The β-glucan quality trait in wheat

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Research

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ABSTRACT
Wheat is one of the most important cereal in the world, providing nutrients for humans and animals. The main objective of the present report is to summarize the knowledge about β-glucan, one of the quality traits of wheat: β-glucan. The β-glucan, main component of dietary fibre, has many health benefits, such as immunomodulatory and cholesterol lower activity, faecal bulking effect, enhanced absorption of certain mineral, prebiotic effects, and reducing type II diabetes. The attention on food quality over quantity is growing in many part of the world so dietary fibre are gaining much interest. Compare to other component of the grain, dietary fibre have not been studied extensively. The present review describes the current status of knowledge about the genetic control of β-glucan accumulation in wheat grain, and the gaps needed to be bridged for better understanding of the genetic architecture of this important trait.

1. Introduction

Due to the revolution of the nutritional concept, food was upgrade as the exclusive supply of nutrient and energy. Those products are, today, raising interest on the market, and they are characterized by fortify content of fibre and antioxidants (Juneja et al. 2019).

Over a decade of intensive research, it has become clear that indigestible complex polysaccharides, namely dietary fibre, from cell walls of pericarp-seed coat and aleurone layers of barley (*Hordeum vulgare*), oat (*Avena sativa*) and wheat (*Triticum aestivum*) grains, can lower the risk of serious, diet-related chronic diseases (Fincher 2009; Fedacko et al. 2019). A large clinical study by European Prospective Investigation into Cancer and Nutrition (EPIC) showed dietary fibre consumption lowers the risk of colon cancer and diverticular diseases (Bingham et al. 2003; Crowe et al. 2011; Ricciardi et al. 2019). Specifically, the most important fibre components in cereal grains are (1,3;1,4)-β-D-glucans, commonly known as β-glucans. Their structural properties are strongly linked to food digestibility, bulking and fermentability (Ain et al. 2018). For example, the viscosity of oat glucan is 9.6 dlg-1, barley and wheat are around 5 dlg-1 (Collins et al. 2010). When eaten, these polysaccharides increase the viscosity of the small intestine contents and therefore slow down enzyme-mediated starch breakdown. This prolongs the food absorption and slows the rate of glucose release after meals, reducing the glycemic index and providing benefit to people with type II diabetes (Allison et al. 2004).

Wheat (*Triticum* spp.) is one of the three major cereal crops and is an excellent source of nutrients (Paznocht et al. 2019). In 2017, world production of wheat was 772 million tons making it the second most-produced cereal after maize (1,135 million tons) (data from FAO, 2017). Cultivated wheats are divided in three main groups based on their ploidy level: diploids, tetraploids and hexaploid. About 95% of the wheat grown worldwide is the hexaploid bread wheat (*Triticum aestivum*). The remaining 5% is the tetraploid durum wheat (*Triticum turgidum*). The latter one is often called pasta wheat to reflect its major end -use (pasta, couscous and some bread flours) (Colasuonno et al. 2017a; Marcotuli et al. 2018) and it is typical of the Mediterranean area. The wheat kernel represents a storehouse of nutrients essential to human diet. The main components of wheat seeds include water (12.5% by weight), starch (70.2%), proteins (12.2%), lipids (1.9%), fibre (1.6%) and minerals (1.6%). This means that wheat kernels have not only a high carbohydrate content but also high vitamin (such as vitamin A, vitamin B and carotenoid pigments) and mineral (sodium, potassium, calcium and magnesium) contents (Hussain et al. 2015; Colasuonno et al. 2017a; Colasuonno et al. 2017b). In this article, we review the efforts made so far towards an understanding of the genetic control of β-glucan content in wheat grain. The studies already made, in wheat and phylogenetic related species, and the future prospects of improving the nutritional quality of wheat grain using marker-assisted selection (MAS) are also briefly discussed.

2. Content of β-glucans in various grain tissues

The β-glucans are abundant in cell walls of *Poaceae* and represent one example of heterogeneous group of glucose polymers in which fine structure is essential for function in the plant cell wall (Burton et al. 2010). β-glucans are unsubstituted and unbranched polysaccharides of β-D-glucopyranosil monomers polymerized through (1,3)- and (1,4)-liknkages. Within the grasses, barley (*Hordeum vulgare*), oat (*Avena sativa*) and rye (*Secale cereale*) grain are rich sources of β-glucans, while wheat and maize (*Zea mais*) have lower concentrations of the polysaccharide (Fincher 2009). In particular, the β-glucan level varies among 0.4-1.4% in wheat, 2-7.8% in oats, 1.2-2% in rye, and it ranges from 2.5% to 11.5% in barley (Izydorczyk and Dexter 2008). The content in barley is notable higher than other cereals. The fibre content is influences by both genetic and environmental factors and theirs interactions (Marcotuli et al. 2018). Several studies showed that β-glucans content increases under hot and dry conditions and in some barley genotypes with anomalous starch composition (waxy or high amylose) (Swanston 1997). The location of β-glucans in wheat and their interaction with other constituents are important for technological process, since they

influence the obtainment of fractions enriched in these polysaccharides and products with a high nutrient content.

Morphologically, each wheat seed contains three distinct parts that are separated during the milling process to produce flour. The different components include endosperm (81-83% by weight), bran (14-15%) and embryo (2-3%). The endosperm, source of white flour, contains the greatest share of starch, proteins (around the 10%), iron and many B-complex vitamins (such as riboflavin, niacin and thiamine). The embryo or the germ, the nascent section of the plant, is usually separated through layers that provide water and solutes from endosperm during germination. The embryo contains minimal quantities of proteins and minerals but a major share of vitamins, especially of the B-complex. The bran is the outer covering of the grain and it consists of aleurone, endocarp, mesocarp and epicarp. The bran contains trace of minerals and indigestible cellulose material, such as the β-glucans. Compared to barley, the distribution of β-glucans throughout the wheat endosperm is less uniform and in low concentration. High concentrations of β-glucans (accounting for about 29% of the dry weight) were found in the aleurone layer (Nemeth et al. 2010).

