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Genetic factors influencing triticale quality for food☆

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ABSTRACT

Triticale is an amphiploid hybrid between wheat and rye. It combines good agronomic performance of wheat with hardiness and resilience to pathogens of rye. Its plasticity to adapt to adverse environmental conditions makes it more suitable for growing under poor conditions compared to wheat and other cereal crops. Since the release of the first cultivars, triticale had a wide range of use from animal feed to industry applications, but there is still a gap in terms of end-use quality for food production between triticale and wheat that limits consumer acceptance, especially in developed countries. Although technological and rheological properties of doughs obtained from triticale flour justify its poor adoption in food production, the high nutritional value conferred by a more balanced amino acid composition and higher content of protein and health promoting compounds are a key strength for human consumption. This review aims to bring out nutritional and technological properties of triticale flours and doughs through a genetic dissection of the major traits determining superior quality characteristics.

1. Introduction

Triticale, originally called *Triticosecale rimpaui* later renamed *xTriticosecale Wittmack*, is an amphiploid hybrid between the seed-bearing parent wheat (*Triticum turgidum* spp. *durum* or *Triticum aestivum*) and the pollen parent rye (*Secale cereale*). The hybridization can produce hexaploid or octoploid genotypes when durum or bread wheat are used to cross with rye, respectively. Specific breeding programs aimed to produce triticale cultivars for commercial purposes were started in Europe, North America, Australia and Canada only in the second half of the 20th century. Until then triticales, especially octoploid genotypes, showed partial floret sterility, high aneuploidy frequency, low grain yield, low test weight, shriveled kernels, pre-harvest sprouting, lodging susceptibility and poor adaptation to diverse environments. In the 1960s, CIMMYT breeders identified a triticale spontaneously outcrossed with a semi-dwarf common wheat variety, which led to a substantial leap forward in terms of grain yield and wider adaptability. Higher grain yield, reduced plant height, and greater grain test weight were the main improved traits of the new hexaploid cultivar Armadillo. The release of improved lines obtained from Armadillo fostered the global diffusion of triticale, especially in North America and Europe. The harvested area significantly increased from 1980s, resulting in a corresponding production increase. In 2020, the world production of triticale was 15,361,341 tonnes on a total area harvested of 3,812,724 ha with an average yield of 4.44 tonnes/ha (40290 hg/ha), slightly higher than that reported in wheat (FAOSTAT data).

On the other hand, to date, triticale flour shows inferior technological quality compared to wheat, therefore it is less frequently used for food production, if not mixed with wheat flour that confers high quality for bread-making. Technological properties of triticale flour and dough remain of a poor end-use quality with a lower utilization in food processing compared to wheat and rye.

However, the high nutritional value of triticale grain may be a strength to a wider diffusion in food industry through the production of healthy foods. Triticale has a protein content similar to wheat, a higher proportion of soluble fibers and a good number of phenolic compounds with antioxidant activity. In particular, the higher content of lysine increases the biological value of proteins resulting in a more balanced amino acid composition compared to wheat. Starch composition, non-starch polysaccharides (NSP), polyphenols and vitamins also

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contribute to the superior nutritional value of triticale flours. The health benefits of consuming nutrients from triticale could drive the development of new cultivars and processing methods more suitable to increase consumer acceptance towards triticale. The focus of the present review article is to provide an overview on end-use quality characteristics of triticale, paying special attention to genetic aspects that control the composition and rheological behavior of doughs.

2. Genetic architecture

2.1. Genomic composition and classification

As an amphipolyploid obtained by crossing wheat species and rye, the ploidy level of triticale may vary from tetraploid (2n = 14 = AARR) to hexaploid (2n = 42 = AABBRR) and octoploid (2n = 56 = AABBDDRR), mainly depending on the parental wheat used in the hybridization. Octoploid triticale genotypes derives from the hybridization between bread wheat (2n = 42 = AABBDD) and rye (2n = 14 = RR), hexaploid genotypes between tetraploid wheat species (2n = 28 = AABB) and rye, otherwise intercrossing octoploid triticales. There are also tetraploid hybrids derived from crosses between hexaploid triticale and rye followed by selfing. Hexaploid varieties are the most widely cultivated around the globe because of their better genomic stability and floret fertility compared to octoploids, which have a better end-use quality due to the presence of D-genome.

