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REVIEW ARTICLE

# Understanding the advances in Sorghum grain quality improvement: An overview

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## Abstract

Sorghum, a crucial cereal crop with versatile applications, is increasingly recognized for its grain quality attributes. The nutritional and biochemical diversity within sorghum, encompassing elements such as iron (Fe), zinc (Zn), proteins, starch, dietary fibers, and ß-carotene, plays a pivotal role in enhancing the quality across diverse sorghum accessions. Breeding programs offer a promising avenue for further improvement in these traits. Additionally, sorghum features a spectrum of phenolic compounds, including tannins and flavonoids, influencing both pigmentation and potential health benefits. The antioxidative properties of these compounds underscore their critical role in promoting health and mitigating oxidative stress. The significance of sorghum is shaped by genetic factors, environmental conditions, ripening stages, and varietal distinctions, highlighting the complex interplay between grain structure, genetics, and nutritional content. As the global demand for diverse, nutritionally rich food sources continues to rise, this review provides insights aimed at deepening our understanding of sorghum's potential as a staple crop with substantial nutritional and health-promoting attributes.

## Keywords

Sorghum grain; phenolic compounds; kafirin; flavonoids; quantitative trait loci; antioxidant activity

## Introduction

Sorghum (*Sorghum bicolor* (L.) Moench), a cereal crop of the Poaceae family serves as an indispensable dietary staple for over 500 million individuals in Africa and Asia (1). It was originated in sub-Saharan Africa, domesticated, and later spread to India and China (2). It is a nutrient-rich, annual diploid crop species (2n=2x=20) and is one of the most significant cereal crops in the world and ranks 5$^{th}$ in terms of production behind maize, rice, wheat, and barley (3). The USA is the top sorghum-producing country contributing 14% whereas India contributes 7 % of the total world production. The major sorghum-producing states in India are Maharashtra, Karnataka, Tamil Nadu, Rajasthan, and Madhya Pradesh (4). As the majority of the human population depends on rice and wheat as their staple food, sorghum being the crop adapted to the dry land conditions can be used to optimize the utilization of dry land and increase the farmers' income. Also, being the C4 crop, sorghum is climate resilient and can be grown in harsh environmental conditions including temperature and water constraints. It is diversified into four main categories: grain sorghum, sweet sorghum, forage sorghum and biomass sorghum, each featuring unique genetic variations, heights, traits and applications (5). Traditionally, sorghum has been utilized in various forms, including whole meal flour and milled fractions for dishes like 'rotis' and gruel. In some instances, sorghum is employed for puffing and creating special dishes, albeit to a limited extent. Sorghum malt is globally used, notably by the Bantu people in Africa where they have a traditional drink known as kafir beer (6). Although the current regional system introduces hybrids, these are less favored for human consumption. In contrast, local and improved landraces are preferred for household consumption because of their superior grain quality, characterized by the bold, white appearance and a sweeter taste (7).

Sorghum shares many of the same essential components as millet and maize, including starch, fat, protein, and non-starch polysaccharides. It is a good source of micro and macronutrients, carotenoids, and polyphenols, as well as bioactive nutrients like vitamin B and fat-soluble vitamins D, E, and K (8). Sorghum has distinct and variety-dependent nutritional qualities. It is gluten-free, has resistant starch and thus can be consumed by people with celiac disease (9). It is well known for having very low digestion of starch and protein and has the potential for controlling obesity and weight. Compared to other cereals, sorghum has high and diverse phenolic compounds including all types with the prevalence of simple phenolic acids, flavonoids, and tannins (10). Identifying the genes regulating the composition of sorghum grains would help modify grain texture and quality to suit current end-use markets and promote the development of new products. This overview delves into the intricate details of sorghum's carbohydrate profile, emphasizing the pivotal role of starch, its granular morphology, and the genetic variations that categorize sorghum grains into waxy and non-waxy types. Beyond carbohydrates, the exploration encompasses the fiber landscape of sorghum, encompassing insoluble and soluble fibers, including notable polysaccharides like β-D-glucans and phytoglycogens. It also extends to the bioactive compounds present in sorghum, which confer the grains with potential health benefits to humans like lowering oxidative stress, anti-cancerous activity, anti-inflammatory action, etc (11). The association studies, combining ability and variability among the diverse sorghum genotypes result in the identification of promising lines with enhanced nutrient contents. Marker trait association as well as the Quantitative Trait Loci (QTLs) was identified in various sorghum accessions for their quality traits. Therefore, this review aims to provide a holistic understanding of sorghum's grain quality, its importance, nutritional composition and therapeutic properties offering insights into its potential benefits for human health by improving its quality attributes through different breeding approaches for alleviating malnutrition in developing countries.

## 1. Sorghum classification and distribution

Sorghum, belonging to the Andropogoneae tribe within the grass family (Poaceae), encompasses approximately 25 species and 5 subgenera. Certain species within this genus have been cultivated for human consumption, utilized as animal fodder, or exploited for industrial purposes. Notably, *Sorghum bicolor* (L.) Moench is a widely cultivated species globally. The remaining species are primarily found in the wild or as weeds, exhibiting varying levels of interspecific compatibility, ranging from 0 % to 100 % (12). The five subgenera identified within Sorghum are Chaetosorghum, Heterosorghum, Parasorghum, Stiposorghum, and Eusorghum. Among these, Eusorghum, which includes the cultivated species, *S. bicolor*, has been further classified into 5 major races (bicolor, durra, kafir, guinea, and caudatum) and 10 intermediate races (Fig. 1) represent hybrid combinations based on panicle characteristics (13). Indian sorghum varieties mainly include the Durra, Caudatum, Guinea, and Guinea-Kafir types, with a smaller amount of bicolor being grown (14). Durra is the primary cultivated sorghum race in India which is also found in Eastern Africa with large, globular grains. High-quality flours can be derived from caudatum, durra, and kafir races, contingent on specific cultivars. The guinea margaritiferum subrace yields excellent grain, which is cooked like rice in Western Africa. In Mali, couscous made with guinea gambicum is highly valued. The white grain forms of *Guinea guineense* are ground into flour, while red grain forms are predominantly used in beer production. *Guinea roxburghii* serves as pop-sorghum in India and high-quality grain in southern Africa (15). In the United States, grain sorghum production is dominated by the Kafir-Caudatum variety. In Nigeria, the Kaura sorghum is classified as Durra-Caudatum, while Zerazeras and Hegaris are considered part of the Caudatum category. In Sudan, the Feterita sorghum ranges across different classifications from Guinea-Caudatum and Caudatum to Durra-Caudatum. Varieties such as broomcorns, sorgos, and Sudan grass are categorized under the bicolor type.