3. β-glucan structure and biosynthesis

One of the main cell wall polysaccharides of wheat grain is (1,3; 1,4)-β-D-glucan, comprising glucose residues joined by (1,3) and (1,4) linkages. Single (1,3) linkages are usually separated by two or three (1,4) connections, but longer sections (up to 14) have been observed in wheat bran (Li et al. 2006). The ratio of the (1,4)- to (1,3)- linkages varies between the species. In wheat the range is from 3.0:1 to 4.5:1; in barley from 2.9:1 to 3.4:1; in rye about 2.7:1; in oats from 1.8:1 to 2.3:1 (Fincher and Stone 2004). The result of this linkage arrangement is an irregular distribution of the chain. For this reason the molecules are not aligned over extended regions and remain in solution when their degree of polymerization (DP) exceeds 1000 (Woodward et al. 1983; Lazaridou and Biliaderis 2007). The asymmetrical conformation is presumably involved in the polysaccharides function

as the gel-like matrix phase component of the cell wall, which allow the wall to be supported but at the same time remain flexible, pliable and porous to permit the transfer of water, nutrients, and other small molecules across the wall during the developmental stages (Fincher 2009). The same asymmetry is responsible for the high viscosity of β-glucan and the beneficial effects on human health and nutrition (Brennan and Cleary 2005). The reason why the β-glucan structures are important is the role in the digestibility of these compounds (Fincher 2009).

The β-glucans biosynthetic pathway has been extensively studied in barley. In particular, (Burton et al. 2010) proposed two phase assembly systems: the first phase involves the assembly of a population of glucose polymers (cellodextrins) linked to a Golgi membrane-associated macromolecules. A population of (1,4)-β-oligoglucosidases is synthetized by cellulose synthase-like CslF or CslH enzymes. The second phase of the model suggests the transfer of the membrane-bound (1,4)-β-oligoglucosidases to the plasma membrane, where they are taken from other enzymes (callose synthase, xyloglucan endotransglycosylase, or CslF isoenzyme) and linked through (1,3)- β-linkages.

4. Genetics of β-glucans

The β-glucan content is a quantitative trait controlled by several loci (QTL) with different impacts. QTL analysis of genes controlling barley mature grain β-glucan content (Han et al. 1995), coupled with the identification of *CslF* genes in a syntenic region of the rice genome, was the first step towards isolating the genes involved in β-glucan biosynthesis.

In barley, using bi-parental mapping populations, grain β-glucan QTL were identified on chromosomes: 1H and 2H (Szűcs et al. 2009), 1HL, 5H and 7HL (Molina-Cano et al. 2007) and 2H, 3H, 6H and 7H (Li et al. 2008). Using association mapping, Shu and Rasmussen (2014) identified genomic regions associated with β-glucan on chromosomes 1H, 4H, 5H, 6H and 7H, and Houston et al. (2014) detected significant association on chromosomes 1H, 2H, 3H, 5H, 6H and 7H. In several studies the region mapped on chromo-

some 7H represented the major QTL explaining up to 39% of the phenotypic variance (Danilova et al. 2018). As for many plant polysaccharides, steady progress has been made in barley suggesting a superfamily of genes involved in the synthesis of these polysaccharides, such as the cellulose synthase-like F (*CslF*) gene family (Burton et al. 2008) and the cellulose synthase (*CesA*) genes (Pear et al. 1996).

Recently, in wheat QTL for β-glucan were mapped on homoeologus group 2 chromosomes (Marcotuli et al. 2017) and on chromosomes 3A, 1B, 5B, and 6D (Manickavelu et al. 2011) using a bi-parental population, and on chromosomes 1A, 2A, 2B, 5B and 7A by genome-wide association mapping (Marcotuli et al. 2016). However, except for a few cases, most of these QTL were not stable across environments. Moreover, the characterization of wheat β-glucan gene families has not been completed.

The lack of major QTL for β-glucan in wheat is the main reason why marker-assisted selection (MAS) has not been used for the improvement of the trait, although the discovery and characterization of the principal genes such as *CslH* and *CslF6* (mapped on chromosome group 5 and 7, respectively) (Nemeth et al. 2010; Cseh et al. 2013; Marcotuli et al. 2018) facilitated the use of MAS. Progress towards breeding for high dietary fibre using MAS are still limited due to the complex expression of the trait in a polyploidy genome such as wheat.

5. Future prospective
In view of the above, major investment in terms of time and resources is needed to increase knowledge regarding the genetic control of the β-glucan content and to find better genetic resources for improvement of nutritional quality of wheat with a highest concentration of fibre. These have been extensively studied in barley for several implication in food process (i.e. malt production and brewing), but in wheat they still represent a complex trait needing of major investigations through new tools application.

High-throughput marker systems (i.e. SNP markers) together to the next-generation sequencing (NGS) techniques may be useful for the genetic dissection, unravelling the genetic control and development of molecular markers associated with major genes and QTL for the trait. In addition, efforts may also be made to exploit alien genetic variation for transfer of desired trait.

Uses of molecular markers in breeding programs and detailed phenotypic analysis of all/new genetic resources assurance tangible benefits through rapid obtainment of the improved varieties with high β-glucan content grains.

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