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Review Article

Molecular Characteristics, Synthase, and Food Application of Cereal β-Glucan

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Cereal β-glucan is a type of valuable dietary fiber that mainly exists in the aleurone, subaleurone, and endosperm of some cereal grains. β-Glucan is acknowledged as a functional food ingredient owing to its multiple health benefits, including the prevention of diabetes, reduction in the incidence of cardiovascular disease, antitumor effects, antioxidant activities, and immunostimulation. It is well documented that cellulose synthase-like *CslF/H/J* genes encode synthases responsible for β-glucan biosynthesis in cereal grains. Recently, β-glucan has been widely applied as an emulsion stabilizer, thickening agent, fat substitute, and bioactive ingredient in the food industry due to its water solubility, viscosity, gelation property, and health benefits. Therefore, the present paper aims to review the molecular characteristics, synthase gene family, and food application of cereal β-glucan in recent years.

1. Introduction

β-Glucan (also known as mixed linkage glucan) is a long-chain polysaccharide consisting of D-glucose monomers linked via β-glycosidic bonds. It is a type of valuable dietary fiber that is widely present in cereals, mushrooms, seaweeds, yeast, and some bacteria [1, 2]. The glycosidic linkages in cereal β-glucan are a combination of β-1, 3 and β-1, 4 glycosidic linkages; hence, it is called (1, 3; 1, 4)-β-glucan. The glycosidic linkages in β-glucan from other sources are a combination of β-1, 3 and β-1, 6 glycosidic linkages; thus, it is called (1, 3; 1, 6)-β-glucan [3]. On the basis of the above molecular structure, β-glucan has a high water binding capacity, resulting in its physicochemical properties, such as solubility, viscosity, and gelation.

β-Glucan is acknowledged as a functional food ingredient owing to its multiple health benefits, including the prevention of diabetes, reduction in the incidence of cardiovascular disease, antitumor effects, antioxidant activities, and immunostimulation [4]. β-Glucan has a positive effect on the management of diabetes by reducing postprandial plasma glucose and insulin levels [5, 6]. It is well documented that consuming β-glucan can lower the risk of coronary heart disease by significantly reducing serum cholesterol levels [7, 8]. Moreover, β-glucan has long been considered an important antitumor agent for its immune-stimulatory and immunomodulatory effects [9]. Recent studies have validated that β-glucan can inhibit the viability and metastasis of cancer cells [10, 11] and promote cancer cell apoptosis [12]. β-Glucan also exerts an immunostimulatory effect by the activation of the mucosal immune system through β-glucan receptor *dectin-1* on macrophages [13]. Due to the various health benefits of β-glucan, many countries, including the United States, the European Union, Canada, Australia, New Zealand, Brazil, and South Korea, have authorized claims to recommend the daily consumption of β-glucan at least 3 g per day or 0.6–1 g per serving [14]. To the best of our knowledge, China has not authorized similar health claims hitherto.

The reported functions of β-glucan have encouraged researchers to investigate the incorporation of β-glucan in various kinds of foods to make functional foods. Furthermore, there has been a breakthrough in the research of β-glucan synthase during the past fifteen years. A comprehensive understanding of the synthase gene family will lay the foundation for improving the β-glucan content in cereals. Hence, the present paper aims to review the molecular characteristics, synthase gene family, and food application of cereal β-glucan in recent years.

2. Common Sources and Molecular Characteristics of Cereal β-Glucan

β-Glucan is predominantly found in the aleurone, subaleurone, and endosperm of some cereals (barley and oat). Cereal β-glucan is a linear polymer of a D-glucose unit that contains two to three consecutive β-1, 4 linkages separated by a β-1, 3 linkage. Many features of β-glucan are different among cereals, such as content, molecular size, and molar ratio (DP3/DP4) (Table 1).