## 2. Sorghum grain structure, appearance, and its genetics

The bran layer that comprises of pericarp and testa, the endosperm, and the germ makes up the sorghum grain (Fig. 2) and their relative proportion varies depending upon variety and environment. Generally, sorghum contains 84.2 % endosperm, 9.4 % germ, and 6.5 % pericarp (16). The sorghum bran generally contains non-starch polysaccharides, a wide range of phenolic compounds, such as flavonoids, phenolic acids, and condensed tannins, as well as certain vitamins, such as carotenoids. Proteins, carbohydrates, and a few vitamins, including vitamin B complex, make up the majority of the endosperm. The germ fraction is primarily made up of lipids and proteins, but it also contains a lot of minerals and vitamins, particularly fat-soluble and complex B vitamins (17, 18). Some sorghum types may also contain a pigmented testa, which is situated between the pericarp and endosperm (17, 19). Genetic and environmental variables mostly determine sorghum quality and appearance. Its caryopsis color and general appearance are influenced by several genetically interrelated elements mentioned in Table 1. Color and thickness of the pericarp, the presence of pigmented testa, and endosperm color all have a major impact on appearance (19). Thus, sorghum can be categorized into 5 types: white, yellow, red, brown and black based on color, phenolic profile and genotypes (Fig. 3).

The 2 genes R and Y are responsible for controlling pericarp color. The combination of these genes expresses the white (R_yy or rryy), lemon yellow (rrY_), or red (R_Y_)

