British Journal of Nutrition (2014), **112**, S4–S13
doi:10.1017/S0007114514002256

Oat β-glucan: physico-chemical characteristics in relation to its blood-glucose and cholesterol-lowering properties

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(Submitted 3 October 2013 – Final revision received 28 May 2014 – Accepted 17 June 2014)

Abstract

The water-soluble, mixed-linkage β-glucan, a form of soluble dietary fibre, is considered the main biologically active component responsible for the capacity of many oat products to lower postprandial glycaemia and fasting plasma cholesterol in human subjects. The present review discusses the physical and chemical properties of oat β-glucan that are considered important predictors of these beneficial metabolic effects. *In vitro* modelling and animal and human studies have provided compelling evidence showing that the ability of oat β-glucan to increase the viscosity of digesta in the gastrointestinal tract (GIT) is a primary determinant of its blood-glucose and cholesterol-lowering properties. Therefore, the chemical structure, molecular weight (MW), the rate and extent of dissolution and solution rheology of oat β-glucan are key factors in determining the physiological function of oat-containing foods. The structure and properties of oat β-glucan vary between species and varieties of oats, and are also affected by the growing and storage conditions and processing of oat grain. In addition, the extraction and analysis methods may also contribute to the variations in the structure, MW, hydration and solution rheology of β-glucan obtained from different laboratories. Recent work has demonstrated that β-glucan solubility in foods depends on the source of the material and processing conditions; solubility may also be subject to changes during food preparation and storage (such as freezing). In conclusion, both the amount and MW of β-glucan that are solubilised in the GIT need to be considered when assessing the blood-glucose and cholesterol-lowering properties of oat-containing foods.

Key words: Oat β-glucan: Soluble fibre: Solubility: Molecular weight: Viscosity: Plasma cholesterol: Blood glucose

Many *in vitro* animal and human studies have shown that water-soluble β-glucan is one of the main bioactive components responsible for a number of the putative health benefits attributed to oat products, as highlighted in the articles in this Supplement of the *British Journal of Nutrition*. The biological behaviour of this polysaccharide is of particular importance in relation to the well-documented effects of oat bran in reducing postprandial glycaemia, insulinaemia and fasting concentrations of the plasma cholesterol (usually the LDL-cholesterol fraction).

The basic chemical structure of oat β-glucan was elucidated as early as the 1960s[(1)] and many aspects of its physiochemical properties have also been known for some time[(2)]. However, the critical role of the physico-chemical properties of oat β-glucan, notably solution rheology, in determining the physiological effects of oat-containing foods has been more difficult to establish, although understanding of this has improved significantly in recent years. As with other types of water-soluble dietary fibre, such as guar gum (a galactomannan-rich leguminous seed flour), oat β-glucan may confer its physiological influence by the combination of a number of mechanisms. The mechanisms involved in modifying digestion kinetics include, but are not limited to[(3–6)], increasing digesta viscosity in the lumen of the gastrointestinal tract (GIT), interacting with starch and other nutrients, interfering with the activity of gut enzymes (e.g. pancreatic α-amylase) and increasing bile salt excretion. For instance, the effects of oat β-glucan and similar forms of fibre on postprandial glycaemia are strongly related to their capacity to reduce the rate of digestion of macronutrients such as starch[(3,7)].

The aim of the present paper is to review the physical and chemical properties of oat β-glucan that have been suggested as potentially influencing gut function and metabolism, a topic covered by other papers in this special issue. The present paper provides some mechanistic insight of the nutritional properties of oat products, with a specific focus on the capacity of oat β-glucan to lower blood-glucose and cholesterol concentrations in human subjects.

Abbreviations: GIT, gastrointestinal tract; MW, molecular weight.

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Molecular structure and conformation

Chemical structure

Oat β-glucan is a linear polymer of D-glucose bonded by β-(1 → 4) and β-(1 → 3) glucosidic linkages. About 90 % of the glucose units are arranged in blocks of β-(1 → 3)-linked cellotriosyl and cellotetraosyl units, with the rest being the longer cellulosic segments (Fig. 1). The ratio of trisaccharides–tetrasaccharides in oat β-glucan is typically 2:1, which is distinctively different from that found in barley (3:1) and wheat (4:1) β-glucans[8,9]. This structural variation leads to differences in some of the physical properties of these β-glucans, which will be discussed in the following sections. A small variation in the trisaccharide–tetrasaccharide ratio has been reported for oat β-glucan, which may arise from several factors including differences between species[10], growing conditions, and extraction and analytical methods. A number of reports have suggested the presence of amino-acid residues[11,12] and inner C-6 carbon-bound phosphomonoesters[13] in the oat β-glucan molecule. However, these additional structural features have not always been observed.

