigation conditions, whereas the cultivar Freedom (grown under the same conditions) had, on average, 7 % higher protein content under non-irrigated conditions.

Results of some studies indicated that the drought stress can reduce oil content by 10–25 % in the seed [219, 221], whereas other reports showed 4 % increased oil content with the water deficit [221, 223]. A multiyear trial conducted by Gao et al. [196] showed that the amount of precipitation had little effect on the oil content of cultivars grown in Michigan. Fatty acid composition was affected in this study, with oleic and linoleic acid being most sensitive to the level of precipitation. The accumulation of oleic acid in the seed had a quadratic relationship with the total precipitation, meaning that its concentration decreased with the increased precipitation up to 302–305 mm (midrange) and then it increased. Conversely, the concentration of linolenic acid was at the maximum when the total precipitation was in the midrange (302–305 mm). Bennet et al. [224] found that irrigation elevated content of isoflavones 2.5 times in soybeans grown in mid-south US, an area characterized by drought and high temperatures during reproductive stages of soybean plant development. These results were confirmed in a greenhouse experiment where high soil moisture was found to increase total isoflavone, daidzein, and genistein contents 1.2 times but did not affect the content of glycitein in soybean seeds [210]. The tocopherol content of soybeans was not significantly affected by the drought stress [214].

Conclusions

In summary, soybean seed contains an array of nutritionally important constituents. Many of them were previously dismissed as antinutrients, but more recent findings suggest they might have significant roles in disease prevention. The structures and quantities of soybean constituents change significantly with genetic and environmental factors, plant maturity, and processing conditions. Effects of environmental factors are complex and have not been elucidated entirely because field trials cannot isolate a single environmental factor and eliminate other confounding factors that influence the soybean crop development. More research studies in a controlled environment are needed to fully understand the effect of these factors on soybean composition. This information will be very important in the forthcoming years when more extreme weather patterns are likely to happen. Despite efforts to develop soybeans lines tailor-made for specific food and non-food applications, specialty soybeans have not been extensively used in practice because of high identity-preservation costs and poor agronomic performance. The recent release of the soybean genome sequence has had a great impact on the understanding of gene function and is expected to bring significant advances in the breeding of soybean.

Acknowledgments The authors thank the United Soybean Board for financial support.

References

1. Orf J (2010) Introduction. In: Bilyeu K, Ratnaparkhe MB, Kole C (eds) Genetics, genomics, and breeding of soybean. CRC Press, Boca Raton
2. United States Department of Agriculture FAS (2011) Oilseeds: world market and trade archives. Full report (10–11). http://www.fas.usda.gov/oilseeds/Current/default.asp. Accessed 11 Jul 2011
3. FAS/USDA, Foreign Agricultural Service (2011) Oilseeds: world market and trade archives. http://www.fas.usda.gov/oilseeds_arc.asp. Accessed 11 Jul 2011
4. USDA (2013) Soybeans: supply, disappearance, and price, US, 1980/81–2012/13. http://usda.mannlib.cornell.edu/MannUsda/viewDocumentInfo.do?documentID=1290. Accessed 11 Mar 2013
5. Iowa State University Extension Service, Agricultural Marketing Resource Center (2013) Soybean oil and biodiesel usage projections and balance sheet. http://www.extension.iastate.edu/agdm/crops/.../biodieselbalancesheet.pdf. Accessed 11 Feb 2013
6. Sugano M (2006) Nutritional implications of soy. In: Sugano M (ed) Soy in health and disease prevention. CRC Press, Boca Raton, pp 1–16
7. Friedman M, Brandon DL (2001) Nutritional and health benefits of soy proteins. J Agric Food Chem 49:1069–1086
8. Kritchevsky D, Chen SC (2005) Phytosterols—health benefits and potential concerns: a review. Nutr Res 25:413–428
9. Jimenez MA, Scarino ML, Vignolini F, Mengheri E (1990) Evidence that polyunsaturated lecithin induces a reduction in plasma cholesterol level and favorable changes in lipoprotein composition in hypercholesterolemic rats. J Nutr 120:659–667
10. Wang T (2008) Minor constituents and phytochemicals of soybeans. In: Johnson L, White P, Galloway R (eds) Soybeans, chemistry, production, processing, and utilization. AOCS Press, Urbana, pp 297–331
11. Schmelz EM, Dillehay DL, Webb SK, Reiter A, Adams J, Merrill AH Jr (1996) Sphingomyelin consumption suppresses aberrant colonic crypt foci and increases the proportion of adenomas versus adenocarcinomas in CF1 mice treated with 1,2-dimethylhydrazine: implications for dietary sphingolipids and colon carcinogenesis. Cancer Res 56:4936–4941
12. Schmelz EM (2000) Dietary sphingomyelin and other sphingolipids in health and disease. Nutr Bull 25:135–139