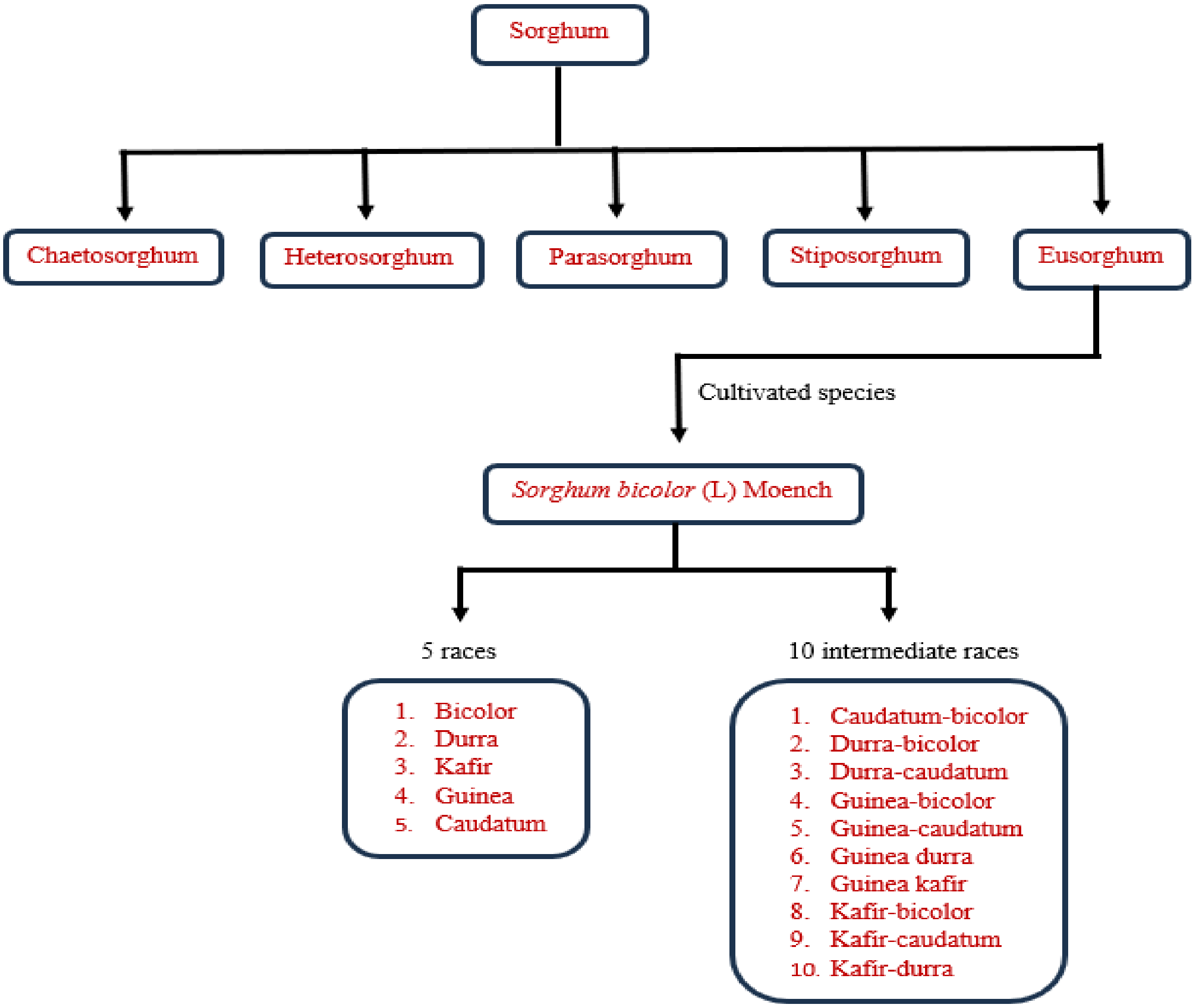


**Fig. 1.** Sorghum classification.

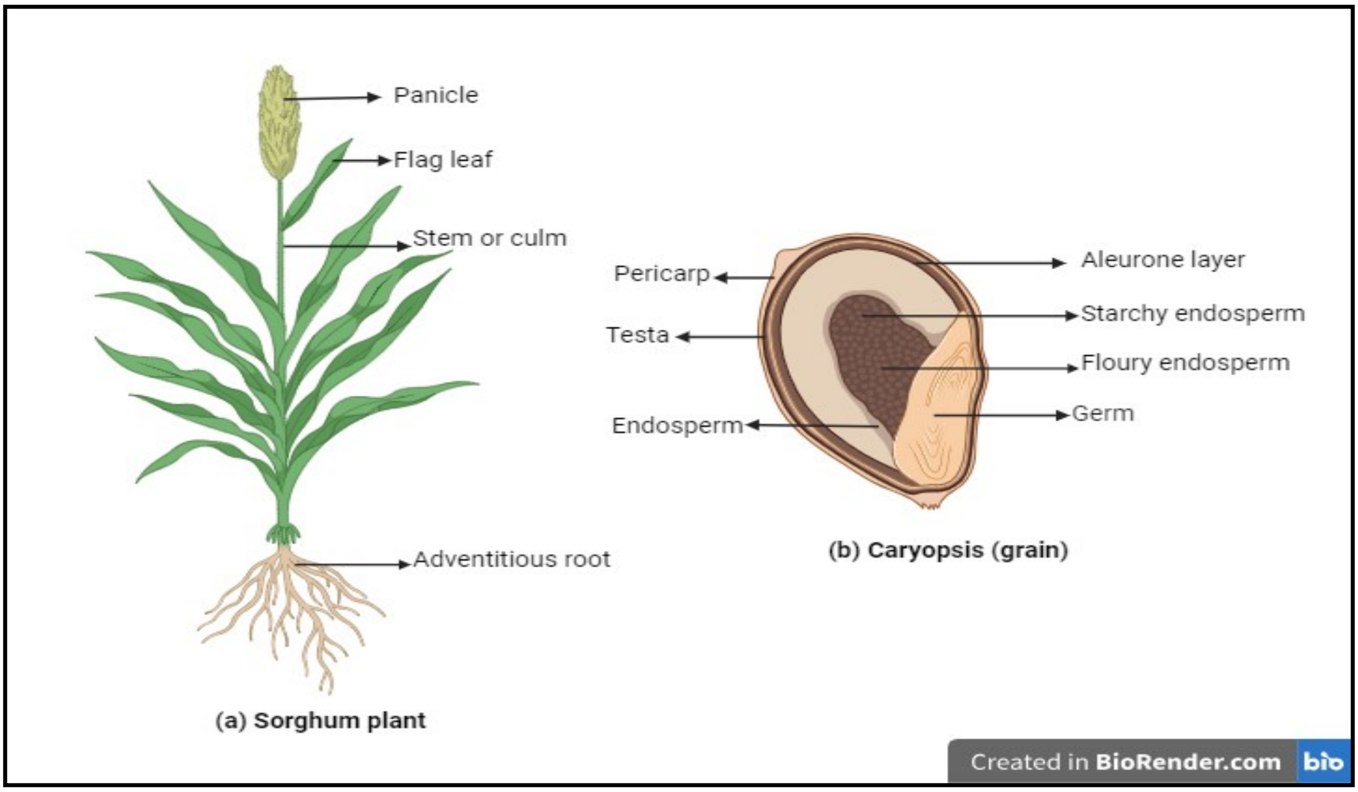


**Fig. 2.** Sorghum plant and grain structure

**Table 1.** Genes and their inheritance patterns associated with sorghum grain traits

| Traits | Genes governing the traits | Inheritance | References |
|---|---|---|---|
| Pericarp color | Y, R | rryy/R_yy : white/colorless<br>rrY_ : yellow<br>R_Y_ : red/black | (20)<br>(21)<br>(22) |
| Testa color | $B_1$,$B_2$ | $B_1$_$B_2$_ : pigmented testa (brown/purple),<br>$B_1$_$b_2b_2$ / $b_1b_1B_2$_ / $b_1b_1b_2b_2$ : non-pigmented testa | (17) |
| Pericarp thickness | Z | Z_: thin pericarp,<br>ZZ : thick pericarp | (17) |
| Color intensity | I (Intensifier gene, only for red and yellow pericarp) | I_: increased intensity,<br>ii : lighter colors | (127) |


**Fig. 3.** Sorghum grain color diversity. A : red grains, B: light red/ orange grains, C: white grains, D: yellow grains, E: black grains.

color. White sorghum has low total phenolic content and tannin and 3-deoxyanthocyanidin levels are extremely low or non-existent (20). Yellow sorghum is greater in total phenolic content and higher in flavanones than white sorghum (21). Red sorghum has a significant amount of phenolic chemicals and condensed tannins. Black sorghum is essentially a unique form of red sorghum at the genetic level, where the pericarp undergoes a transformation to black under the influence of solar radiation during maturation. The pericarp of black sorghum contains a high concentration of phenolic compounds, notably 3-deoxyanthocyanidin (22). The presence of a pigmented testa layer is governed by $B_1$ and $B_2$ genes. Condensed tannins are found in sorghums classed as type III (also known as brown or bird-resistant sorghum) that have pigmented testa ($B_1$_$B_2$_) and a dominant spreader (S_) gene. Pericarp thickness is controlled by the Z gene ranging from 8 to 160 mm (23), and varies within an individual kernel. Sorghum carrying homozygous recessive (rr) genes have thick mesocarp. The presence of a thick pericarp typically masks the color of the testa and endosperm, resulting in kernels that appear chalky due to the existence of small starch granules in the pericarp (23). The Wx gene impacts endosperm starch composition. The dominant Wx allele balances amylose and amylopectin, while the recessive wx allele creates a waxy endosperm rich in amylopectin (24). The genetics of important sorghum grain quality traits such as grain size, grain shape, and grain lustre were studied. While grain size and grain shape are governed by dominant genes that are polygenic in nature, the grain lustre trait is under the control of complementary recessive genes (25).

## 3. Nutritional Composition and Functional Attributes of Sorghum Grain

Carbohydrates are the most abundant component of sorghum grain, followed by proteins, lipids, fiber, dietary fiber, and ash (26). On average, 100 g of the grain consists of approximately 72.1 g carbohydrates, 12.4 g water, 10.6 g proteins, 6.7 g fibers, and 3.5 g fats, providing an estimated energy of around 1,377 kJ (27).

### 3.1 Polysaccharides: Starch, fibers, and their significance

Sorghum is rich in starch, primarily stored in the endosperm, with granule morphology varying between floury and corneous regions, as observed (28). The granules in the corneous endosperm are smaller and possess a more angular shape, while those in the floury endosperm are larger and exhibit a spherical form. Starch consists of amylose and amylopectin and their proportion affects the functional and nutritional attributes of sorghum starch and starch-derived products. Amylose plays a role in starch thermal characteristics like gelatinization and pasting (29). Foods high in amylose have been demonstrated to have a lower glycemic index, which promotes various health benefits, including improved diabetes and obesity control (30). Corneous endosperm starch had less amylose than floury endosperm starch (31). Genetic diversity in amylose concentration is evident, with levels ranging from 24 to 33 % in 95 Zimbabwean sorghum landraces and 16.1 % to 55.8 % in 55 different genotypes (32, 33). The majority of sorghum grains contain 20-30 % amylose, which is common for normal cereal grains (28). Sorghum grains are categorized as waxy and non-waxy, with waxy grains containing a higher amount of amylopectin and minimal amylose (up to 5 %) and exhibiting distinctive characteristics like higher starch digestibility, more susceptible to enzymatic degradation, etc (34, 35). Moreover, Waxy sorghum starch has quick cooking, high peak viscosity, and low stability during cooking. It resists gel formation and retrogradation (36).

Apart from being a source of carbohydrates, sorghum is rich in fibers, both insoluble (cellulose and lignin) and soluble (arabinoxylans, β-glucans), that are located in the pericarp and endosperm cell walls and account for 6 to 15 g per 100 g of grain (37) with significant phenolic acids like p-coumaric and ferulic acids (38). The β-D-glucan content in sorghum grain varies from 0.12 % (39) to ≈0.09 % with Glucan A and B identified as water-soluble glucans (40). A few varieties, such as sweet sorghum, contain water-soluble polysaccharides called phytoglycogens, with the mutant gene "su" being homologous to sweet corn (41). The average chain length of sorghum phytoglycogen is 9.4–13.4 and the content can reach up to 13.2 % of the grain.