Molecular weight and conformation

The molecular weight (MW) and conformation of oat β-glucan are important because they can largely determine many other physical properties, including the solubility, solution viscosity and viscoelasticity and gelation properties. For instance, high MW oat β-glucan does not form a gel, but gels can be produced from samples with reduced MW under certain conditions[14,15]. All the studies so far have indicated that oat and other cereal β-glucans adopt overall an extended random coil conformation in aqueous solution[16–18]. Oat β-glucan, like all other natural polysaccharides, has a MW distribution that is polydisperse. This means that, instead of one unique value (as in proteins), a wide MW distribution exists in each polymer sample. Therefore, depending on the method used for the measurement, various MW averages are obtained to describe a polymeric material. The weight-average MW and number-average MW (M_w and M_n) are the most frequently encountered values for β-glucans, which are often measured, for example, by static light-scattering and osmotic pressure measurements, respectively[12,19,20]. High-performance size exclusion chromatography has been extensively used in recent years for characterisation of β-glucan. When connected with multi-detectors (using reflective index, light scattering and viscometry), the high-performance size exclusion chromatography method can provide a range of molecular parameters in addition to the MW distribution and average MW[21]. The method of specific dye binding of calcofluor to cereal β-glucans offers a unique way of determining the MW of β-glucan by high-performance size exclusion chromatography. The post-column detection of calcofluor binding to β-glucan makes it possible to measure β-glucan in the presence of other polysaccharides that do not bind this fluorescent stain[22,23]. This is especially useful in making comparisons between different food products and extracts containing β-glucan, because purification of β-glucan is not necessary before the measurement.

$$\ldots{}^4G_1{}^3G_1[{}^4G_1{}^4G_1{}^3G_1]_m\,[{}^4G_1{}^4G_1{}^4G_1{}^3G_1]_n\,{}^4G_1{}^4G_1{}^4G_1{}^4G_1\ldots$$

Fig. 1. Chemical structure of oat β-glucan. G represents a glucose unit and the numbers indicate the linkage sites; the ratio of *m*/*n* is approximately 2.

Factors that affect the molecular weight

The MW of β-glucan in common oat grain (*Avena sativa* L.), which is the main commercial species, is influenced by the variety and growing conditions[24,25]. It has not been possible to directly measure the MW of β-glucans in the cell-wall matrix of oat grain. The MW of β-glucan in groats or flour is subject to changes caused by endogenous hydrolytic enzymes, and various processing and storage factors. Because endo-β-glucanases are present in oat seeds[26], inactivation of these enzymes (such as by IR heating, steaming or boiling in aqueous ethanol) is considered essential to obtain high MW β-glucan extracts from the oat-grain cell walls[27,28]. The reported MW of β-glucan is also therefore subject to significant variations, as a result of differences in the conditions used for extraction and purification of the polysaccharide. The MW obtained for purified oat β-glucans through a well-designed process to minimise molecular depolymerisation is in the range of 2×10^6 to 3×10^6 Da. It is known that the MW of β-glucan can be decreased as a result of food preparation such as bread-making[29], baking of muffins or cookies[30,31], and extensive extrusion[32]. Åman *et al.*[33] reported that the MW of β-glucan was preserved in rolled oats, oat bran and different types of oat-bran concentrate, porridge and pancakes, whereas the degradation of β-glucan was observed in bread, pasteurised apple juice, pasta and teacake (see Decker *et al.*[34] in this Supplement for more examples).

Solubility and extractability

Content and location in oat grain

The β-glucan contents in oat groats vary considerably with cultivars and growing conditions. It has been shown that a 2- to 3-fold variation in the β-glucan content exists among oat cultivars[10,25,35]. A number of surveys from different parts of the world revealed that the β-glucan contents were in the range of 1·8–5·5 % of the total dry weight of the oat groat, and frequently in the range of 4·5–5·5 %[10,36,37]. Higher β-glucan contents of up to 7 % have also been reported for some oat varieties[34].

Oat β-glucan is primarily located in the cell walls of the starchy endosperm (Fig. 2). The endosperm cell walls of oats[38] have a layered structure. In this layered structure, there is a relatively thin outer layer, consisting of mainly water-insoluble polysaccharides such as cellulose, glucomannan and arabinoxylan, and a thick inner layer of water-soluble polysaccharide, most of which consist of the mixed linkage β-glucan plus a small amount of soluble arabinoxylan. The cell wall of the subaleurone layer is usually much thicker than that of the inner endosperm[39] and is rich in β-glucan. A relatively thin layer of

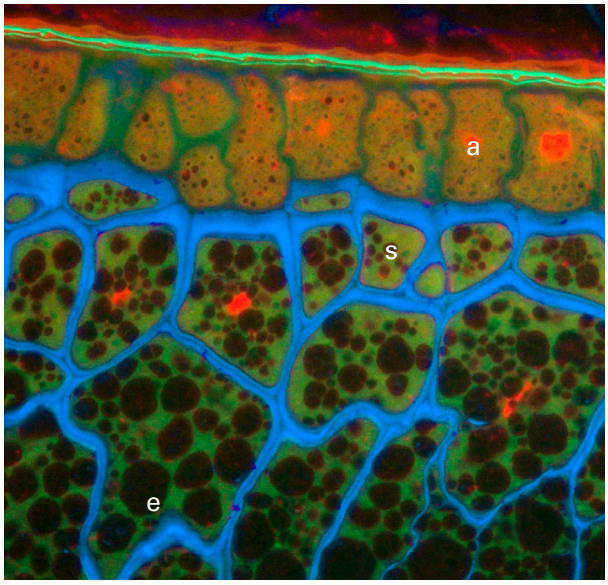

Fig. 2. β-Glucan in the cell wall of oat stained with calcofluor. a, aleurone; s, subaleurone; e, endosperm. (Courtesy of S. Shea Miller, Agriculture and Agri-Food Canada.)