13. Birt D, Merrill A Jr, Barnett T, Enkvetchakul B, Pour P, Liotta D, Geisler V, Menaldino D, Schwartzbauer J (1998) Inhibition of skin carcinomas but not papillomas by sphingosine, *N*-methylsphingosine, and *N*-acetylsphingosine. Nutr Cancer 31:119–126
14. Berra B, Colombo I, Sottocornola E, Giacosa A (2002) Dietary sphingolipids in colorectal cancer prevention. Eur J Cancer Prev 11:193
15. Dillehay DL, Webb SK, Schmelz EM, Merrill AH Jr (1994) Dietary sphingomyelin inhibits 1,2-dimethylhydrazine-induced colon cancer in CF1 mice. J Nutr 124:615–620
16. Imaizumi K, Tominaga A, Sato M, Sugano M (1992) Effects of dietary sphingolipids on levels of serum and liver lipids in rats. Nutr Res 12:543–548

17. Kobayashi T, Shimizugawa T, Osakabe T, Watanabe S, Okuyama H (1997) A long-term feeding of sphingolipids affected the levels of plasma cholesterol and hepatic triacylglycerol but not tissue phospholipids and sphingolipids. Nutr Res 17:111–114
18. Olivera A, Rivera J (2005) Sphingolipids and the balancing of immune cell function: lessons from the mast cell. J Immunol 174:1153–1158
19. Anderson JW, Baird P, Davis RH Jr, Ferreri S, Knudtson M, Koraym A, Waters V, Williams CL (2009) Health benefits of dietary fiber. Nutr Rev 67:188–205
20. Thompson LU, Zhang L (1991) Phytic acid and minerals: effect on early markers of risk for mammary and colon carcinogenesis. Carcinogenesis 12:2041–2045
21. Vucenik I, Shamsuddin AKM (2003) Cancer inhibition by inositol hexaphosphate (IP6) and inositol: from laboratory to clinic. J Nutr 133:3778S–3784S
22. Ferry S, Matsuda M, Yoshida H, Hirata M (2002) Inositol hexakisphosphate blocks tumor cell growth by activating apoptotic machinery as well as by inhibiting the Akt/NFkappaB-mediated cell survival pathway. Carcinogenesis 23:2031–2041
23. Sakai T, Kogiso M (2008) Soy isoflavones and immunity. J Med Invest 55:167–173
24. Murphy P (2008) Soybean proteins. In: Johnson L, White P, Galloway R (eds) Soybeans: chemistry, production, processing, and utilization. AOCS Press, Urbana, pp 229–269
25. Vincent A, Fitzpatrick LA (2000) Soy isoflavones: are they useful in menopause? Mayo Clin Proc 75:1174–1184
26. Weaver CM, Cheong JMK (2005) Soy isoflavones and bone health: the relationship is still unclear. J Nutr 135:1243–1247
27. Wolf W (1972) Soybean ultrastructure and its relationship to processing. In: Inglett GE (ed) Symposium: seed proteins. AVI Pub. Co., Westport, pp 231–241
28. Liu K (1997) Soybeans: chemistry, technology, and utilization. Chapman & Hall, New York
29. Kawamura S (1967) Quantitative paper chromatography of sugars of the cotyledon, hull, and hypocotyl of soybeans of selected varieties. Kagawa Univ Fac Tech Bull 18:117–131
30. Krishnan HB (2001) Biochemistry and molecular biology of soybean seed storage proteins. J New Seeds 2:1–25
31. Nielsen N, Bassüner R, Beaman T (1997) The biochemistry and cell biology of embryo storage proteins. In: Larkins R, Vasil I (eds) Cellular and molecular biology of plant seed development. Kluwer Academic Publishers, Dordrecht, pp 151–220
32. Zarkadas CG, Gagnon C, Gleddie S, Khanizadeh S, Cober ER, Guillemette RJD (2007) Assessment of the protein quality of fourteen soybean [*Glycine max* (L.) Merr.] cultivars using amino acid analysis and two-dimensional electrophoresis. Food Res Int 40:129–146
33. Badley R, Atkinson D, Hauser H, Oldani D, Green J, Stubbs J (1975) The structure, physical and chemical properties of the soy bean protein glycinin. Biochimica et Biophysica Acta (BBA) Protein Struct 412:214–228
34. Wolf W, Briggs D (1985) Studies on the cold-insoluble fraction of the water-extractable soybean proteins. II. Factors influencing conformation changes in the 11 S component. Arch Biochem Biophys 76:377–393
35. Adachi M, Takenaka Y, Gidamis AB, Mikami B, Utsumi S (2001) Crystal structure of soybean proglycinin A1aB1b homotrimer. J Mol Biol 305:291–305
36. Adachi M, Kanamori J, Masuda T, Yagasaki K, Kitamura K, Mikami B, Utsumi S (2003) Crystal structure of soybean 11S globulin: glycinin A3B4 homohexamer. Proc Natl Acad Sci 100:7395
37. Maruyama N, Tecson-Mendoza E, Maruyama Y, Adachi M, Utsumi S (2007) Molecular design of soybean proteins for enhanced food quality. In: Clay D, Pierce F (eds) Functional foods and biotechnology. CRC Press, Boca Raton, pp 26–46
38. Thanh VH, Shibasaki K (1978) Major proteins of soybean seeds. Subunit structure of beta-conglycinin. J Agric Food Chem 26:692–695
39. Wadahama H, Iwasaki K, Matsusaki M, Nishizawa K, Ishimoto M, Arisaka F, Takagi K, Urade R (2012) Accumulation of β-conglycinin in soybean cotyledon through formation of disulfide bonds between α′and α subunits. Plant Physiol 158(3):1395–1405
40. KangII J, Matsumura Y, Mori T (1991) Characterization of texture and mechanical properties of heat-induced soy protein gels. J Am Oil Chem Soc 68:339–345
41. Utsumi S, Matsumura Y, Mori T (1997) Structure-function relationships of soy proteins. In: Damodaran S, Paraf A (eds) Food proteins and their applications. Marcel Dekker Inc., New York, pp 257–291
42. Herman E (2005) Soybean allergenicity and suppression of the immunodominant allergen. Crop Sci 45:462–467
43. Ogawa T, Tsuji H, Bando N, Kitamura K, Zhu YL, Hirano H, Nishikawa K (1993) Identification of the soybean allergenic protein, Gly m Bd 30 K, with the soybean seed 34-kDa oil-body-associated protein. Biosci Biotechnol Biochem 57:1030