### 3.2 Sorghum Protein Composition: Distribution, Classes and Nutritional Implications

Sorghum protein distribution reveals that approximately 80 %, 16 %, and 3 % are found in the endosperm, germ, and pericarp respectively (42). The major protein fractions in sorghum include prolamin proteins, particularly kafirins, and non-prolamin proteins like globulins, glutelins, and albumins. Prolamin proteins, primarily situated in the endosperm's protein bodies, constitute the majority of the protein fraction, with nitrogen fertilizer significantly increasing prolamin levels in sorghum and millets (43). Sorghum exhibits greater hardness compared to other food grains, attributed to its elevated prolamin concentration ranging from 3.6 % to 5.1 % and lysine content ranging from 1.06 to 3.64 (44). Kafirins are categorized into α-, β-, γ- and δ-kafirins and makeup 48 % to 70 % of sorghum grain's total protein content (45), exhibiting high polymerization and resistance to enzymatic digestion in the digestive tract (46). The corneous endosperm has higher kafirin levels, while the opaque endosperm contains more albumins and globulins, with equal glutelin concentration in both forms (47). Glutelins, the second-largest high molecular protein fraction located in the endosperm's protein matrix (48). Sorghum proteins are lysine-deficient burich in glutamic acid, leucine and proline. Cultivars from breeding programs exhibit 52 % to 115 % higher lysine compared to conventional varieties (42). Earlier studies reported crude protein levels of 8 % to 12.5 %. At the same time, a recent examination of 19 sorghum genotypes showed significant variation, emphasizing the impact of landrace selection in developing biofortified sorghum, with high-protein genotypes PYPS 2 and PYPS 13 emerging from landraces PSLRC 2 and PSLRC 21 (49).

### 3.3 Carotenoids in Sorghum: Endosperm Color and Composition

Carotenoids are the characteristic yellow or orange pigments present in various seeds, leaves, and plant materials. In sorghum, particularly in the endosperm, show a significant association with grain color. Sorghum is broadly categorized into white endosperm, with low carotenoid levels, and yellow endosperm, with elevated carotenoid levels, primarily lutein and zeaxanthin (50). Yellow endosperm sorghum demonstrates higher carotenoid content, with zeaxanthin identified as the predominant carotenoid in most varieties and β-carotene exclusively found in yellow endosperm genotypes (51). Lutein and zeaxanthin are highlighted as the most prevalent carotenoids in grain sorghum, although at concentrations lower than those in yellow maize (52, 53). Enhanced bioavailability of provitamin A, specifically β-carotene, has been documented in certain transgenic sorghum lines, with 5 Quantitative Trait Loci identified on chromosomes 1, 2, and 10. Yellow endosperm sorghum exhibits higher levels of lutein, zeaxanthin, and β-carotene compared to white endosperm types, with crossbreeding resulting in inbreds with intermediate carotenoid values (54). A study underscored zeaxanthin as the predominant carotenoid in most sorghum varieties, with β-carotene or provitamin A activity exclusively identified in yellow endosperm genotypes (51). Other carotenoids present in smaller proportions include α-cryptoxanthin, β-cryptoxanthin, and α-carotenes (52, 53). A study investigated carotenoid and pro-vitamin A content in sorghum accessions with different pericarp pigments using LC-MS (55). Among the 5 identified carotenoids,3 (α-carotene, β-carotene and β-cryptoxanthin) are vitamin A precursors. Sorghum with yellow pericarp exhibited the highest total carotenoid content, while brown or yellow pericarp varieties had the highest β-carotene. White pericarp sorghum had the lowest carotenoid levels. Pro-vitamin A content was highest in yellow pericarp, followed by brown and white pericarp varieties. The study suggests that breeding sorghum with specific pericarp pigments may help to prevent vitamin A deficiency in regions where sorghum is a staple crop.

### 3.4 Mineral Composition of Sorghum Grains: Fe and Zn Variability and Genetic Insights

Sorghum grains have been extensively studied for their iron (Fe) and zinc (Zn) content due to their essential role in human nutrition. Research has consistently shown significant variability in the mineral content of sorghum grains among different varieties investigated the genetic and environmental impact on iron, zinc, and phytate in food sorghum, emphasizing the importance of understanding the factors influencing the availability of these minerals in sorghum varieties. Fe ranged from 30 to 113 mg/kg, Zn from 11 to 44 mg/kg, and phytate from 0.4 to 3.5 % and Fe and Zn did not consistently link to genetics but varied across locations, indicating environmental impact (56). Additionally, there are substantial differences in mineral content among different sorghum varieties, with greater Fe and Zn in red and black varieties compared to white (57). A study was conducted in a total of 19 sorghum genotypes derived from 11 superior landraces, where significant variations in the concentration of total and available Fe and Zn were found. Most sorghum genotypes demonstrated elevated levels of iron (ranging from 14.21 to 28.41 mg/100 g) and zinc (ranging from 4.81 to 8.16 mg/100 g). Thus, this study identified high Fe and Zn-containing landraces which underscores the potential of utilizing them for biofortification purposes.

Moreover, quantitative trait loci (QTLs) and candidate genes associated with high grain Fe and Zn concentrations in sorghum, provide insights into the genetic basis of mineral accumulation in sorghum grains (58). Twenty-three sorghum landrace accessions representing 5 distinct color types: white, buff, red, brown, and purple collected from 5 different countries, revealed significant variability among the accessions in terms of Fe and Zn levels, whereas no significant differences were observed in the Mn and Na contents (59). The concentration of Fe ranged from 25 µg/g to 42 µg/g, with the highest recorded concentration being 42 µg/g and the lowest at 25 µg/g. Zn concentrations exhibited variation within the range of 18 µg/g to 30 µg/g. In an assessment of the zinc (Zn) and iron (Fe) content in 29 accessions, specifically selected for their elevated mineral levels, as part of the screening process involving over 2200 sorghum lines, the iron content ranged from 26 to 60 mg/kg, while the zinc content varied between 21 and 57 mg/kg (60).

## 4. Antinutritional Factors in Sorghum: Implications for Nutrient Accessibility and Bioavailability

In addition to examining the nutritional composition, it is crucial to consider the accessibility of nutrients for consumers, particularly given the variation in naturally occurring antinutritional factors that diminish the nutritional value of sorghum compared to wheat or maize (61). These factors include phytates, enzyme inhibitors, condensed tannins, and others, collectively compromising the digestibility of the grain. Phytic acids or phytates form complexes with essential dietary minerals like calcium, zinc, iron, and magnesium, rendering them less available for absorption (62). This process involves the chelation of positively charged minerals, such as iron and zinc, resulting in insoluble complexes and reduced mineral absorption. Besides, the phytate forms complexes with proteins, slowing the digestion rate and impeding their bioavailability (63).

Primarily serving as a reservoir of phosphorus and inositol, phytates in sorghum are predominantly located in the aleurone layer (phytin bodies or aleurone grains) and to a lesser extent, in the germ. Abrasive decortication of sorghum can remove 40 to 50 % of phytate and total phosphorus. The levels of phytate-phosphorus in 30 sorghum varieties ranged from 0.17 % to 0.38 %, constituting 80 % to 87 % of the total phosphorus in the kernel (64). Some low phytic acid-containing landraces, such as Malkhed-1, Nalwar-2, and the variety Phule Maulee, have been identified (65). Because of these anti-nutrient interactions and sorghum's low bioavailability in comparison to other grains (66), maximizing the potential of nutrient-rich landraces and genotypes such as PSLRC-2, PSLRC-3, PSLRC-9, PYPS 2 and PYPS 13 by reducing anti-nutritive factors should be a priority, particularly in Asia and Sub-Saharan Africa, where malnutrition and nutritional deficiencies are common in women and children (49).