β-glucan is also found in the inner layer of the aleurone cell walls. This inner layer is surrounded by a thick insoluble outer layer, which in turn makes the β-glucan less readily soluble compared with the endosperm β-glucan[38,39].

Solubility and its determination

In the literature, the term 'solubility' for a polysaccharide does not represent the true thermodynamic equilibrium solubility. Rather, it is used to refer to the property of a polysaccharide in a solid form or contained in a solid food matrix to disperse in a liquid medium (often water) and form a homogeneous dispersion under specified conditions. It is sometimes used interchangeably with the word 'extractability' of the polysaccharides. Solubility is usually expressed by the percentage of the dissolved fraction relative to the total amount of the polysaccharide in the original solid matrix under specific conditions (such as temperature).

The solubility of β-glucan in water has been tested recently under different conditions of processing and laboratory measurements[40]. The choice of the method depends on the objective of the investigation. Clearly, it is only meaningful to compare the solubility of different β-glucans, and indeed other polysaccharide preparations, under the same conditions. In order to establish reliable methods for the preparation of β-glucan concentrates with maximum yields and minimal depolymerisation, several studies have been carried out to compare extractability of β-glucan under various conditions. Different extraction schemes have been developed based on these studies for laboratory or commercial production of β-glucan, and the methods have been reviewed previously[41,42]. The extractability of β-glucan was found to be strongly dependent on many factors, such as temperature, pH and the presence of digestive enzymes. When the health benefits of β-glucan as a soluble fibre are of primary interest, the solubility properties of β-glucan under conditions close to the gut environment are highly relevant. Because animal and human trials are expensive and time-consuming, having an *in vitro* method as a pre-screening tool to evaluate the properties of β-glucan in oat products is very useful.

There are two main types of *in vitro* methods used to evaluate the solubility of β-glucan in foods. One of these is designed to simulate physiological conditions of digestion in the upper GIT[30,43] of human subjects. For a typical example of such a procedure, see the online supplementary materials. This method involves incubating test foods with a series of digestive enzymes at human body temperature (37°C) and appropriate pH levels for defined periods to simulate the acidic and neutral conditions in the stomach and small intestine, respectively. The solubilised β-glucan in the supernatant can then be quantitatively measured by the method of Jørgensen & Aastrup[44], and the total β-glucan content in the same sample can be measured by the method of McCleary & Glennie-Holmes[45]. A similar procedure has been developed by directly measuring the viscosity developed during the simulated digestion process. This allows the contribution of solubility and MW of β-glucan to the viscosity to be accounted for simultaneously[46]. Another procedure, which adapts essentially the method of Asp *et al.*[47], was developed initially for the isolation of water-soluble NSP[40]. This method involves a de-starching process during which the samples are treated at boiling temperature to allow starch gelatinisation. The starch and protein are then hydrolysed by various enzymes, and β-glucan is precipitated from the supernatants by alcohols. A similar approach to this is the use of hot-water extraction at 100°C with only a heat-stable α-amylase and 0·28 mg/ml $CaCl_2$ added[23,25,33]. Few direct comparisons have been made among the results from these methods. Because it is known that increasing extraction temperature increases the solubility of the polymer[40], the amount of solubilised β-glucan is likely to be lower using *in vitro* physiological extraction than that obtained using the hot-water extraction method[30]. Further work is required, therefore, to investigate the precise relationship between *in vitro* measurements of β-glucan solubility and polysaccharide dissolution *in vivo*.

Factors that influence solubility

Sources. As mentioned earlier, most β-glucan in the oat groat is located in the inner layer of the cell wall that is enclosed by an insoluble cellulosic and hemicellulosic outer layer. It is generally less water soluble than extracted β-glucan material. Because the cell walls in the inner endosperm are thinner than in the aleurone and subaleurone layers, it appears that β-glucan in the milled whole groat is more easily extracted than that in oat bran[30,38]. For example, Beer *et al.*[30] has found that the proportion of soluble β-glucan extracted from oat brans and rolled oats, by hot-water extraction in conjunction with a heat-stable α-amylase treatment, was 30–65 and 70 %, respectively (Table 1). Under physiological conditions, the percentage of extractable β-glucan was also noticeably higher in rolled oats than in bran samples.

Table 1. The β-glucan content and the percentage and molecular weight of extracted β-glucan from oat bran and rolled oats using hot water (90°C for 2 h with Termamyl) or physiological *in vitro* digestion method[30]

Sample	β-Glucan (g/100 g)	β-Glucan extracted (% of total)		Molecular weight ($\times 10^{-3}$ Da)	
		Hot water	Physiological	Hot water	Physiological
Bran A	13·4	51·3	12·9	1400	1100
Bran B	8·9	56·7	25·1	1600	1800
Bran C	7·6	64·1	28·7	1800	1900
Bran C*	ND	30·2	ND	1800	
Rolled oats*	4·2	69·5	33·4	1500	1500

ND, not determined.
* Samples cooked before extraction.