44. González R, Polo F, Zapatero L, Caravacaj F, Carreira J (1992) Purification and characterization of major inhalant allergens from soybean hulls. Clin Exp Allergy 22:748–755
45. Ogawa T, Bando N, Tsuji H, Nishikawa K, Kitamura K (1995) Alpha-subunit of beta-conglycinin, an allergenic protein recognized by IgE antibodies of soybean-sensitive patients with atopic dermatitis. Biosci Biotechnol Biochem 59:831–833
46. Burks A, Cockrell G, Connaughton C, Guin J, Allen W, Helm R (1994) Identification of peanut agglutinin and soybean trypsin inhibitor as minor legume allergens. Int Arch Allergy Immunol 105:143–149
47. Liener IE (1994) Implications of antinutritional components in soybean foods. Crit Rev Food Sci Nutr 34:31–67
48. George M, Bhide S, Thengane R, Hosseini G, Manjaya J (2008) Identification of low lectin mutants in soybean. Plant Breed 127:150–153
49. Gerde J, White PJ (2008) Lipids. In: Johnson L, White P (eds) Soybeans, chemistry, production, processing, and utilization. AOCS Press, Urbana, pp 193–227
50. Peregrine EK, Sprau GL, Cremeens CR, Handly P, Kilen TC, Smith JR, Thomas DA, Sarins JD, Nelson RL (2008) Evaluation of the USDA soybean germplasm collection: maturity group V (FC 30265-PI 612614) and maturity groups VI–VIII (PI 416758-PI606432B). US Department of Agriculture Technical Bulletin No. 1920, pp 1–367
51. Peregrine EK, Sprau GL, Cremeens CR, Nelson RL, Orf JH, Thomas DA (2008) Evaluation of the USDA soybean germplasm collection: maturity groups 000–IV (PI 578371-PI612761). US Department of Agriculture Technical Bulletin No. 1919, pp 1–155
52. Hill JL, Peregrine EK, Sprau GL, Cremeens CR, Nelson RL, Kenty MM, Kilen TC, Thomas DA (2001) Evaluation of the USDA soybean germplasm collection: maturity groups VI–VIII (FC 03.659–PI 567.235B). US Department of Agriculture Technical Bulletin No. 1894, pp 1–130
53. Hill JL, Peregrine EK, Sprau GL, Cremeens CR, Nelson RL, Orf JH, Thomas DA (2005) Evaluation of the USDA soybean germplasm collection: maturity groups 000–IV (PI507670-PI 574486). US Department of Agriculture Technical Bulletin No. 1914, pp 1–131
54. Rotundo JL, Borrás L, Westgate ME, Orf JH (2009) Relationship between assimilate supply per seed during seed filling and soybean seed composition. Field Crops Res 112:90–96
55. Weih M (2003) Trade-offs in plants and the prospects for breeding using modern biotechnology. New Phytol 158:7–9
56. Burton J, Carter T, Wilson R (1999) Registration of 'Prolina' soybean. Crop Sci 39:294–295

57. Chen P, Ishibashi T, Dombek DG, Rupe JC (2011) Registration of R05-1415 and R05-1772 high-protein soybean germplasm lines. J Plant Reg 5:410–413
58. Carter TE, Rzewnicki PE, Burton JW, Villagarcia MR, Bowman DT, Taliercio E, Kwanyuen P (2010) Registration of N6202 soybean germplasm with high protein, favorable yield potential, large seed, and diverse pedigree. J Plant Reg 4:73–79
59. Panthee DR, Pantalone VR (2006) Registration of soybean germplasm lines TN03–350 and TN04–5321 with improved protein concentration and quality registration by CSSA. Crop Sci 46:2328–2329
60. Berry T, Becker D, Rasmussen O, Jensen A, Norton H (1962) The limiting amino acids in soybean protein. J Anim Sci 21:558–561
61. Yaklich RW (2001) β-Conglycinin and glycinin in high-protein soybean seeds. J Agric Food Chem 49:729–735
62. Thakur M, Hurburgh CR (2007) Quality of US soybean meal compared to the quality of soybean meal from other origins. J Am Oil Chem Soc 84:835–843
63. Krishnan HB (2005) Engineering soybean for enhanced sulfur amino acid content. Crop Sci 45:454–461
64. Oltmans-Deardorff SE, Fehr WR, Shoemaker RC (2013) Marker-assisted selection for elevated concentrations of the α′ subunit of β-conglycinin and its influence on agronomic and seed traits of soybean. Crop Sci 53:1–8
65. Jenkinson JE, Fehr WR (2010) Agronomic and seed characteristics of soybean lines with alleles for modified glycinin concentration. Crop Sci 50:1896–1903
66. Fukushima D (2001) Recent progress in research and technology on soybeans. Food Sci Technol Res 7:8–16
67. Bernard R, Nelson R, Cremeens C (1991) USDA soybean genetic collection: isoline collection. Soybean Genet Newsl 18:27–57
68. Herman EM, Helm RM, Jung R, Kinney AJ (2003) Genetic modification removes an immunodominant allergen from soybean. Plant Physiol 132:36–43
69. Joseph LM, Hymowitz T, Schmidt MA, Herman EM (2006) Evaluation of germplasm for nulls of the immunodominant allergen P34/Gly m Bd 30 k. Crop Sci 46:1755–1763
70. Bilyeu K, Ren C, Nguyen HT, Herman E, Sleper DA (2009) Association of a four-basepair insertion in the P34 gene with the low-allergen trait in soybean. Plant Gen 2:141–148
71. Wilson R, Burton J, Pantalone V, Dewey R (2002) New gene combinations governing saturated and unsaturated fatty acid composition in soybean. In: Gardner H, Kuo TM (eds) Lipid biotechnology. CRC Press, Boca Raton, pp 95–114
72. Pokorný J, Schmidt Š (2011) Plant lipids and oils. In: Sikorski Z, Kolakowska A (eds) Chemical and functional properties of food lipids. CRC Press, Boca Raton, pp 249–271
73. Yadav N (1996) Genetic modification of soybean oil quality. In: Verma D, Shoemaker R (eds) Soybean: genetics, molecular biology, and biotechnology. CAB International, Wallingford, pp 165–188