Triticale genotypes are classified as 'primary triticale' in case of hybrids obtained by crossing wheat and rye, and as 'secondary triticale' obtained in different ways; intercrossing primary triticale lines, crossing primary or secondary triticales with wheat and rye or crossing primary triticales with secondary triticales (Oettler, 2005). Octoploids (AABBDDRR) are obtained only as primary triticale. Hexaploid triticales (AABBRR) exist either as primary triticale when obtained by crossing *Triticum* tetraploid species with diploid rye or as secondary triticale in the case of intercrossing octoploid triticale genotypes that revert to the hexaploid level.

Triticale hybrid does not always contain one complete diploid set of chromosomes derived from each parent. These types are classified as 'substituted' triticales. In contrast to 'complete' triticales, which have complete sets of chromosomes derived from both parental species, 'substituted' triticales retain different proportion of the rye genome; R-chromosomes or a segment of an R-chromosome can be substituted with an entire chromosome or with a chromosome segment from wheat species.

2.2. Chromosome constitutions

Intercrossing different primary or secondary triticales as well as backcrossing triticale with wheat species induce recombination and chromosomal rearrangements between wheat and rye genomes, producing substituted genotypes. Although genotypes with all rye chromosomes (AABBRR) show higher adaptive advantages than substituted types, the resulting chromosomal combinations of substituted lines have produced, very often, a substantial gain in agronomic performance, fitness and grain quality. Currently, chromosome substitution lines are very spread among triticale populations, in which A-, B- and R-chromosomes are replaced, mainly, by D-genome of common wheat and *Aegilops* species. The first reported triticale substitution line was Armadillo, in which the 2R chromosome of rye was substituted by 2D chromosome of wheat. This is the most frequent substitution in modern triticale, which led to a substantial increase of yield and agronomic performance, but on the other hand has resulted in narrowing genetic base. Later, substitution lines in which A-, B- and R-chromosomes are substituted by D-chromosomes were produced with the aim to improve the end-use quality of triticale (Lukaszewski et al., 1987; Lukaszewski and Curtis, 1992, 1994; Lukaszewski, 2003, 2006).

Lukaszewski and Curtis (1992, 1994) used a set of aneuploids carrying 1DL arm and the triticale substitution line Rhino 5D(5B) to transfer the *Glu-D1* locus from chromosomes 1R and 1A in the cv Rhino. Because the translocation of the entire chromosome arms, 1D(1A), 1D (1B) and 1D(1R) caused the decline of agronomic performance, substitution lines 1R.1D 5D(5B) were used to transfer only the *Glu-D1* locus of 1DL chromosome arm to 1R of triticale cultivar Presto (Lukaszewski, 2003, 2006). The resultant triticale substitution lines showed a substantial increase in the SDS-sedimentation value compared to triticale cv. Presto. The SDS-sedimentation test is an indicator of gluten strength that varies depending on protein quantity and quality.

The bottleneck limiting triticale breeding is the availability of genetic variability because it is a relatively newly synthesized species. Producing new amphiploid genotypes by introducing new genes from parental forms (*Triticum* and *Secale*) and related species (*Aegilops*) and the use of new gene editing tools might provide the best ways to increase genetic variability in triticale.

3. Nutritional value and grain quality

3.1. Grain composition

Triticale spikes are generally awned like rye and durum wheat. Grains are more elongated than durum wheat and often wrinkled like rye. Triticale has a chemical composition of caryopsis between wheat and rye but on average has a higher concentration of health promoting compounds compared to the other cereals, such as lysine, dietary fiber and antioxidant compounds.