Processing and food preparation. The solubility of β-glucan from oat bran varies largely because of different processing conditions in addition to varietal differences[48]. Using an *in vitro* digestion model to simulate human digestion, Beer *et al.*[30] found that only 12–33 % of total β-glucan in bran and rolled oats was solubilised, whereas Tosh *et al.*[32] reported a slightly higher solubility value of 39 % in a commercial oat bran. When the oat bran was incorporated into an extruded cereal, the solubility of β-glucan increased markedly from 39 to 67 % in breakfast cereals prepared under mild extrusion conditions. Further increases in the extrusion temperature and mechanical disruption resulted in a complete solubilisation of β-glucan, although the process was accompanied by a >10-fold decrease in MW. Microscopy observations clearly showed that extrusion disrupted the cell-wall structure from which β-glucan labelled by calcofluor was released and dispersed into the food matrix (Fig. 3). Zhang *et al.*[49] also reported that extrusion improved the solubility of β-glucan in oat bran. Johansson *et al.*[40] have shown that the baking of wheat bread with oat bran and subsequent drying of the bread decrease the amount of β-glucan solubilised, whereas the cooking of oat flakes as porridge increases it. Also, fermentation of oat bran by rye sourdough was shown to increase the solubility of oat β-glucan[40,50].

The presence of endogenous enzymes, mainly β-glucanase, can have both detrimental and beneficial effects, the former being a depolymerisation of β-glucan and the latter being an increase in polymer solubility[51]. In a study by Tosh *et al.*[52], β-glucanase at different concentrations was added to the wheat dough containing oat bran to produce muffins containing different MW β-glucans. A decrease in MW of β-glucan from 2 200 000 to 400 000 Da led to an increase in the solubility of β-glucan in oat-bran muffins from 44 to 57 %. This phenomenon is in agreement with dissolution studies showing that the hydrolysis of a similar water-soluble polysaccharide, such as guar galactomannan, significantly increased solubilisation of the polymer[53]. However, when the MW was reduced further to 120 000 Da, the solubility of β-glucan decreased to as low as 26 %. The authors suggested that the subsequent diminution of β-glucan solubility at very low MW (120 000 Da) was due to a stronger self-association of the depolymerised β-glucan, thus leading to the formation of insoluble aggregates. It is also worth speculating that the interaction of β-glucan with other food components, especially proteins via the Maillard reaction, might have contributed to the low solubility. Lower MW polysaccharides seem to possess an increased reactivity towards proteins[54] and other components found in foods[15,55].

Storage. Storage conditions have been shown to alter the solubility of β-glucan in oat-containing products. Beer *et al.*[30] noticed that frozen storage reduced the amount of extractable (soluble) β-glucan in oat muffins and the degree of reduction depended on the other ingredients in the formulation. After 8 weeks of storage, there was up to a 50 % decrease in the extractable β-glucan in the muffins. A more recent study demonstrated that taking fresh muffins through a number of freeze–thaw cycles, each consisting of 14 h at −18°C and 10 h at room temperature, progressively reduced

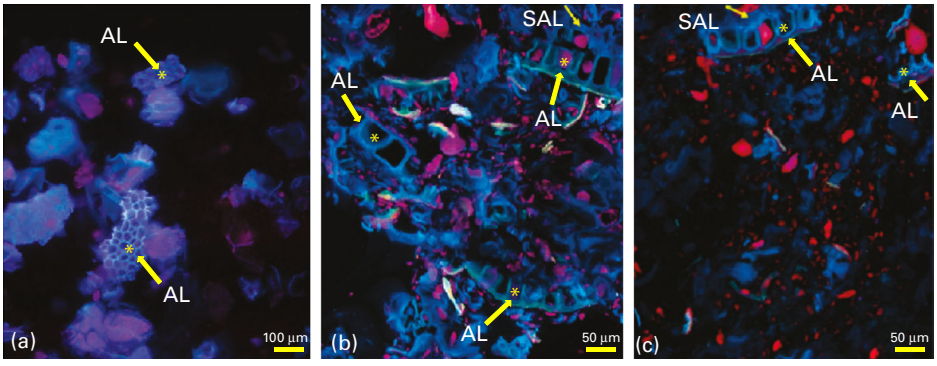

Fig. 3. Cryosections of test cereals, stained with calcofluor and mounted in acid fuchsin, showing that extrusion disrupted the cell wall structure, during which β-glucan (blue stain) was released and dispersed into the food matrix. (a) Premix (control); (b) after moderate extrusion and (c) after extensive extrusion. AL, aleurone cells; SAL, subaleurone cell walls. (Adapted from Tosh *et al.*[32], with permission).

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β-glucan solubility in the muffins. After four cycles of freeze–thaw treatment, the extractable β-glucan was reduced by over 50 %[56]. The authors ascribed the loss of solubility of β-glucan during frozen storage to the reorganisation of β-glucan chains due to intermolecular interactions (mostly stabilised by hydrogen bonding), which are likely to lead to increased ordered structure[14].