## 5. Phenolic Compounds in Sorghum: Diversity, Distribution and Health Implications

Phenolic compounds, which contain at least one aromatic ring and one or more hydroxyl groups, are categorized into soluble compounds like flavonoids, quinones, and phenylpropanoids within the plant cell vacuole. They also include insoluble compounds such as lignins, condensed tannins, and hydroxycinnamic acid, which are attached to the cell wall (67). These compounds contribute significantly to the antioxidant properties of sorghum, with potential health benefits linked to chronic disease prevention such as breast and colon cancer as well as diabetes (68). The composition of phenolic compounds in sorghum is influenced by factors such as variety, genotype, pericarp color, and grain testa pigmentation (69). The range of the phenolic compounds estimated in various sorghum accessions is mentioned in Table 2.

Phenolic acids, constituents of the grain's endosperm, pericarp, and testa exist in both free and bound and are abundant in sorghum grains, with ferulic acid being the most prevalent in the bound form (70, 71). Phenolic acids, the simplest yet abundant phenolic compounds present in all sorghum grains, exhibit a total concentration ranging from 445 to 2850 µg/g (72). Notable phenolic acids reported in sorghum include gallic, vanillic, protocatechuic, cinnamic, p-coumaric, p-hydroxybenzoic, syringic, ferulic, caffeic, and sinapic acids (73- 75). Studies on sorghum genetic resources reveal a wide range of total polyphenol content, with ferulic acid consistently exhibiting the lowest content among examined phenolic compounds (76). Higher total phenol levels in specific sorghum genotypes under salinity stress suggest a potential adaptive mechanism for mitigating sub-cellular damage during stress conditions (77). Variability in Total Phenolic Content (TPC) is observed among sorghum accessions from different countries (78). Genotypes with red and brown pericarp show elevated levels of total proanthocyanidin and total phenolic content, contributing to heightened antioxidant activities (79). Sorghum polyphenol extracts have antioxidant properties and show inhibition of the activity of cholesterol biosynthesis-

**Table 2.** Total phenol content (TPC), Total flavonoid content (TFC), and Total tannin content (TTC) ranges in different sorghum accessions

| Sorghum source | Extract solvent | TPC Range (mg GAE/g) | TFC Range | TTC Range | References |
|---|---|---|---|---|---|
| Moroccan ecotypes | Methanol | 125.86 - 314.91 | 4.53 - 14.04 mg GAE/g | - | (128) |
| Kenyan varieties | Methanol | 7.9 - 29.6 | - | - | (109) |
| Australian varieties | Methanol | 0.24 - 11.50 | - | - | (129) |
| Senegalese varieties | Methanol | 0.22 - 0.57 | - | - | (130) |
| Genetic resources collected from 5 countries | Methanol | 16.33 - 231.21 | 16.46 - 67.71 mg QE/g | - | (76) |
| Accessions from 15 regions | Methanol | 9.97 - 333.58 | 10.35 - 252.67 mg QE/g | - | (78) |
| Breeding lines | Methanol | 0.29 - 10.38 | - | 0.68 - 434.22 mg CE/g | (131) |
| Black sorghum lines | Methanol | 5 - 20 | - | - | (22) |
| Black sorghum hybrids | | 9 - 17 | - | 14 - 19 mg CE/g | |
| Korean sorghum landraces | Methanol | 1.17 - 10.23 | - | 0.12 - 428.95 mg CE/g | (132) |
| Sorghum landraces | Methanol | 1.37 - 9.20 | - | 25.18 - 408.84 mg CE/g | (133) |
| Sorghum genotypes | | 173.68 - 1040.73 | - | 1.13 - 12.4 mg/100 g | (79) |

related enzymes (80). Biologically active compounds linked to sorghum polyphenols have been shown to lower blood LDL (low-density lipoprotein) cholesterol levels and elevate HDL (high-density lipoprotein) cholesterol, demonstrating significant hypocholesterolemic effects. Sorghum's cholesterol-lowering impact has been recognized compared to cereals like wheat, oats and millet as the sorghum diet reduced the absorption of cholesterol in the intestine (81). In a study, it was found that sorghum extracts reduce cholesterol levels by influencing the expression of proteins involved in hepatic cholesterol metabolism (82).

Tannins, a diverse group of polyphenolic polymers, exhibit varying molecular weights and complexity and are associated with numerous health benefits, including antioxidant properties, anticancer activities, and cardioprotective effects (83). Despite their positive health effects, tannins also possess anti-nutritional properties, hindering protein digestibility and iron absorption through complex formation (84). Influenced by phenol-protein ratios, tannins form soluble and insoluble complexes with proteins and impact carbohydrates in sorghum, including hemicellulose, cellulose, starch, and pectin (85). Sorghum predominantly contains condensed tannins also known as proanthocyanidins, with hydrolyzable tannins found in various plants demonstrating diverse biological capacities (86, 87). Sorghum tannins, mainly condensed, vary significantly among varieties, with black testa varieties having the highest content (88). Sorghum varieties are classified into three types based on tannin content, with Type I having low levels, Type II moderate levels, and Type III high levels. Type I sorghums, characterized by recessive $B_1$ and/or $B_2$ genes ($B_1\_b_2b_2$, $b_1b_1B_2\_$, or $b_1b_1b_2b_2$), Type II sorghums possess dominant $B_1$ and $B_2$ genes but a homozygous recessive S gene ($B_1\_B_2\_ss$) and Type III sorghums, with dominant $B_1$, $B_2$ and S genes ($B_1\_B_2\_S\_$) (17, 89).

Sorghum grains harbor condensed or non-hydrolyzable tannins with varied degrees of polymerization degrees, including dimers, oligomers, and polymers of catechins, exhibiting variations in flavanol interlinkages, phenolic hydroxylation patterns and the configuration of the hydroxylated C-ring C3 center of the flavan-3-ol building block (90). The primary unit of condensed tannins is (epi)catechin, accompanied by significant units like (epi)gallocatechin, (epi)gallocatechin gallate, and (epi)afzelechin (91). Specifically, procyanidins, a type of condensed tannin in sorghum grains, act as potent radical scavengers, significantly enhancing antioxidant capacity. Variability in condensed tannin levels is observed among sorghum bran varieties, with coarse sorghum bran exhibiting the highest content (179.77 mg/100 g) and fine sorghum bran having the lowest content (172.38 mg/100 g). This variability may be attributed to factors such as ripening stage, varietal differences, climatic conditions, or their interplay (92).