2.1. Common Sources of Cereal β-Glucan. Among cereals, barley and oat have the highest β-glucan content, ranging from 2.2% to 19.8% and 2.2%–7.8%, respectively [3, 15, 16, 18]. Other cereals, such as wheat, rice, and maize, also contain β-glucan but in much lower amounts (Table 1). Previous studies have demonstrated that variations in β-glucan content are mainly caused by species and cultivars. Although the β-glucan content in ordinary barley cultivars is between 4% and 11% [26], a genotype containing as high as 19.8% has been reported [16]. In addition to species and cultivars, environmental conditions also have a significant effect on β-glucan content. Some studies have verified that warm and dry weather conditions enhance the β-glucan content [27, 28]. Given that a great amount of β-glucan is located in the outer layer of the grain, such as aleurone and subaleurone, the processing is another factor that affects the final β-glucan content in addition to the factors mentioned above. It is noteworthy to mention that β-glucan is distributed primarily in the endosperm in barley grains in comparison to in the aleurone layers of oat grains; thus, pearling has little effect on the β-glucan content in barley [29, 30].

2.2. Molecular Weight of Cereal β-Glucan. The molecular weight of β-glucan is reported to be scattered in the range of $31–2700 \times 10^3$ in barley, $65–3100 \times 10^3$ in oat, $21–1100 \times 10^3$ in rye, $43–758 \times 10^3$ in wheat, and 36×10^3 in sorghum [17, 19]. The big variations in the molecular weight of β-glucan are attributed to varietal and environmental factors, extraction and purification protocols, and analytical methodologies [2, 26]. The molecular weight of β-glucan can largely determine some other physical characteristics, such as viscosity and solubility, thereby affecting its functional properties. Previous research has indicated that high molecular weight (HMW) barley β-glucan can delay gastric emptying due to increased viscosity, resulting in a reduced glycemic response and diet-induced thermogenesis [31]. Otherwise, low molecular weight (LMW) barley β-glucan was ineffective in lowering glycemic responses [32]. Wang et al. demonstrated that the consumption of HMW barley β-glucan rather than that of LMW β-glucan altered the composition of gut microbiota and consequently reduced the risk markers of cardiovascular disease [33].

2.3. Molar Ratio of Cereal β-Glucan. The structure of cereal β-glucan, also known as (1, 3; 1, 4)-β-glucan, can be defined by digestion with specific (1, 3; 1, 4)-β-glucan endohydrolase, which only hydrolyzes the β-1, 4 linkage adjacent to the β-1, 3 linkage, releasing oligosaccharides with a degree of polymerization (DP) of mainly DP3 (cellotriose) and DP4 (cellotetraose) [34, 35]. The molar ratio of DP3/DP4 is quite variable among cereals (Table 1). In addition to species, the molar ratio is associated with genotype and growth environment. High β-glucan cultivar and drier environment have led to a lower molar ratio in oat [36]. The molar ratio is a unique feature of each cereal, and it affects the solubility and the viscosity of β-glucan in the solution. For instance, oat β-glucan with a lower molar ratio (1.5–2.3) is more soluble than barley and wheat β-glucan with a higher molar ratio (2.6 and 3.2) [25].

3. β-Glucan Synthase in Cereals

During the past fifteen years, considerable progress has been made in the synthesis mechanism of β-glucan. The quantitative trait loci (QTL) for the β-glucan content of barley grains have been identified extensively, such as the major QTL on chromosome 2H [37, 38], 3H [38], 4H [39], and 7H [40–43]. The β-glucan synthase gene families have been reported in rice, barley, wheat, oat, maize, and sorghum (Table 2). By comparative genomics analysis between rice and barley, six cellulose synthase-like *CslF* genes have been found in the syntenic region that is a major QTL for β-glucan content on barley chromosome 2H. After the introduction of two of these *CslF* genes (*OsCslF2* and *OsCslF4*) to *Arabidopsis*, a species without *CslF* genes and β-glucan, the low β-glucan levels have been detected by a β-glucan-specific antibody, indicating the participation of *OsCslF* genes in β-glucan biosynthesis [44]. Through a similar experimental approach, cellulose synthase-like *HvCslH1* [51] and cellulose synthase-like *HvCslJ* [52] have also been proved to be capable of directing β-glucan synthesis.