74. Bahrami G (2009) Trans and other fatty acids: effects on endothelial functions. In: Watson R (ed) Fatty acids in health promotion and disease causation. AOCS Press, Urbana, pp 3–43
75. Chen S, Kritchevsky D, Baer D (2007) Trans fatty acid effect on cardiovascular disease: animal and human studies. In: List G, Kritchevsky D, Ratnayake N (eds) Trans fats in foods. AOCS Press, Urbana, pp 1–37
76. Wang T, Hammond EG, Fehr WR (1997) Phospholipid fatty acid composition and stereospecific distribution of soybeans with a wide range of fatty acid composition. J Am Oil Chem Soc 74:1587–1594
77. Zeisel SH (1992) Choline: an important nutrient in brain development, liver function and carcinogenesis. J Am Coll Nutr 11:473–481
78. Lagarda M, Garcia-Llatas G, Farré R (2006) Analysis of phytosterols in foods. J Pharm Biomed Anal 41:1486–1496
79. Sattler SE, Cahoon EB, Coughlan SJ, DellaPenna D (2003) Characterization of tocopherol cyclases from higher plants and cyanobacteria. Evolutionary implications for tocopherol synthesis and function. Plant Physiol 132:2184–2195
80. Kamal-Eldin A, Appelqvist LÅ (1996) The chemistry and antioxidant properties of tocopherols and tocotrienols. Lipids 31:671–701
81. Ujiie A, Yamada T, Fujimoto K, Endo Y, Kitamura K (2005) Identification of soybean varieties with high α-tocopherol content. Breed Sci 55:123–125
82. Guzman GJ, Murphy PA (1986) Tocopherols of soybean seeds and soybean curd (tofu). J Agric Food Chem 34:791–795
83. Kumar V, Rani A, Dixit AK, Bhatnagar D, Chauhan G (2009) Relative changes in tocopherols, isoflavones, total phenolic content, and antioxidative activity in soybean seeds at different reproductive stages. J Agric Food Chem 57:2705–2710
84. Dolde D, Vlahakis C, Hazebroek J (1999) Tocopherols in breeding lines and effects of planting location, fatty acid composition, and temperature during development. J Am Oil Chem Soc 76:349–355
85. Yoshida H, Kanrei S, Tomiyama Y, Mizushina Y (2006) Regional characterization of tocopherols and distribution of fatty acids within soybean seeds (*Glycine max* L.). J Food Lipids 13:12–26
86. Yoshida H, Takagi S, Ienaga H, Tsuchiya C (1998) Regional distribution of tocopherols and fatty acids within soybean seeds. J Am Oil Chem Soc 75:767–774
87. Almonor G, Fenner G, Wilson R (1998) Temperature effects on tocopherol composition in soybeans with genetically improved oil quality. J Am Oil Chem Soc 75:591–596
88. Gerde J, Hardy C, Fehr W, White PJ (2007) Frying performance of no-trans, low-linolenic acid soybean oils. J Am Oil Chem Soc 84:557–563
89. List G, Mounts T, Orthoefer F, Neff W (1996) Potential margarine oils from genetically modified soybeans. J Am Oil Chem Soc 73:729–732
90. Cahoon EB (2003) Genetic enhancement of soybean oil for industrial uses: prospects and challenges. AgBioForum 6:11–13
91. Yamada T, Takagi K, Ishimoto M (2012) Recent advances in soybean transformation and their application to molecular breeding and genomic analysis. Breed Sci 61:480–494
92. Clemente TE, Cahoon EB (2009) Soybean oil: genetic approaches for modification of functionality and total content. Plant Physiol 151:1030–1040
93. Fehr WR (2007) Breeding for modified fatty acid composition in soybean. Crop Sci 47:S-72–S-87
94. Flores T, Karpova O, Su X, Zeng P, Bilyeu K, Sleper DA, Nguyen HT, Zhang ZJ (2008) Silencing of GmFAD3 gene by siRNA leads to low α-linolenic acids (18:3) of fad3-mutant phenotype in soybean [*Glycine max* (Merr.)]. Transg Res 17:839–850
95. Takagi Y, Rahman S (1996) Inheritance of high oleic acid content in the seed oil of soybean mutant M23. Theor Appl Genet 92:179–182
96. Rahman SM, Kinoshita T, Anai T, Takagi Y (2001) Combining ability in loci for high oleic and low linolenic acids in soybean. Crop Sci 41:26–29
97. Alt JL, Fehr WR, Welke GA, Sandhu D (2005) Phenotypic and molecular analysis of oleate content in the mutant soybean line M23. Crop Sci 45:1997–2000
98. Burton JW, Wilson RF, Rebetzke GJ, Pantalone VR (2006) Registration of N98–4445A mid-oleic soybean germplasm line registration by CSSA. Crop Sci 46:1010–1012

99. Bachlava E, Cardinal AJ (2009) Correlation between temperature and oleic acid seed content in three segregating soybean populations. Crop Sci 49:1328–1335
100. Primomo VS, Falk DE, Ablett GR, Tanner JW, Rajcan I (2002) Genotype × environment interactions, stability, and agronomic performance of soybean with altered fatty acid profiles. Crop Sci 42:37–44
101. Scherder CW, Fehr WR (2008) Agronomic and seed characteristics of soybean lines with increased oleate content. Crop Sci 48:1755–1758
102. Spear JD, Fehr WR, Schnebly SR (2013) Agronomic and seed traits of soybean lines containing the high-oleate transgene DP-305423-1. Crop Sci 53:906–912
103. Schlueter JA, Vasylenko-Sanders IF, Deshpande S, Yi J, Siegfried M, Roe BA, Schlueter SD, Scheffler BE, Shoemaker RC (2007) The FAD2 gene family of soybean. Crop Sci 47:S-14–S-26
104. Buhr T, Sato S, Ebrahim F, Xing A, Zhou Y, Mathiesen M, Schweiger B, Kinney A, Staswick P (2002) Ribozyme termination of RNA transcripts down-regulate seed fatty acid genes in transgenic soybean. Plant J 30:155–163
105. Graef G, LaVallee BJ, Tenopir P, Tat M, Schweiger B, Kinney AJ, Van Gerpen JH, Clemente TE (2009) A high-oleic-acid and low-palmitic-acid soybean: agronomic performance and evaluation as a feedstock for biodiesel. Plant Biotechnol J 7:411–421