Flavonoids, primarily concentrated in sorghum bran, exhibit diverse types and concentrations influenced by factors such as pericarp color, thickness, and the presence of pigmented testa (93). Representing the most abundant and diverse class of phenolic compounds in sorghum, flavonoids, with recognized health benefits including antioxidant, anticancer, anti-inflammatory, and gastroprotective properties, exist in both free (soluble) and bound forms (94). Specific flavonoid compounds identified in sorghum include flavan-4-ols, flavanones, flavonols, and dihydroflavonols, with notable content in red and black sorghums (22, 89, 95). Sorghum is a primary source of rare flavonoids known as 3-deoxyanthocyanins, contributing to red-to-black pigmentation in various plant parts. Particularly, black sorghum grains exhibit elevated levels of these compounds in the bran, ranging from 4 to 16 mg/g (96). Significant variability in total flavonoid content among sorghum landraces underscores their diversity. The diversity in flavonoid levels among sorghum landraces may result not only from genetic differences but also from variations in collection sites, indicating an influence of environmental factors on flavonoid concentration, as observed in the study conducted (97). The flavonoid concentrations in 8 sorghum genotypes revealed significant variations influenced more by genotype than environmental factors (98). In black sorghum, four 3-deoxy anthocyanidin compounds, including apigeninidin (AP), luteolinidin (LUT), 7-methoxyapigeninidin (7-MeO-AP) and 5-methoxyluteolinidin (5-MeO-LUT), exhibited diversity in locations and genotypes. Flavones, yellow-colored flavonoids present in sorghum grain with varying concentrations influenced by factors such as pericarp color and thickness, with red and yellow pericarp sorghums often associated with elevated flavone levels (21, 99). A study conducted on 8 sorghum varieties in Austria aimed to assess their antioxidant content and activity. Flavonoids were detected in quantities ranging from 27.03 µg/g (Kalatur variety) to 87.52 µg/g (Huggo variety) (100). On another note, sorghum flavonoids are pivotal for resisting biotic stress. Various diet-based feeding experiments have underscored the importance of testing flavonoids and phenolics against challenging herbivores, implicating these compounds in host plant resistance (101). Notably, research indicates that flavonoids in sorghum adversely affect Fall armyworm larval growth and survival, induce changes in the peritrophic membrane of the larval midgut and mitigate herbivory damage (102, 103) The role of sorghum flavonoids in resisting corn leaf aphids (CLA) *Rhopalosiphum maidis* was studied and how the sorghum flavonoids, controlled by the yellow seed1 (*y1*) gene, repel CLA (106). Sorghum with functional *y1* alleles accumulated flavonoids, deterring CLA, while those lacking *y1* alleles attracted more aphids. Flavonoids from functional *y1* plants increased CLA mortality compared to those from plants lacking *y1* alleles or controls. This underscores the significance of *y1*-regulated flavonoids in sorghum's defense against CLA.

## 6. Sorghum Phenolics: Antioxidant, Anticancer and Antidiabetic Properties

Sorghum and its co-products have gained recognition as valuable sources of nutraceuticals and functional foods, owing to their high content of phenolic compounds, some of the most significant naturally occurring antioxidants and chemopreventive agents (104, 105). The antioxidant activity of sorghum phenolics, assessed through various widely-used *in vitro* assays such as Oxygen radical absorbance capacity (ORAC), Ferric reducing antioxidant power (FRAP), 2,2'-azino-bis(3-ethylbenzothiazoline-6-sulphonic acid) (ABTS) and 1,1-diphenyl-2-picrylhydrazyl (DPPH), contributes significantly to the associated health benefits (106). However, it is important to acknowledge the limitations of these assays in directly translating to *in vivo* antioxidant capacity, considering the complexities of the physiological environment like pH, temperature, bioavailability, and metabolism. Sorghum phenolic compounds act as natural antioxidants, protecting biomolecules from oxidative damage caused by reactive oxygen species, making sorghum grains a valuable source of readily available antioxidants through dietary intake (107). Pigmented sorghum varieties, in particular, exhibit significantly higher antioxidant activity compared to red wheat (108). Recent studies have highlighted strong correlations between phenolic compounds and antioxidant activities in sorghum, with flavonoids and tannins demonstrating significant associations with FRAP and total antioxidant activity (97). Beyond direct antioxidant effects, sorghum phenolics, including 3-deoxyanthocyanidins and condensed tannins, offer additional health benefits through mechanisms such as induction of endogenous detoxifying enzymes and acting as free radical "sinks" to mitigate oxidative stress (11, 109, 110). Sorghum, known for its rich content of specific compounds, including phenolic extracts, demonstrates potential anticancer properties as evidenced by *in vitro* and animal studies, showcasing the ability to reduce and inhibit cancer cell proliferation in the colon, liver, and esophagus (111). Flavones in sorghum, exhibiting estrogenic effects, contribute to *in vitro* anticancer effects, while 3-deoxyanthocyanins in black sorghum show similar properties. The presence of condensed tannins in sorghum, particularly in brown sorghum bran, may play a crucial role in cancer prevention by inhibiting aromatase associated with breast cancer, thereby impeding the formation of cancer growth stimuli (112). Sorghum bran, recognized for its abundance of phenolic substances, is also beneficial for individuals at risk of diabetes due to its low glycemic index (113). In studies investigating the antidiabetic properties of sorghum phenol, sorghum phenolic extract significantly reduced plasma glucose concentrations in diabetic rats, comparable to the effectiveness of the antidiabetic drug glibenclamide (114, 115). Additionally, tannin-rich polyphenolic extracts from sorghum grain demonstrated inhibitory activity against α-amylase and α-glucosidase enzymes, with *in vivo* studies showing significant hypoglycemic activity in diabetic rats, reducing various metabolic parameters (114, 116).

## 7. Breeding for improving the sorghum grain quality

Sorghum, renowned for its substantial genetic diversity, serves as a valuable resource for breeding programs, particularly in the context of enhancing nutritional profiles. A comprehensive analysis of 265 sorghum accessions over 3 years, revealed substantial variation in grain protein (8.1-18.8 %), fat (1.0-4.3 %), and starch (61.7-71.1 %) content (117). The study identified high heritability for protein, followed by fat and starch, highlighting significant genetic contributions to trait variation. Specific races exhibited distinct compositions, with durras/bicolor-durras from Ethiopia/India having the highest protein and fat, while kafirs from the USA/India/South Africa displayed the lowest protein and the highest starch content. These findings not only offer new genetic sources for enhancing sorghum nutrition but also provide insights into the genetic architecture influencing grain composition variation.

A total of 108 sorghum landraces from Tigray, Ethiopia, along with 2 improved varieties, Melkam and Dekeba, were analyzed for genetic diversity and associations in grain yield and nutritional traits. Significant variations were observed among genotypes in all studied traits. The average starch, protein, ash, zinc, iron, calcium and magnesium contents were 65.1 %, 10.3 %, 1.9 %, 35.3 ppm, 36.8 ppm, 243 ppm and 1096.8 ppm respectively. LR14, LR65, LR10, LR23 and LR38 exhibited the highest values for these traits. Strong associations were found among traits and ten promising landraces were selected based on Genotype x yield x trait (GYT) analysis for potential use in breeding programs in Tigray and similar environments (118).

A study conducted a study employing three sets of full diallel crosses with 15 parents to investigate the inheritance patterns of grain iron (Fe) and zinc (Zn) concentrations in sorghum (119). It was found that the genetic regulation of grain zinc (Zn) concentrations, primarily governed by additive gene effects, suggests the efficacy of progeny selection for Zn enhancement. Conversely, grain iron (Fe) concentrations were influenced predominantly by non-additive gene effects, emphasizing the potential of heterosis breeding in addition to progeny selection for increased Fe levels. A study further contributed by developing 12 new hybrids, revealing the importance of non-additive gene action in improving nutritional traits, with some crosses outperforming parents for both Fe and Zn concentrations without yield penalties (120).