As in wheat, mature kernels are composed of bran, germ and endosperm. The seed coat, composed of outer aleurone layer and pericarp, is thicker than wheat. The endosperm represents over 80% of the kernel and carbohydrates are the major components (70% of the total dry matter). The protein content ranges from about 8% to 16%, non-starch dietary fiber is between wheat and rye, ranging from about 10% to 16%, and lipids (1–2%), vitamins and micronutrients (1–2%) are present in small amounts. The chemical and nutritional composition of triticale kernels is positioned between wheat and rye (Table 1).

3.1.1. Starch

Similar to wheat and higher compared to rye, starch accounts from 60% to 70% of the starchy endosperm in triticale (Dennett and Trethowan, 2013; Langó et al., 2018b; Rakha et al., 2011; Sirat et al., 2022; Watanabe et al., 2019). It consists of two glucan polymers in the form of water-insoluble granules; amylose, that is a linear polymer of glucose with long-chain branches, and amylopectin, a highly branched polymer. The amylose to amylopectin ratio and the morphology and the structure of starch granules strongly influence technological properties of flour and dough digestibility. Starches represent the main source of energy provided by cereals in human nutrition and they are classified as ready digestible starch (RDS), slowly digestible starch (SDS) and resistant starch (RS). Langó et al. (2018a) reported the amylose content varying

Table 1
Whole flour composition of triticale, wheat and rye grain. Quantity is reported as percentage of dry matter.

	% WHOLE FLOUR		
	TRITICALE	**WHEAT**	**RYE**
Carbohydrates	>70%	>70%	>70%
Starch	60–75%	64–80%	55–70%
Amylose	12.8–35.1%	29–33%	25–28.9%
Protein	8.6–16.3%	11.5–14.1%	9.6–14.5%
Dietary fiber	10–16.3%	9.6–15.5%	13.7–20.6%
SDF	0.6–2.8%	2.2–2.5%	4.3–4.5%
IDF	9.3–14.3%	11.4–12.4%	13.1–14.4%
Lipids	1–2.4%	1–2%	1–2%
Ash	1–2%	1–2%	1–2%
Polyphenols	0.2–0.7%	0.2–0.4%	0.4–0.7%

from 23.9% to 34.5% in a set of hexaploid triticales, with an average similar to rye (28.9%) and lower than wheat (32.5%). Similar results were obtained by Navarro-Contreras et al. (2014) comparing protein and starch content of substituted and complete triticales to durum wheat and rye. Triticale cultivars showed similar amounts of amylose to rye but lower compared to wheat, and the amylose content in substituted types was lower than complete types. Dennett et al. (2009) observed high degree of variation in amylose content (ranging from 12.8% to 35.1%) among a selection of 247 triticale lines.

In cereals, starch is deposited in three distinct types of granules, based on the shape and size: A-type (diameter >15 μm) large and lenticular, B-type (diameter <15 μm) smaller and spherical and C-type (diameter 5 μm) polymorphs of A- and B-types. In the set of hexaploid triticales analyzed by Langó et al. (2018b), all genotypes showed a higher volume of A-type granules compared to wheat and rye. Triticale starch granules are often larger than those of wheat and other cereals with the A-type granules representing the highest proportion of the total granules. The ratio of A-type to B-type granules is biased toward A-type and is directly correlated with the increase in amylose percentage. Although the amylose content of large starch granules is higher than small granules, the absolute amylose content of triticale is lower than wheat (Ao and Jane, 2007).

Starch synthesis, composition and morphology can vary not only based on genotypes but also based on environments and growing conditions. Langó et al. (2018b) reported that the starch content of some triticales grown under Hungarian conditions were lower than the content obtained in other studies conducted under different conditions on the same genotypes.