106. Brace RC, Fehr WR, Schnebly SR (2011) Agronomic and seed traits of soybean lines with high oleate concentration. Crop Sci 51:534–541
107. Boersma JG, Gillman JD, Bilyeu KD, Ablett GR, Grainger C, Rajcan I (2012) New mutations in a delta-9-stearoyl-acyl carrier protein desaturase gene associated with enhanced stearic acid levels in soybean seed. Crop Sci 52:1736–1742
108. Zhang P, Burton JW, Upchurch RG, Whittle E, Shanklin J, Dewey RE (2008) Mutations in a Δ-stearoyl-ACP-desaturase gene are associated with enhanced stearic acid levels in soybean seeds. Crop Sci 48:2305–2313
109. Pantalone V, Wilson R, Novitzky W, Burton J (2002) Genetic regulation of elevated stearic acid concentration in soybean oil. J Am Oil Chem Soc 79:549–553
110. Ruddle P, Cardinal A, Upchurch RG, Arellano C, Miranda L (2013) Agronomic effects of mutations in two soybean Δ9–stearoyl-acyl carrier protein-desaturases. Crop Sci 53:1887–1893
111. Oltmans-Deardorff SE, Fehr WR, Welke GA, Shoemaker RC, Graham MA (2013) Molecular mapping of the mutant fap4(A24) allele for elevated palmitate concentration in soybean. Crop Sci 53:106–111
112. De Vries BD, Fehr WR, Welke GA, Dewey RE (2011) Molecular characterization of the mutant fap3(A22) allele for reduced palmitate concentration in soybean. Crop Sci 51:1611–1616
113. Fehr W, Welke G, Cianzio S, Duvick D, Hammond E (1991) Inheritance of reduced palmitic acid content in seed oil of soybean. Crop Sci 31:88–89
114. Middelbos I, Fahey G (2008) Soybean carbohydrates. In: Johnson L, White P, Galloway R (eds) Soybeans, chemistry, production, processing, and utilization. AOCS Press, Urbana, pp 269–296
115. Karr-Lilienthal LK, Grieshop CM, Spears JK, Fahey GC Jr (2005) Amino acid, carbohydrate, and fat composition of soybean meals prepared at 55 commercial US soybean processing plants. J Agric Food Chem 53:2146–2150
116. AOAC (1990) Official methods of analysis (total dietary fiber in foods), 15th edn. Sec. 985.29
117. AOAC (1999) Official methods of analysis (total soluble and insoluble dietary fiber in foods), 16th edn. Sec. 991.43
118. AACC (2000) Official methods of analysis (total dietary fiber) 10th edn. Sec. 32-05, pp Sec. 32-05
119. AACC (2000) Official methods of analysis (total dietary fiber-rapid gravimetric method) 10th edn. Sec. 32-06
120. AACC (2000) Official methods of analysis (determination of soluble, insoluble, and total dietary fiber in foods and food products) 10th edn. Sec. 32-07
121. AACC (2000) Official methods of analysis (insoluble and soluble dietary fiber in oat products-enzymatic-gravimetric method) 10th edn. Sec. 32-21
122. Redondo-Cuenca A, Villanueva-Suárez MJ, Mateos-Aparicio I (2008) Soybean seeds and its by-product okara as sources of dietary fibre. Measurement by AOAC and Englyst methods. Food Chem 108:1099–1105
123. Lee CH, Oh SH, Yang EJ, Kim YS (2006) Effects of raw, cooked, and germinated small black soybean powders on dietary fiber content and gastrointestinal functions. Food Sci Biotechnol 15:635–638
124. Tosh SM, Yada S (2010) Dietary fibres in pulse seeds and fractions: characterization, functional attributes, and applications. Food Res Int 43:450–460
125. AACC (2000) Official methods of analysis (crude fiber in flours, feeds, and feedstuffs) 10th edn. Sec. 32-20
126. AOAC (2006) Official methods of analysis [fiber (crude) in animal feed and pet food], 18th edn. Sec. 978.10
127. Brumm T (2004) Quality and grading factors of IP soybeans. In: Bern C, Brumm TJ (eds) Managing grain after harvest. Department of Agricultural and Biosystems Engineering, Iowa State University, Ames
128. Naeve SL, Orf JH, O'Neill T (2006) Quality of the United States soybean crop: 2006. Report to the American Soybean Association and US Soybean Export Council quality mission to Asia, Nov 13–21, 2006
129. Van Soest P, McQueen R (1973) The chemistry and estimation of fibre. Proc Nutr Soc 32:123–131
130. Jung HJG (1997) Analysis of forage fiber and cell walls in ruminant nutrition. J Nutr 127:810S–813S
131. Hollung K, Overland M, Hrustic M, Sekulic P, Miladinovic J, Martens H, Narum B, Sahlstrom S, Sorensen M, Storebakken T, Skrede A (2005) Evaluation of nonstarch polysaccharides and oligosaccharide content of different soybean varieties (*Glycine max*) by near-infrared spectroscopy and proteomics. J Agric Food Chem 53:9112–9121
132. Redonco-Cuerca A, Villanueva-Suárez MJ, Rodríguez-Sevilla MD, Mateos-Aparicio I (2006) Chemical composition and dietary fibre of yellow and green commercial soybeans (*Glycine max*). Food Chem 101:1216–1222
133. Grieshop CM, Fahey GC Jr (2001) Comparison of quality characteristics of soybeans from Brazil, China, and the United States. J Agric Food Chem 49:2669–2673
134. Karr-Lilienthal LK, Grieshop CM, Merchen NR, Mahan DC, Fahey GC Jr (2004) Chemical composition and protein quality comparisons of soybeans and soybean meals from five leading soybean-producing countries. J Agric Food Chem 52:6193–6199
135. Wilson L, Birmingham VA, Moon DP, Snyder HE (1978) Isolation and characterization of starch from mature soybeans. Cereal Chem 55:661–670
136. Saldivar X, Wang Y-J, Chen P, Hou A (2011) Changes in chemical composition during soybean seed development. Food Chem 124:1369–1375