Additionally, sorghum's adaptability to diverse environments contributes to its significant polyphenol diversity. This diversity presents opportunities for biofortification and crop enhancement, integrating desirable traits into elite varieties, but requires quantitative phenotyping to identify alleles responsible for quantitative variation in grain polyphenols (121). An average total polyphenol concentration of 7.00 mg GAE/g, with mean proanthocyanidin and 3-deoxyanthocyanidin concentrations at 7.73 mg CE/g and 27.40 abs/mL/g respectively was earlier reported (122), showcasing the potential for diverse polyphenolic content in sorghum grains. More advances have been achieved in breeding sorghum varieties (ATx3363 and BTx3363 germplasms) with elevated levels of 3-deoxyanthocyanidins in the grain pericarp while maintaining satisfactory grain yield (123). Moreover, different studies related to the correlation between quality traits of sorghum are mentioned in Table 3.

## 8. QTL mapping, Association mapping and GWAS in Sorghum for quality traits

Sorghum, a versatile crop used for food, animal feed, biofuels and more, exhibits diverse quality traits influenced by complex genetic architectures. Association mapping and Genome-Wide Association Studies (GWAS) offer powerful tools to unravel the genetic basis of these traits, aiding in targeted breeding and improvement. QTLs for different quality traits have been reported and recorded in the

**Table 3.** Pearson's correlation between different quality traits (phenolic compounds, macro and the micronutrients, Estimated glycemic index) in sorghum

| Trait 1 | Trait 2 | Correlation | References |
|---|---|---|---|
| Total phenols | Proanthocyanidins | Strong positive correlation | (122) |
| Total phenols | 3-deoxyanthocyanidins | Weak positive correlation | |
| Grain weight | Proanthocyanidins | No significant correlation | |
| Grain weight | 3-deoxyanthocyanidins | No significant correlation | |
| Grain weight | Total phenols | Small negative correlation | |
| Phosphorus | Magnesium | Strong positive correlation | (59) |
| Phosphorus | Potassium | Weak positive correlation | |
| Phosphorus | Protein | Weak positive correlation | |
| Iron | Zinc | Significant positive correlation | |
| Iron | Manganese | Significant positive correlation | |
| Phosphorus | Calcium | No significant correlation | |
| Phosphorus | Iron | Significant positive correlation | |
| Calcium | Sodium | Significant positive correlation | |
| Protein | Magnesium | Significant positive correlation | |
| Zinc | Magnesium | Significant positive correlation | |
| Zinc | Phosphorus | Significant positive correlation | |
| Manganese | Zinc | Significant positive correlation | |
| Protein | Zinc | Significant positive correlation | (134) |
| Iron | Zinc | Strong positive correlation | |
| Total starch | Estimated glycemic index | Significant positive correlation | (135) |
| Non-resistant starch | Estimated glycemic index | Significant positive correlation | |
| ß- glucan | Estimated glycemic index | Significant negative correlation | |
| Flavonoids, phenolic compounds, antioxidant activity | Estimated glycemic index | Significant negative correlation | |

**Table 4.** Quantitative trait loci (QTLs) identified for different nutritional and therapeutic traits

| Traits | QTLs/Gene | Chromosome number | Population studied | References |
|---|---|---|---|---|
| Starch | QGSTR1.1 | 1 | BTx623/Rio | (136) |
| | QPRCN3.1 | 3 | | |
| | QGSTR3.4, QGSTR3.2 QGSTR3.3 | 3 | RTx430/Sureno | (137) |
| | QGSTR1.2, QGSTR1.3 | 1 | ICRISAT mini core collection, landraces, Chinese cultivars | (138) |
| | QGSTR3.5 | 3 | | |
| | QGSTR4.3 | 4 | | |
| | QGSTR4.2 | 4 | Diversity panel | (126) |
| | QGSTR3.1 | 3 | Diverse set | (125) |
| Proteins | QPRCN1.1 | 1 | BTx623/Rio | (136) |
| | QPRCN1.4 | 1 | | |
| | QPRCN2.15, QPRCN2.20, QPRCN2.16, QPRCN2.29, QPRCN2.4, QPRCN2.17, QPRCN2.11, QPRCN2.10, QPRCN2.5, QPRCN2.2, QPRCN2.12, QPRCN2.6, QPRCN2.35, QPRCN2.32, QPRCN2.7, QPRCN2.3, QPRCN2.13, QPRCN2.24, QPRCN2.14, QPRCN2.1, QPRCN2.8, QPRCN2.9, QPRCN2.33, QPRCN2.18, QPRCN2.19, QPRCN2.25, QPRCN2.30, QPRCN2.21, QPRCN2.22, QPRCN2.28, QPRCN2.31, QPRCN2.27, QPRCN2.26, QPRCN2.23 | 2 | Sorghum Association Panel (SAP) | (139) |
| | QPRCN9.1 | 9 | RTx430/Sureno | (137) |
| | QPRCN10.2, QPRCN10.3, QPRCN10.1 | 10 | | |
| | QPRCN9.2 | 9 | | |
| | QPRCN5.1 | 5 | Diversity Panel | (140) |
| | QPRCN2.36, QPRCN2.38, QPRCN2.37, QPRCN2.39 | 2 | | |

| | | | | |
|---|---|---|---|---|
| Carotenoids | QGRCC2.2, QGRCC2.3, QGRCC2.4, QGRCC2.5 | 2 | | |
| | QGRCC3.2, QGRCC3.5, QGRCC3.4, QGRCC3.3 | 3 | | |
| | QGRCC4.2 | 4 | | |
| | QGRCC5.1, QGRCC5.2 | 5 | | |
| | QGRCC6.1, QGRCC6.2 QGRCC6.3, QGRCC6.29 QGRCC6.4, QGRCC6.7, QGRCC6.9, QGRCC6.8, QGRCC6.6, QGRCC6.10, QGRCC6.11,QGRCC6.31, QGRCC6.12, QGRCC6.13, QGRCC6.14, QGRCC6.15, QGRCC6.16, QGRCC6.17, QGRCC6.30, QGRCC6.18, QGRCC6.19, QGRCC6.20, QGRCC6.21, QGRCC6.22, QGRCC6.23, QGRCC6.24, QGRCC6.25, QGRCC6.26, QGRCC6.27, QGRCC6.28 | 6 | Sorghum Association Panel (SAP) | (141) |
| | QGRCC7.3, QGRCC7.4 | 7 | | |
| | QGRCC1.1, QGRCC1.2, QGRCC1.3, QGRCC1.4, QGRCC1.5 | 1 | | |
| | QGRCC4.1 | 4 | | |
| | QGRCC6.1 | 6 | KS115/Macia | (50) |
| | QGRCC7.1, QGRCC7.2 | 7 | | |
| | QGRCC10.1, QGRCC10.2, QGRCC10.3, QGRCC10.5, QGRCC10.6 | 10 | | |