Isolation and purification. The extent and rate of dissolution of isolated and purified β-glucan powders has not been well investigated, in contrast to materials such as galactomannan-rich guar-gum powders[53,57,58]. Panahi *et al.*[59] showed that an oat β-glucan concentrate (60 % of β-glucan on dry weight basis) prepared by an alcohol-based enzymic technique had better solubility and higher MW than the product produced by a conventional aqueous extraction process. It has long been known that the solubility of isolated β-glucan is influenced by the drying method. Freeze-dried oat and wheat β-glucans are sometimes difficult to dissolve in water[9]; the replacement of water molecules with isopropanol before drying (the so-called solvent exchange process) is critical to ensure good solubility of β-glucan isolates. The effect of MW on the solubility of β-glucan isolates therefore also depends on the way in which the isolate is prepared. In general, the ease of solubilisation of a polymer decreases as MW increases. This behaviour was demonstrated clearly with guar galactomannan powders where an inverse relationship between the dissolution rate and MW was observed[53]. Recently, Kim & White[7] reported that the solubility of a β-glucan isolate decreased with an increase in MW in a starch suspension after *in vitro* digestion. This is not always the case with oat β-glucan isolates, however. When the solvent exchange stage before drying is omitted, low-MW β-glucan molecules can potentially form stronger polymer–polymer interactions than the high-MW molecules do, which may then lead to a low solubility.

Rheological properties in aqueous medium

Viscoelastic properties of β-glucan solution

A freshly prepared and fully hydrated oat β-glucan solution behaves as a typical neutral random-coil polysaccharide solution. The viscosity of a polysaccharide solution depends on the structure, MW and polymer concentration, as well as conditions of measurement, such as shear rate and temperature. The shear rate dependence of viscosity for oat β-glucan has been extensively studied[2,60]. In terms of conditions in the GIT, shear rate is related to the degree of mixing of fluid (digesta) caused by peristalsis, although flow patterns in the gut are obviously much more complex. Fig. 4 shows the steady shear-flow profiles for solutions of a high MW (2×10^6 Da) oat β-glucan at different concentrations[60]. At low β-glucan concentrations (approximately lower than the overlap concentration c^*), the solution viscosity does not change with respect to shear rate, a form of behaviour that is typical of a Newtonian fluid. At high concentrations, however, shear-thinning behaviour is observed, meaning that the viscosity decreases with an increasing shear rate. Because of the shear-rate dependence of viscosity, the solution viscosities of different samples have to be compared at the same shear rate, most usefully the value at 'zero' shear rate is preferred. In heterogeneous systems containing a polysaccharide gum and insoluble particulates, which are common in food suspensions or ingested food mixed with digestive fluids (i.e. digesta) in the gut, more complex rheological behaviour is seen. For instance, if there is a high fractional volume of insoluble particulates present, the suspensions exhibit shear-thinning even at low shear rates (i.e. loss of the Newtonian plateau) and also substantial increases in viscosity are observed[61,62]. For calculation of the zero-shear viscosity from the flow profiles, see online supplementary material. As seen in the literature, most researchers, in an effort to simplify the

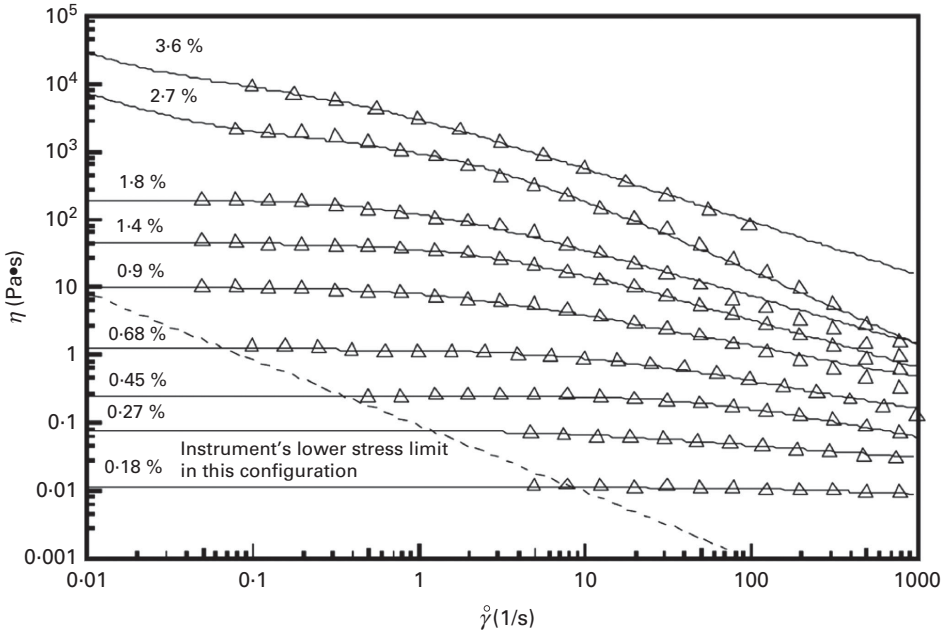

Fig. 4. Apparent viscosity (η) *v.* shear rate ($\dot{\gamma}$) for different concentrations of oat β-glucan solutions. (Re-printed, with permission, from Ren *et al.*[60]).

method and obtain reproducible data, remove the particulate material by centrifugation before taking viscosity readings, because the presence of insoluble material can seriously interfere with measurements. Moreover, a single measurement of viscosity is often performed at an arbitrary shear rate (see Table 2). This is because the shear rates that occur in the intestinal lumen of human subjects and experimental animals following a meal containing a polysaccharide gum are not known and may vary at different regions of the gut and at different postprandial times. Also, zero shear viscosity is not always readily obtainable due to instrumental limitations. Caution is therefore needed when comparing viscosity data from different laboratories.