137. Kuo TM, Van Middlesworth JF, Wolf WJ (1988) Content of raffinose oligosaccharides and sucrose in various plant seeds. J Agric Food Chem 36:32–36
138. Obendorf RL, Zimmerman AD, Ortiz PA, Taylor AG, Schnebly SR (2008) Imbibitional chilling sensitivity and soluble carbohydrate composition of low raffinose, low stachyose soybean seed. Crop Sci 48:2396–2403
139. Hartwig E, Kuo TM, Kenty MM (1997) Seed protein and its relationship to soluble sugars in soybean. Crop Sci 37:770–773

140. Hou A, Chen P, Alloatti J, Li D, Mozzoni L, Zhang B, Shi A (2003) Agronomic and seed characteristics of soybean with reduced raffinose and stachyose. Crop Sci 45:589–592
141. Kumar V, Rani A, Goyal L, Dixit AK, Manjaya J, Dev J, Swamy M (2010) Sucrose and raffinose family oligosaccharides (RFOs) in soybean seeds as influenced by genotype and growing location. J Agric Food Chem 58:5081–5085
142. Hymowitz T, Collins FI, Panczner J, Walker WM (1972) Relationship between the content of oil, protein and sugar in soybean seed. Agron J 64:613–616
143. Hou A, Chen P, Shi A, Zhang B, Wang Y-J (2009) Sugar variation in soybean seed assessed with a rapid extraction and quantification method. Int J Agron 484571:8. doi:10.1155/2009/484571
144. Dust JM, Gajda AM, Flickinger EA, Burkhalter TM, Merchen NR, Fahey GC Jr (2004) Extrusion conditions affect chemical composition and in vitro digestion of select food ingredients. J Agric Food Chem 52:2989–2996
145. Maughan P, Maroof MAS, Buss G (2000) Identification of quantitative trait loci controlling sucrose content in soybean (*Glycine max*). Mol Breed 6:105–111
146. Taira H (1990) Quality of soybeans for processed foods in Japan. Jpn Agric Res Quart 24:224–230
147. Liying Z, Li D, Qiao S, Johnson EW, Li B, Thacker PA, Han IK (2003) Effects of stachyose on performance, diarrhoea incidence and intestinal bacteria in weanling pigs. Arch Tierernahr 57:1–10
148. Krause D, Easter R, Mackie R (1994) Fermentation of stachyose and raffinose by hind-gut bacteria of the weanling pig. Lett Appl Microbiol 18:349–352
149. Dey P (1985) D-Galactose-containing oligosaccharides. In: Dev P, Dixon RA (eds) Biochemistry of storage carbohydrates in green plants. Academic, London, pp 53–127
150. Obendorf RL, Zimmerman AD, Zhang Q, Castillo A, Kosina SM, Bryant EG, Sensenig EM, Wu J, Schnebly SR (2009) Accumulation of soluble carbohydrates during seed development and maturation of low-raffinose, low-stachyose soybean. Crop Sci 49:329–341
151. Konno S (1979) Changes in chemical composition of soybean seeds during ripening. Jpn Agric Res Quart 13:186–194
152. Yazdi-Samadi B, Rinne R, Seif R (1977) Components of developing soybean seeds: oil, protein, sugars, starch, organic acids, and amino acids. Agron J 69:481–486
153. Saravitz DM, Pharr DM, Carter TE Jr (1987) Galactinol synthase activity and soluble sugars in developing seeds of four soybean genotypes. Plant Physiol 83:185
154. Stevenson DG, Doorenbos RK, Jane J, Inglett GE (2006) Structures and functional properties of starch from seeds of three soybean [*Glycine max* (L.) Merr.] varieties. Starch Stärke 58:509–519
155. Hitz WD, Carlson TJ, Kerr PS, Sebastian SA (2002) Biochemical and molecular characterization of a mutation that confers a decreased raffinosaccharide and phytic acid phenotype on soybean seeds. Plant Physiol 128:650–660
156. Parsons C, Zhang Y, Araba M (2000) Nutritional evaluation of soybean meals varying in oligosaccharide content. Poult Sci 79:1127–1131
157. Baker K, Utterback P, Parsons C, Stein H (2011) Nutritional value of soybean meal produced from conventional, high-protein, or low-oligosaccharide varieties of soybeans and fed to broiler chicks. Poult Sci 90:390–395
158. Suarez FL, Springfield J, Furne JK, Lohrmann TT, Kerr PS, Levitt MD (1999) Gas production in humans ingesting a soybean flour derived from beans naturally low in oligosaccharides. Am J Clin Nutr 69:135–139
159. Raboy V, Dickinson DB (1993) Phytic acid levels in seeds of glycine max and *G. soja* as influenced by phosphorus status. Crop Sci 33:1300–1305
160. Anderson RL, Wolf WJ (1995) Compositional changes in trypsin inhibitors, phytic acid, saponins and isoflavones related to soybean processing. J Nutr 125(3 Suppl):581S–588S
161. Raboy V, Dickinson DB (1987) The timing and rate of phytic acid accumulation in developing soybean seeds. Plant Physiol 85:841
162. Oltmans SE, Fehr WR, Welke GA, Raboy V, Peterson KL (2005) Agronomic and seed traits of soybean lines with low-phytate phosphorus. Crop Sci 45:593–598
163. Israel D, Burton J, Kwanyuen P (2006) Genetic variability for phytic acid phosphorus and inorganic phosphorus in seeds of soybeans in maturity groups V, VI, and VII. Crop Sci 46:67–71
164. Cromwell GL, Coffey RD (1991) Phosphorus-a key essential nutrient, yet a possible major pollutant-its central role in animal nutrition. In: Lyons TP (ed) Biotechnology in the feed industry. Alltech Technical Publications, Nicholasville, pp 133–145
165. Raboy V, Dickinson DB, Below FE (1984) Variation in seed total phosphorus, phytic acid, zinc, calcium, magnesium, and protein among lines of *Glycine max* and *G. soja*. Crop Sci 24:431–434