CslF6, the most highly and widely expressed *CslF* gene in barley, wheat, and rice [53–57], is the predominant gene for the synthesis of the majority of β-glucan in cereals. Three independent barley β-glucanless mutants have shown the cosegregation of the β-glucan deficiency phenotype with the single nucleotide mutation in *HvCslF6* coding sequence (CDS) region, demonstrating a unique role for *HvCslF6* in β-glucan biosynthesis [48, 49]. This has been further confirmed by the transient expression of wild-type *HvCslF6* (which can synthesize β-glucan) and mutant *HvCslF6* (which cannot synthesize β-glucan) in *Nicotiana benthamiana* (*N. benthamiana*) leaves [49]. Additionally, the overexpression of *HvCslF6* under the control of an endosperm-specific promoter has increased the β-glucan content and altered its fine structure in barley grains [47]. On the contrary, the downregulation of *TaCslF6* by RNA interference (RNAi) has resulted in decreased β-glucan content in

Table 1: Common sources and molecular characteristics of cereal β-glucan.

Source	Content (% w/w)	Molecular weight (g/mol)	Molar ratio (DP3/DP4)	References
Barley	2.2–19.8	$31–2700 \times 10^3$	1.8–3.5	[15–17]
Oat	2.2–7.8	$65–3100 \times 10^3$	1.5–2.3	[3, 17, 18]
Rye	1.0–2.7	$21–1100 \times 10^3$	1.9–3.0	[17, 19]
Wheat	0.18–1.8	$43–758 \times 10^3$	2.8–4.5	[17, 20–22]
Sorghum	0.1–1.7	36×10^3	2.1–3.0	[19, 23]
Maize	0.8–1.7	—	2.5	[24, 25]
Rice	0.02–0.13	—	1.18	[21, 24]

Table 2: List of genes confirmed to function in β-glucan synthesis in cereals.

Gene	Promoter	Gene source	Transgenic host	Approach	Function	Reference
OsCslF2	*CaMV 35S*	Rice	Arabidopsis	HE	Synthesize β-glucan ≤ 0.1% (w/w) in leaves.	[44]
OsCslF4	*CaMV 35S*	Rice	Arabidopsis	HE	Synthesize β-glucan ≤ 0.1% (w/w) in leaves.	[44]
OsCslF6	*CaMV 35S*; secondary cell wall-specific; senescence-associated	Rice	Arabidopsis	HE	Accumulate high-level β-glucan with poor growth by the 35S and secondary cell wall promoter; accumulate high-level β-glucan with normal growth by the senescence-associated promoter.	[45]
OsCslF6	—	Rice	—	Mutant	Reduce more than 97% β-glucan.	[46]
HvCslF4	*CaMV 35S*	Barley	Barley	OE	Increase up to 50% β-glucan in grain and raise the DP3 / DP4 ratio.	[47]
HvCslF6	—	Barley	—	Mutant	Completely lack β-glucan in the endosperm and aleurone layers of cell walls.	[48, 49]
HvCslF6	*CaMV 35S*; endosperm-specific	Barley	Barley	OE	Increase high-level β-glucan in leaves but has little effect on gain β-glucan by the 35S promoter; increase more than 80% β-glucan in grains and reduce the DP3/DP4 ratio by the endosperm-specific promoter.	[47]
HvCslF6	*CaMV 35S*	Barley	*N. benthamiana*	HE	Synthesize β-glucan about 1.62% (w/w) in leaves with a DP3/DP4 ratio of 1.40.	[21]
HvCslF6	—	Barley	Barley	Knockout	Reduce more than 97% β-glucan in grains.	[50]
HvCslH1	*CaMV 35S*	Barley	Arabidopsis	HE	Synthesize β-glucan 0.00015%–0.016% (w/w) in leaves and stems.	[51]
HvCslJ	*CaMV 35S*	Barley	*N. benthamiana*	HE	Synthesize β-glucan ≤ 0.1% (w/w) in leaves.	[52]
TaCslF6	Endosperm-specific	Wheat	Wheat	RNAi	Decrease β-glucan by 30%–52% in the endosperm.	[53]
TaCslF6	*CaMV 35S*	Wheat	*N. benthamiana*	HE	Synthesize β-glucan approximately 0.6%–2.0% (w/w) in leaves with a DP3/DP4 ratio of 1.60.	[21]
AsCslF6	*CaMV 35S*	Oat	*N. benthamiana*	HE	Synthesize β-glucan approximately 0.59% (w/w) in leaves with a DP3/DP4 ratio of 1.09.	[21]
ZmCslF6	*CaMV 35S*	Maize	*N. benthamiana*	HE	Synthesize β-glucan approximately 1.59% (w/w) in leaves with a DP3/DP4 ratio of 1.07.	[21]
SbCslF6	*CaMV 35S*	Sorghum	*N. benthamiana*	HE	Synthesize β-glucan approximately 3.8%–5.9% (w/w) in leaves with a DP3/DP4 ratio of 0.93.	[21]