Solution viscosity is affected by the polymer concentration (c) and MW in a power-law relationship: $\eta \sim (c[\eta])^n$. The intrinsic viscosity, $[\eta]$, is a measure of hydrodynamic volume of the individual molecule in solution and is related to MW by, for instance, the Mark–Houwink relationship ($[\eta] = k\ \mathrm{MW}^{\alpha}$, where k and α are constants). Therefore, the parameter $c[\eta]$ represents the space occupancy of the polymer molecules in the solution by taking into account both concentration and MW factors. Fig. 5 is a double logarithmic plot of $\eta_{sp,0}$ (the specific viscosity at zero shear rate) *v.* the parameter $c\eta$ for oat β-glucan solutions. This plot consists of two linear regions connected by a continuous transition region starting at $c[\eta]$ approximately 1. The concentration at this point is designated c^*, which corresponds to the concentration at which individual β-glucan molecules begin to overlap. For example, for two β-glucans of MW 1 million Da and 0·1 million Da, the c^* values are approximately 0·1 and 0·5 %, respectively. At $c < c^*$, the solution is classified as being in a dilute regime and the relationship $\eta_{sp,0} \sim c^{1\cdot1}$ holds; whereas at $c > c^*$, the solution is classified as being in a semi-dilute regime and $\eta_{sp,0} \sim c^{4\cdot4}$. It is well known that the viscosity of β-glucan solution changes more markedly with concentration in the semi-dilute solution than it does in dilute solution. The zero-shear viscosity at the critical concentration is approximately 1 mPa·s (Fig. 5). In most clinical trials that showed positive blood-glucose and cholesterol-lowering effects, the viscosity (as estimated *in vitro* in the shear rate range 10–30 s^{-1}) is considerably higher than this value (Table 2), although the *in vivo* viscosity may be different from that measured *in vitro*[63]. According to Wood[41], the (*in vitro* viscosity) dose–response for the glycaemic response of β-glucan is in the range of 20–2000 mPa·s (at shear rate 30 s^{-1}). When the viscosity is lower than 20 mPa·s, no glucose-lowering effect is observed, whereas when the viscosity is higher than 2000 mPa·s, no further reductions in blood glucose are seen. In other words, the metabolic response appears to reach a plateau above 2000 mPa·s. This highlights the importance that changes in MW have on the viscosity of β-glucan products, which in turn determines their physiological activity.

It must be emphasised that *in vitro* viscosities of polysaccharides might not accurately reflect the viscosities of these polymers when present in the GIT. The level of viscosity required to achieve a specific physiological effect has not been carefully reviewed and systematically studied. There are no data available on the direct measurements of luminal viscosity of oatmeals. However, studies by Marciani *et al.*[64,65] on locust bean gum, a source of water-soluble galactomannan with rheological properties similar to high MW oat β-glucan, provides some useful comparative information. In these studies, the gastric-content samples were obtained after ingestion of meals containing different doses of locust bean gum using nasogastric intubation and aspiration, and the viscosity was measured *in vitro* by a viscometer. This group also used an echo-planar MRI technique to measure the *in vivo* gastric lumen viscosity, which allowed viscosity to be measured non-invasively[64]. A good correlation was obtained between the rheological data from *in vitro* viscometry and echo-planar MRI. Table 2 lists the viscosity of test meals that have demonstrated positive physiological functions. Taking these data into consideration, along with the recommended minimum dose of oat β-glucan used for achieving significant physiological effects, the viscosity of the luminal digesta seems to fall within the lower end range of a semi-dilute regime (see Fig. 5).

From the analysis of data from Lan-Pidhainy *et al.*[56], it was found that the viscosity was related to concentration exponentially by an exponent of 1·51, although the soluble β-glucan concentration was well within the range of the dilute regime. This is due, at least in part, to the existence of particulate materials, which are known to raise the viscosity of a solution/suspension as explained by Rayment *et al.*[61]. It is well documented that cereal β-glucan tends to form macromolecular aggregates in aqueous solutions[20,21,66]. Moreover, the low-MW oat β-glucan aggregates more easily than their high-MW counterparts[8,14,15]. Low-MW β-glucan solutions have been shown to have a 'yield stress flow' behaviour at very low shear rates giving higher than expected apparent viscosity values, which is attributed to the presence of β-glucan aggregates (Fig. 4)[2,60].

Impact on the blood-glucose and cholesterol-lowering properties

The mechanisms by which oat β-glucan and other soluble fibres elicit their physiological effects on carbohydrate and lipid metabolism are discussed in the article on oats and CVD risk markers by Thies *et al.*[67] in this Supplement. Although several mechanisms have been proposed, the ability of the soluble polysaccharide to increase the viscosity of the gut digesta, and thus to delay nutrient absorption from the gut, is believed to be a key factor[3,68]. Wood *et al.*[63] first demonstrated an inverse linear relationship between peak postprandial blood glucose and insulin increments and log (viscosity) in healthy subjects who consumed glucose drinks containing extracted and purified β-glucan samples of different doses and MW values. A number of studies also reported that high-viscosity β-glucan drinks significantly attenuated postprandial glycaemia, but low-viscosity β-glucan showed no such effect[59]. A similar relationship was reported when β-glucan was incorporated into a food matrix such as baked goods and breakfast cereals[69,70]. Recently, an inverse linear relationship between glycaemic responses and *in vitro* viscosity of extracted β-glucan, as measured under simulated physiological conditions, was clearly demonstrated in healthy subjects consuming bread[71], muffins[52,72] and granolas[73] containing oat or barley β-glucans.