166. Israel D, Kwanyuen P, Walker D, Burton J (2007) Response of low seed phytic acid soybeans to increases in external phosphorus supply. Crop Sci 47:2036–2046
167. Kwanyuen P, Burton JW (2005) A simple and rapid procedure for phytate determination in soybeans and soy products. J Am Oil Chem Soc 82:81–85
168. Kumar V, Rani A, Rajpal S, Srivastava G, Ramesh A, Joshi OP (2005) Phytic acid in Indian soybean: genotypic variability and influence of growing location. J Sci Food Agric 85:1523–1526
169. Chen BHY, Morr CV (1985) Solubility and foaming properties of phytate-reduced soy protein isolate. J Food Sci 50:1139–1142
170. Wilcox JR, Premachandra GS, Young KA, Raboy V (2000) Isolation of high seed inorganic P, low-phytate soybean mutants. Crop Sci 40:1601–1605
171. Yuan FJ, Zhao HJ, Ren XL, Zhu SL, Fu XJ, Shu QY (2007) Generation and characterization of two novel low phytate mutations in soybean (*Glycine max* L. Merr.). Theor Appl Genet 115:945–957
172. Hammond E, Johnson LA, Su C, Wang T, White PJ (2005) Soybean oil. In: Shahidi F (ed) Bailey's industrial oil and fat products. Wiley, New York, pp 577–653
173. Wang H, Murphy PA (1994) Isoflavone composition of American and Japanese soybeans in Iowa: effects of variety, crop year, and location. J Agric Food Chem 42:1674–1677
174. Lee SJ, Ahn JK, Kim SH, Kim JT, Han SJ, Jung MY, Chung IM (2003) Variation in isoflavone of soybean cultivars with location and storage duration. J Agric Food Chem 51:3382–3389
175. Kudou S, Fleury Y, Welti D, Magnolato D, Uchida T, Kitamura K, Okubo K (1991) Malonyl isoflavone glycosides in soybean seeds (*Glycine max* MERRILL). Agric Biol Chem 55:2227–2233
176. Kim J, Hong SB, Jung WS, Yu CY, Ma KH, Gwag JG, Chung IM (2007) Comparison of isoflavones composition in seed, embryo, cotyledon and seed coat of cooked-with-rice and vegetable soybean (*Glycine max* L.) varieties. Food Chem 102:738–744
177. Wang HJ, Murphy PA (1996) Mass balance study of isoflavones during soybean processing. J Agric Food Chem 44:2377–2383
178. Murphy PA, Song T, Buseman G, Barua K, Beecher GR, Trainer D, Holden J (1999) Isoflavones in retail and institutional soy foods. J Agric Food Chem 47:2697–2704
179. Setchell K (1998) Phytoestrogens: the biochemistry, physiology, and implications for human health of soy isoflavones. Am J Clin Nutr 68:1333S–1346S
180. Shi A, Chen P, Zhang B, Hou A (2010) Genetic diversity and association analysis of protein and oil content in food-grade soybeans from Asia and the United States. Plant Breed 129:250–256

181. Hurburgh CR, Brumm TJ, Guinn JM, Hartwig RA (1990) Protein and oil patterns in US and world soybean markets. J Am Oil Chem Soc 67:966–973
182. Weber CR (1950) Inheritance and interrelation of some agronomic and chemical characters in an interspecific cross in soybeans, *Glycine max* × *G. ussuriensis*. Iowa Agric. Exp. Stn Res. Bull. No. 374
183. Gibson L, Mullen R (1996) Soybean seed composition under high day and night growth temperatures. J Am Oil Chem Soc 73:733–737
184. Weiss M, Weber C, Williams L, Probst A (1952) Correlations of agronomic characters and temperature with seed compositional characters in soybean, as influenced by variety and time of planting. Agron J 44:289–297
185. Piper EL, Boote KI (1999) Temperature and cultivar effects on soybean seed oil and protein concentrations. J Am Oil Chem Soc 76:1233–1241
186. Cherry JH, Bishop L, Hasegawa PM, Lefflert H (1985) Differences in the fatty acid composition of soybean seed produced in northern and southern areas of the USA. Phytochemistry 24:237–241
187. Zhe Y, Lauer JG, Borges R, de Leon N (2010) Effects of genotype × environment interaction on agronomic traits in soybean. Crop Sci 50:696–702
188. Murphy SE, Lee EA, Woodrow L, Seguin P, Kumar J, Rajcan I, Ablett GR (2009) Genotype × environment interaction and stability for isoflavone content in soybean. Crop Sci 49:1313–1321
189. Jenkinson JE, Fehr WR (2010) Influence of locations and planting dates on protein composition of soybean lines with modified beta-conglycinin and glycinin concentration. Crop Sci 50:1805–1810
190. Karlin J (2012) Change in where US soybeans are planted over past 25 years. http://www.dtnprogressivefarmer.com/dtnag/common/link.do;jsessionid=0B34BBF75ADAAE85A2C29CEDCCBB558E.agfreejvm2?symbolicName=/ag/blogs/template1&blogHandle=agfundamental&blogEntryId=8a82c0bc35e51c22013659b6ba090487. Accessed 16 May 2012
191. Yamaya A, Endo Y, Fujimoto K, Kitamura K (2007) Effects of genetic variability and planting location on the phytosterol content and composition in soybean seeds. Food Chem 102:1071–1075
192. Anthony P, Malzer G, Sparrow S, Zhang M (2012) Soybean yield and quality in relation to soil properties. Agron J 104:1443–1458
193. Abbasi MK, Tahir MM, Azam W, Abbas Z, Rahim N (2012) Soybean yield and chemical composition in response to phosphorus–potassium nutrition in Kashmir. Agron J 104:1476–1484
194. Krueger K, Goggi AS, Mallarino AP, Mullen RE (2013) Phosphorus and potassium fertilization effects on soybean seed quality and composition. Crop Sci 53:602–610
195. Farmaha BS, Fernández FG, Nafziger ED (2012) Soybean seed composition, aboveground growth, and nutrient accumulation with phosphorus and potassium fertilization in no-till and strip-till. Agron J 104:1006–1015