HE, heterologous expression; OE, overexpression; RNAi, RNA interference.

the endosperm of wheat [53], and the *cslf6* knockout mutant has displayed more than 97% reduction of β-glucan in rice [46]. Recently, a series of CRISPR/Cas9-induced mutations in the members of the *CslF/H* gene family have been generated. β-Glucan has only been absent in the grain of *cslf6* knockout lines, whereas *cslf3*, *cslf9*, and *cslh1* knockout lines have similar β-glucan content to the wild-type [50]. Hence, *CslF6* is a crucial β-glucan synthase gene for engineering the accumulation of β-glucan in cereals.

However, there is a dosage effect negatively correlating β-glucan levels with plant growth. Transgenic plants overexpressing *CslF6* under the constitutive *CaMV 35S* promoter have accumulated high-level β-glucan with severe growth and developmental defect [45, 47]. The negative effects of elevated β-glucan accumulation on plant growth have been prevented by the spatial-temporal regulation of *CslF6* expression under the control of senescence-associated promoter or endosperm-specific promoter [45, 47].

As mentioned above, the molar ratio (DP3/DP4) of β-glucan varies and is a unique feature of each cereal. The *CslF6* from *Brachypodium*, wheat, and barley has produced β-glucan with a relatively high DP3/DP4 ratio, while *CslF6* from maize, oat, rice, and sorghum has generated β-glucan with a relatively low DP3/DP4 ratio. By generating a series of chimeric constructs between four *CslF6* cDNAs, it has been found that the transmembrane helices 4 (TMH4) of the membrane pore region of CslF6 can control the DP3/DP4 ratio and the fine structure of β-glucan. Point mutation constructs have further confirmed the isoleucine-to-leucine (I/L) change in the TMH4 of CslF6 to be responsible [21]. Furthermore, the glycine-to-aspartic acid (G/D) difference between barley and sorghum in the catalytic region of CslF6 has also been defined to dramatically influence the DP3/DP4 ratio of β-glucan [58].

4. Food Application of Cereal β-Glucan

Recently, β-glucan has been widely applied as an emulsion stabilizer, thickening agent, fat substitute, and bioactive ingredient in the food industry due to its water solubility, viscosity, gelation property, and health benefits [1, 3, 59]. Some of these functional products are favored by consumers owing to their improved quality together with low cholesterol and hypoglycemia properties [60–62]. Notwithstanding, incorporating β-glucan into some food products is still a challenge due to the possible negative effects on the textural quality, sensory characteristics, and shelf life of foods [63, 64]. The effects of β-glucan on food quality and consumer acceptance in various food products will be discussed in the following sections.

4.1. Traditional Chinese Food. Noodle is a traditional Chinese food made from refined wheat flour that is low in dietary fiber, vitamins, minerals, and other important nutrients [65]. Thus, various ingredients including β-glucan are added to improve the health benefits of wheat flour noodles. Noodle incorporated with 30% banana flour and 10% oat β-glucan has exhibited an increase in total dietary fiber and essential minerals, thereby decreasing the glycemic index and carbohydrate digestibility rate [66]. Oat flour, famous for its high β-glucan content, has also been supplemented to wheat flour to produce oat-fortified noodles. Noodle formulations containing 10%–30% oat flour have led to increased β-glucan content and noodle firmness together with decreased noodle lightness and color stability [67]. In addition, more than 50% of wholemeal oat flour (with high-level β-glucan) has been added into wheat flour and other ingredients (compensating for diluted gluten) to make oat-based white salted noodles, resulting in increased pasting viscosities and noodle hardness [68].