Table 2. Examples of viscosity (η) measured at specific shear rates ($\dot{\gamma}$) and temperature (temp.) of oat-containing meals tested in human studies, which have demonstrated positive postprandial blood-glucose lowering (PGL) and cholesterol-lowering (CL) effects

Type of food	Extraction method	β-Glucan dose (g)	β-Glucan M_p or M_w* ($\times 10^{-6}$ Da)	η (at $\dot{\gamma}$, and temp.) (mPa·s)	Metabolic effects shown	Reference
Glucose drink with β-glucan extract	Drink before consumption	1·8	ND	23 (30 s^{-1}, 25°C)	PGL	Wood *et al.*[63]
		3·6		159 (30 s^{-1}, 25°C)		
		7·2		1940 (30 s^{-1}, 25°C)		
Oat bran muffin	Physiological extraction at 37°C[30]	8	1·8–2·8	15·2 (30 s^{-1}, 37°C)	PGL	Lan-Pidhainy *et al.*[56]
		12	2·0–2·7	17·8 (30 s^{-1}, 37°C)		
Oat bran muffin	Physiological extraction at 37°C[30]	4	2·2	5·9 (30 s^{-1}, 37°C)	PGL	Tosh *et al.*[52]
		8	2·2	29·8 (30 s^{-1}, 37°C)		
Glucose drink with β-glucan concentrate	2 h hydration of the drink mix at 37°C	6	ND	3200 (12·9 s^{-1}, 37°C)	PGL	Panahi *et al.*[59]
Cereal with oat bran	Physiological extraction at 37°C[30]	3	2·2	2930 (30 s^{-1}, 37°C)	CL	Wolever *et al.*[81]
		3	0·53	800 (30 s^{-1}, 37°C)		
		4	0·85	1670 (30 s^{-1}, 37°C)		
Cereal with oat bran	Physiological extraction at 37°C[30]	8	2·2*	2930 (30 s^{-1}, 37°C)	PGL	Brummer *et al.*[69]
		8	0·92*	1700 (30 s^{-1}, 37°C)		
		8	0·63*	800 (30 s^{-1}, 37°C)		
Granola bar with oat bran and rolled oats	Physiological extraction at 37°C[30]	6·2	2·1	796 (30 s^{-1}, 37°C)	PGL	Regand *et al.*[73]
		6·2	0·43	66 (30 s^{-1}, 37°C)		

M_p, peak molecular weight; M_w, weight average molecular weight; values with *indicate M_w only; ND, not determined.

In a recent human intervention trial using extruded breakfast cereal containing oat β-glucan of various MW values, Wolever *et al.*[74] demonstrated an inverse relationship between serum LDL-cholesterol and log (viscosity), as measured by *in vitro* extraction under physiological conditions. These studies provide convincing evidence that the ability of β-glucan and other viscous polysaccharides to increase the digesta viscosity in the GIT is a key factor in determining their blood-glucose and cholesterol-lowering effects. In addition to this rheological mechanism, direct interference of soluble fibre with the biochemical degradation of starch[73,75,76] and bile-acid binding[5] have been reported to contribute to these beneficial effects on metabolism.

Although numerous human trials have been carried out to test oat β-glucans from various sources and present in different forms of foods, only some of these studies showed reductions in blood-cholesterol and -glucose concentrations[77–79]. This discrepancy can be attributed to a range of factors, apart from the β-glucan dosage used, that may potentially affect the amount and MW of solubilised β-glucan in the GIT by influencing the alimentary viscosity. Regand *et al.*[72] reported that depolymerisation of β-glucan in bread and pasta reduced its efficacy in attenuating the peak blood-glucose response in healthy human subjects. The same group also found that an extruded oat-based breakfast cereal given at a dose of 3 g of oat β-glucan/d with a high ($2{\cdot}2 \times 10^6$ Da) or medium ($0{\cdot}5 \times 10^6$ Da) MW lowered LDL-cholesterol similarly (5 %), but the efficacy was reduced by 50 % when MW was reduced to $0{\cdot}2 \times 10^6$ Da[74]. Kerckhoffs *et al.*[31] also demonstrated that the cholesterol-lowering effect of β-glucan from oat bran administered in orange juice diminished when the same β-glucan is incorporated into bread and cookies. Depolymerisation of β-glucan and/or reduced solubility in food may account for the attenuation in efficacy reported for the latter products. Moreover, it has been shown that the reduced solubility induced by freeze–thaw cycling[56] or gelation[80] decreased the efficacy of β-glucan in lowering postprandial glycaemic responses in human subjects. These studies provide compelling evidence that the physico-chemical properties of oat β-glucan play a crucial role in determining its physiological functions. Thus, reduced solubility and/or MW of β-glucan might be responsible for some of the published studies that failed to show positive metabolic effects of oat products.