196. Gao J, Hao X, Thelen KD, Robertson GP (2009) Agronomic management system and precipitation effects on soybean oil and fatty acid profiles. Crop Sci. 49:1049–1057
197. Robinson AP, Conley SP, Volenec JJ, Santini JB (2009) Analysis of high yielding, early-planted soybean in Indiana. Agron J 101:131–139
198. Hu M, Wiatrak P (2012) Effect of planting date on soybean growth, yield, and grain quality: review. Agron J 104:785–790
199. Bellaloui N, Mengistu A (2008) Seed composition is influenced by irrigation regimes and cultivar differences in soybean. Irrigation Sci 26:261–268
200. Howell RW, Cartter JL (1958) Physiological factors affecting composition of soybeans: II. Response of oil and other constituents of soybeans to temperature under controlled conditions. Agron J 50:664–667
201. Keirstead C (1952) Marketing study of factors affecting the quantity and value of products obtained from soybeans. United States Dept. of Agriculture, Production and Marketing Administration, Fats and Oils Branch, US Government Printing Office, Washington, DC
202. Serreti C (1993) Influence of high protein, genotype, and environment on protein quality of soybean. Kansas State University, Manhattan
203. Kane MV, MacKown CT, Grabau LJ, Steele CC, Hildebrand DF (1997) Early-maturing soybean cropping system: III. Protein and oil contents and oil composition. Agron J 89:464–469
204. Naeve SL, Huerd SC (2008) Year, region, and temperature effects on the quality of Minnesota's soybean crop. Agron J 100:690–695
205. Wolf R, Cavins J, Kleiman R, Black L (1982) Effect of temperature on soybean seed constituents: oil, protein, moisture, fatty acids, amino acids and sugars. J Am Oil Chem Soc 59:230–232
206. Ren C, Bilyeu KD, Beuselinck PR (2009) Composition, vigor, and proteome of mature soybean seeds developed under high temperature. Crop Sci 49:1010–1022
207. Carrera C, Martínez MJ, Dardanelli J, Balzarini M (2011) Environmental variation and correlation of seed components in nontransgenic soybeans: protein, oil, unsaturated fatty acids, tocopherols, and isoflavones. Crop Sci 51:800–809
208. Cheesbrough T (1989) Changes in the enzymes for fatty acid synthesis and desaturation during acclimation of developing soybean seeds to altered growth temperature. Plant Physiol 90:760–764
209. Caldwell CR, Britz SJ, Mirecki RM (2005) Effect of temperature, elevated carbon dioxide, and drought during seed development on the isoflavone content of dwarf soybean [*Glycine max* (L.) Merrill] grown in controlled environments. J Agric Food Chem 53:1125–1129
210. Lozovaya VV, Lygin AV, Ulanov AV, Nelson RL, Daydé J, Widholm JM (2005) Effect of temperature and soil moisture status during seed development on soybean seed isoflavone concentration and composition. Crop Sci 45:1934–1940
211. Kitamura K, Igita K, Kikuchi A, Kudou S, Okubo K (1991) Low isoflavone content in some early maturing cultivars, so-called "summer-type soybeans" [*Glycine max* (L) Merrill]. Jpn J Breed 41:651–654
212. Tsukamoto C, Shimada S, Igita K, Kudou S, Kokubun M, Okubo K, Kitamura K (1995) Factors affecting isoflavone content in soybean seeds: changes in isoflavones, saponins, and composition of fatty acids at different temperatures during seed development. J Agric Food Chem 43:1184–1192
213. Vlahakis C, Hazebroek J (2000) Phytosterol accumulation in canola, sunflower, and soybean oils: effects of genetics, planting location, and temperature. J Am Oil Chem Soc 77:49–53
214. Britz SJ, Kremer DF (2002) Warm temperatures or drought during seed maturation increase free α-tocopherol in seeds of soybean [*Glycine max* (L.) Merr.]. J Agric Food Chem 50:6058–6063
215. Meckel L, Egli DB, Philips RE, Radcliffe D, Leggett JE (1984) Effect of moisture stress on seed growth in soybeans. Agron J 76:647–650
216. Rotundo JL, Westgate ME (2010) Rate and duration of seed component accumulation in water-stressed soybean. Crop Sci 50:676–684
217. Dornbos D, Mullen R (1992) Soybean seed protein and oil contents and fatty acid composition adjustments by drought and temperature. J Am Oil Chem Soc 69:228–231
218. Kumar V, Rani A, Solanki S, Hussain SM (2006) Influence of growing environment on the biochemical composition and physical characteristics of soybean seed. J Food Compos Anal 19:188–195

219. Rotundo JL, Westgate ME (2009) Meta-analysis of environmental effects on soybean seed composition. Field Crops Res 110:147–156
220. Carrera C, Martínez MJ, Dardanelli J, Balzarini M (2009) Water deficit effect on the relationship between temperature during the seed fill period and soybean seed oil and protein concentrations. Crop Sci 49:990–998
221. Specht J, Chase K, Markwell J, Germann M, Lark K, Graef G, Macrander M, Orf J, Chung J (2001) Soybean response to water. Crop Sci 41:493–509
222. Rose I (1988) Effects of moisture stress on the oil and protein components of soybean seeds. Crop Pasture Sci 39:163–170
223. Boydak E, Alpaslan M, Hayta M, Gerçek S, Simsek M (2002) Seed composition of soybeans grown in the Harran region of Turkey as affected by row spacing and irrigation. J Agric Food Chem 50:4718–4720
224. Bennett JO, Yu O, Heatherly LG, Krishnan HB (2004) Accumulation of genistein and daidzein, soybean isoflavones implicated in promoting human health, is significantly elevated by irrigation. J Agric Food Chem 52:7574–7579