Steamed bread (*Mantou*), another traditional Chinese staple food, is also made from refined wheat flour and accounts for 40% of wheat consumption in China [69]. Steamed bread incorporated with 30% barley flour has presented significant improvements in the amount of β-glucan (from 0.03% to 1.03%), hardness, and chewiness, but decreases in the specific volume, brightness, and whiteness index of steamed bread [70]. Steamed bread with the addition of less than 3 g/100 g oat β-glucan has produced a comparable overall consumer acceptance, while an oat β-glucan addition of 5 g/100 g has reduced the consumer acceptance but decreased the *in vitro* starch digestibility and predicted glycemic index [71].

4.2. Milk Products. β-Glucan is a functional bioactive component in the production of yogurt. Yogurt incorporated with β-glucan has exhibited faster proteolysis, lower release of large peptides, and more free amino acids [72]. The addition of barley β-glucan (0.5, 1, 1.5, and 2%, w/v) has significantly enhanced the separation, viscosity, texture profile, and sensory characteristics of full-fat yogurt during storage [62].

Oat milk has also increased the β-glucan content while maintaining the sensory evaluation similar to the control drink [73]. Nonetheless, the incorporation of oat β-glucan into milk is challenged by the thermodynamic incompatibility between milk proteins and β-glucan, thereby limiting its application [64, 74]. Additionally, β-glucan has been used as a fat substitute to produce low-fat cheese, which has resulted in softer cheese with decreased melt time and sensory scores [75].

4.3. Baking Products. Nowadays, β-glucan is preferred as a thickening and structure-making agent applied in gluten-free bakery products due to its prohealth benefits. The application of oat β-glucan (with an optimized percentage of 2.63%) in gluten-free yeast-leavened cake has achieved positive effects on texture, volume, and sensory acceptance [61]. Similarly, gluten-free yeast-leavened cake with 5%–20% high-in-β-glucan oat fiber powder has shown improved springiness, cohesiveness, porosity, and volume [76].

β-Glucan-enriched biscuits, containing 5.2 g/100 g β-glucan from barley flour, have been more acceptable to consumers, with sensory responses being similar to the control [77]. The addition of β-glucan to bread has also been widely tested, but its effect on loaf volume, bread firmness, rate of staling, and consumer acceptance has varied depending on certain conditions, including molecular weight, concentration, and source of β-glucan [63, 78–81].

4.4. Meat Products. β-Glucan is applied as a fat substitute in some meat products, such as beef patties, burgers, and sausages. Oat β-glucan gel (13.45%) can be effectively applied as a fat replacer in low-fat beef patties by retaining fat and moisture, thereby increasing the cooking yield [82]. The addition of inulin gel (IG) and oat β-glucan (βG) mixtures (3%-IG and 0.3%-βG, 6%-IG and 0.6%-βG) could be a valuable alternative to improve the stability, texture, and adhesiveness of low-fat meat emulsions [83]. Low-fat beef burgers, containing 2.2% β-glucan, have exhibited improved texture parameters and cooking properties along with enhanced nutritional characteristics [84]. Oat β-glucan (OG) and marine collagen peptide (MCP) mixed gel (OG/MCP ratio 10 : 1) in low-fat sausage (50% fat reduced) has significantly increased the springiness and chewing, while the taste and overall palatability of such sausage have been comparable with those of the control [85].

5. Conclusions and Future Perspectives

β-Glucan from cereal grains is a valuable dietary fiber that has numerous health-promoting applications. Its health benefits and physicochemical characteristics are conducive to its application in various food products. In China, people pay considerable attention to health and functional food nowadays. The application of β-glucan in traditional Chinese food, such as noodles and steamed bread, is a trend. Nevertheless, wheat and rice, as the main food sources of humans, have a less amount of β-glucan compared with barley and oat. Therefore, future research should focus on improving the β-glucan content in wheat and rice grains. Molecular weight and molar ratio should also be considered due to their effects on the solubility and viscosity of β-glucan and subsequently on the final food products. With further studies on the β-glucan synthase gene family, it is promising to improve the β-glucan content and modify its molar ratio by marker-assisted breeding and molecular design breeding in the future.

Data Availability

All the data generated or analyzed during this study are included in this article.

Conflicts of Interest

All the authors declare that there are no conflicts of interest.

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