| | | | | |
|---|---|---|---|---|
| Polyphenol | QPCGA1.2, QPCGA1.1 | 1 | Sorghum Association Panel (SAP) | (117) |
| | QPCGA2.1, QPCGA2.2 | 2 | | |
| | QPCGA4.11, QPCGA4.12, QPCGA4.14, QPCGA4.15, QPCGA4.8, QPCGA4.6, QPCGA4.16, QPCGA4.13, QPCGA4.7, QPCGA4.1, QPCGA4.10, QPCGA4.2, QPCGA4.5, QPCGA4.9, QPCGA4.3, QPCGA4.4 | 4 | | |
| | QPCGA5.2, QPCGA5.3, QPCGA5.1 | 5 | | |
| | QPCGA7.3, QPCGA7.4, QPCGA7.1, QPCGA7.2, QPCGA7.5 | | | |
| | QPCGA8.1 | 8 | | |
| | QPCGA7.7, QPCGA7.6 | 7 | | |
| | QPCGA6.1 | 6 | | |
| | QPCGA4.32, QPCGA4.31, QPCGA4.25, QPCGA4.27, QPCGA4.29, QPCGA4.28, QPCGA4.30 ,QPCGA4.26, QPCGA4.24, QPCGA4.22, QPCGA4.20, QPCGA4.23, QPCGA4.21, QPCGA4.17, QPCGA4.19, QPCGA4.18 | 4 | Diverse landraces and *S.bicolor x S. halepense* RIL | (142) |
| | QPCGA1.4, QPCGA1.5, QPCGA1.3 | 1 | | |
| Tannins | QTANN4.13, QTANN4.14, QTANN4.15, QTANN4.16, QTANN4.17, QTANN4.18 | 4 | NAM (BTx623 x Niu Shen Zui, Hong Ke Zi & Kaoliang) - JLM | (143) |
| | QTANN2.4 | 2 | | |
| | QTANN10.1 | 10 | | |
| | QTANN1.1 | 1 | Diversity panel | (126) |
| | QTANN2.2, QTANN2.3 | 2 | | |
| | QTANN3.2, QTANN3.3 | 3 | | |
| | QTANN4.10, QTANN4.11, QTANN4.12 | 4 | | |
| | QTANN5.3 | 5 | | |
| | QTANN7.4 | 7 | | |
| | QTANN8.1 | 8 | | |
| | QTANN9.2 | 9 | | |
| | QTANN2.1 | 2 | Sorghum Association Panel (SAP) | (117) |
| | QTANN3.1 | 3 | | |
| | QTANN4.9, QTANN4.7, QTANN4.2, QTANN4.6, QTANN4.8, QTANN4.4, QTANN4.3, QTANN4.5 | 4 | | |
| | QTANN5.1, QTANN5.2 | 5 | | |
| | QTANN7.3, QTANN7.1, QTANN7.2 | 7 | | |
| | QTANN9.1 | 9 | | |

**Source:** Sorghum QTL Atlas | OZ Sorghum (aussorgm.org.au) (124)

Sorghum QTL Atlas (http://aussorgm.org.au/sorghum-qtl-atlas/) (124) and the identified QTLs for some traits are also mentioned in Table 4.

A study on candidate gene association mapping in a diverse set of 300 sorghum accessions to evaluate marker-trait associations related to 10-grain quality traits, using 1290 single nucleotide polymorphisms (SNPs) separated the panel into 5 subpopulations (125). Variations were observed in kernel hardness, acid detergent fiber and total digestible nutrients among the subpopulations. Following the model testing, association analysis between 333 SNPs in candidate genes and/or loci and grain quality traits revealed eight significant marker-trait associations (Table 5).

Genome-wide association study in genotypes of grain sorghum identified significant SNPs associated with tannins, starch and amino acids, revealing 14, 15 and 711 genetic loci respectively (126). Notably, SNPs for tannins colocalized with known loci, while those for starch linked to the sucrose phosphate synthase gene. Homologs of *opaque1* and *opaque2* genes associated with amino acids were also identified. Promising candidate genes were mapped to metabolic pathways and biosynthetic pathways for aspartate and branched-chain amino acids were reconstructed. Such a study provides valuable insights into the genetic basis of grain quality traits in sorghum, serving as a foundation for further validation studies.

## Conclusion and Future Prospects

Sorghum being a climate-resilient crop, is raising significant attention as a future grain option due to its agricultural benefits in the face of climate change as well as the beneficial effects of its bioactive compounds on human health. This comprehensive review consolidates the current knowledge on the advances in sorghum grain quality improvement, covering various aspects such as grain structure, appearance, genetics, nutritional composition, functional attributes and the diverse components contributing to sorghum's nutritional value. The exploration of polysaccharides, proteins, carotenoids, minerals, phenolic compounds and antinutritional factors provides a thorough understanding of the complex interplay influencing sorghum grain quality. Specifically, sorghum stands out for its abundance and diversity of phenolic compounds, unique among cereal grains. Considerable research has explored sorghum's phenolic profile, with most studies concentrating on overall content (such as total phenolic, flavonoids or condensed tannins) using colorimetric methods, rather than individual phenolics. The review also highlighted the multifaceted properties of sorghum phenolics, emphasizing their antioxidant, anticancer and antidiabetic potential. However, the majority of evidence comes from *in vitro* studies, indicating a need for additional *in vivo* and potentially clinical research to validate these health advantages, along with exploring interactions between bioactive compounds and their underlying mechanisms. Integrating association mapping and genome-wide association studies (GWAS) in sorghum provides valuable insights into the genetic basis of quality traits, paving the way for targeted breeding strategies. The identification of quantitative trait loci (QTLs) associated with nutritional and therapeutic traits adds a crucial dimension to sorghum breeding efforts. Continued research in this field will likely unveil further opportunities for optimizing sorghum grain quality and harnessing its full potential for the global food and nutritional security of people from developing and underdeveloped countries.

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## Authors' contributions

Anamika Dhar collected the literature and wrote the article. B. Meena Kumari contributed by suggesting the idea for writing the review and compilation of the content. D. Kavithamani helped in summarizing and revising the manuscript. N. Manikanda Boopathi helped in editing and

**Table 5.** Association of the eight significant Single nucleotide polymorphisms (SNPs) in a candidate gene/locus with the quality traits

| Marker | Locus/Gene | Chromosome | Trait | $R_{LR}^2$ (%) value |
|---|---|---|---|---|
| SB00116.3 | SSIIa | 10 | Kernel hardness | 8 |
| SB00214.1 | pSB1700 | 3 | Kernel hardness | 10 |
| SB00214.2 | pSB1700 | 3 | Kernel hardness | 10 |
| SB00156.1 | pSB0289 | 3 | Ca content | 6 |
| SB00054.1 | PRC1044 | 6 | Ca content | 6 |
| SB00068.1 | pSB0140 | 6 | P content | 5 |
| SB00086.1 | pSB1120 | 3 | Starch | 9 |
| SB00115.3 | SSIIb | 4 | Starch | 10 |

**Source:** Sukumaran *et al.* (125)

summarizing the manuscript. P. Meenakshi provided information related to the biochemical aspects.

All authors read and approved the final manuscript.

## Compliance with ethical standards

**Conflict of interest:** Authors do not have any conflict of interest to declare.

**Ethical issues:** None.

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