Conclusions and future research

Based on the results of physiological and human studies to date, there is strong evidence to show that oat β-glucan lowers total and LDL-cholesterol and attenuates postprandial glycaemia and insulinaemia when it is ingested in sufficiently high doses and at a suitably high MW. The physico-chemical properties of oat β-glucan, namely MW and solubility, should be considered when assessing the physiological properties. Oat β-glucan concentrates or isolates have shown similar beneficial effects to oat bran and rolled oats, provided that detrimental processing conditions are avoided.

The current recommended intake of ≥ 3 g/d β-glucan by US Food and Drug Administration does not ensure a significant decrease in blood cholesterol, because the quantity of

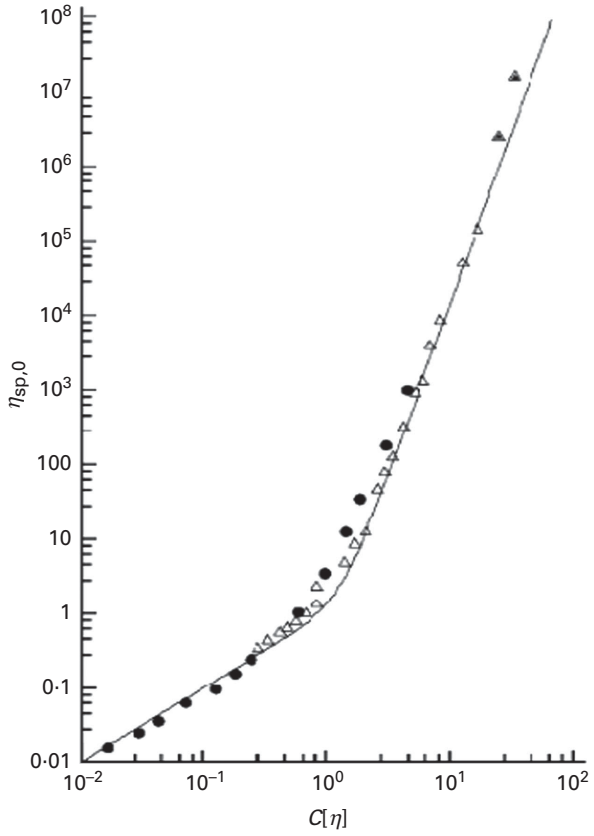

Fig. 5. Log $\eta_{sp,0}$ (the specific viscosity at zero shear rate) *v.* log $c[\eta]$ for oat β-glucan. ●: data of Doublier & Wood[2]; Δ: data from Ren *et al.*[60]. (Reprinted, with permission, from Ren *et al.*[60]).

β-glucan ingested does not solely determine the physiological efficacy. It is the amount and MW of β-glucan that become solubilised in the GIT that determines, to a large extent, the blood-glucose and cholesterol-lowering properties. Clear inverse linear relationships have been demonstrated between the *in vitro* log (viscosity) of drink or extracts from solid foods and postprandial blood-glucose or fasting blood-cholesterol concentrations. It appears that there is a range of viscosity values over which β-glucan exhibits such biological activities, although the minimum and maximum values for this range need to be defined. There is little doubt that *in vitro* evaluation can be effectively used to screen oat products in order to increase the likelihood of success in achieving beneficial biological effects in human subjects. How the viscosity of drinks or extracts measured *in vitro* corresponds to the *in vivo* viscosity developed in the GIT is not straightforward. A combination of factors, including the dilution effects of digestive fluids, enzymic degradation of β-glucan and interaction of this polymer with other food components, is likely to influence the *in vivo* viscosity. Direct measurements of viscosity in the human gut have not yet been carried out on ingested oat products, as has been done with other polysaccharides such as the leguminous galactomannans (locust bean gum)[64,65]. Accordingly, the minimum *in vivo* viscosity that is required to achieve desirable metabolic effects is currently unknown.

The development of inexpensive and palatable oat-containing products, which are still physiologically effective, is needed in the future. To facilitate this, it is necessary to establish a standardised protocol to characterise β-glucan products, which provides sufficient physico-chemical data to allow useful comparisons and interpretations to be made of the results obtained in various human studies.

Supplementary material

To view supplementary material for this article, please visit http://dx.doi.org/10.1017/S0007114514002256

Acknowledgements

The authors thank Shea Miller at Agriculture and Agri-Food Canada (AAFC) for providing Fig. 2 and Peter Butterworth (Kings College London), Simon Ross-Murphy (University of Nottingham), and Steve Cui and Susan Tosh of AAFC for helpful feedback on various drafts of the present paper. The authors dedicate this review to the late Peter Wood, a close colleague and friend of both the authors, for his huge research contribution to the structure, properties and nutritional effects of oat β-glucan. Q. W. received an honorarium from Quaker Oats Company (a subsidiary of PepsiCo, Inc.) for attending the workshop in May 2012 to discuss the content of the supplement. Research in the laboratory of P. R. E. was funded by the Biotechnology and Biological Sciences Research Council, UK.

Author contributions: Q. W. drafted the paper and P. R. E. contributed to writing and editing the paper.

This paper was published as part of a supplement to British Journal of Nutrition, publication of which was supported by an unrestricted educational grant from Quaker Oats Co. (a subsidiary of PepsiCo Inc.). The papers included in this supplement were invited by the Guest Editor and have undergone the standard journal formal review process. They may be cited.

The Guest Editor to this supplement is Roger Clemens. The Guest Editor declares no conflict of interest.

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