3.1.2. Dietary fiber

Kernel dietary fiber has major health benefits and can be classified according to the water solubility in soluble (SDF) and insoluble (IDF) dietary fiber. SDF accounts for about 10%–20% of the total dietary fiber and consists mostly of non-cellulosic polysaccharides, whereas IDF mainly includes structural cell wall components and represents 80%–85% of the total dietary fiber. Total dietary fiber content in triticale, ranging from 10 to 17% (Agil and Hosseinian, 2014; Fraś et al., 2016; Langó et al., 2018b), is more genetically variable than environmentally dependent (Langó et al., 2017; Rakha et al., 2011). The highest total dietary fiber content is found in rye followed by triticale and then wheat, 18.91%, 16.3% and 15.05% of dry weight, respectively. The soluble fraction in triticale is higher than wheat, especially water-extractable arabinoxylans and fructans (Fraś et al., 2016; Rakha et al., 2011). Arabinoxylan and hemicelluloses (especially β-glucans) are predominant fiber in cereals and can be present either as soluble or insoluble fractions. Arabinoxylans accounts for about 40% of the total dietary fiber in triticale (Dennett et al., 2013; Rakha et al., 2011), and their amount is reported to be similar or higher than wheat in different triticale cultivars, though lower than rye (Dennett et al., 2013; Makarska et al., 2008; Rakha et al., 2011). Fructans are one of the major components of the SDF ranging from 1.5 to 3% of the total dietary fiber content in triticale cultivars (Rakha et al., 2011). They are associated with both positive and negative health effects; fructans positively affect gut microbiota and antioxidant activity but, on the other hand, can trigger gastrointenstinal disorders like other FOODMAPs (Fermentable Oligosaccharides, Disaccharides, Monosaccharides and Polyols). Cellulose content is slightly lower compared to fructans, and lignin is also present in considerable amounts.

Although non-starch polysaccharides are major components of dietary fiber, starch, in the form of RS, also provides a good amount of IDF. Among cereals like barley, oat, rye and wheat, the highest level of RS was identified in triticale (Mikulikova and Kraic, 2006). Most of the dietary fiber is contained in the seed pericarp and aleurone layer, thus, after milling and based on the type of milling process, a large part is lost and the average content of dietary fiber decreases by over 50%. Otherwise, technological processing involving temperature variations and dough fermentations produce changes in dietary fiber content and composition, resulting in a slight increase compared to refined flours at the expense of a decrease in starch content (Fraś et al., 2016). The higher dietary fiber content compared to wheat contributes to an increase in the nutritional value of triticale, encouraging its use in human nutrition as health benefit food. On the other side, the lower content compared to rye, especially arabinoxylans content, promotes its use in animal feed.

3.1.3. Protein

The content of proteins in triticale grains is highly variable (8.6%–16.3%) as affected by genotypes, environments and agronomic practices (Dennett et al., 2013; Fraś et al., 2016; Jonnala et al., 2010b; Langó et al., 2017; Pattison et al., 2014; Rakha et al., 2011; Sirat et al., 2022; Tohver et al., 2005; Watanabe et al., 2019). Breeding efforts for the improvement of yield and grain morphology resulted in an increase of starch content in modern triticale cultivars, at the expense of proteins, in comparison with early genotypes. A large part of triticale proteins is contained in the outer aleurone layer and pericarp, therefore removed by the milling process. The endosperm contains three distinct protein fractions: albumins/globulins, gliadins and glutenins. Albumins and globulins, referred to as non-gluten forming proteins, are represented by enzymes and physiologically active proteins. Gliadins are classified as α/β-, γ- and ω-gliadins whereas glutenins include High Molecular Weight Glutenin Subunits (HMW-GS) and Low Molecular Weight Glutenin Subunits (LMW-GS). HMW-GS can be further classified in x-type subunits and y-type subunits based on the number of cysteine residues. They are known as gluten forming protein and represent the main storage proteins. Triticale also contains secalin subunits (HMW-SS and LMW-SS) that act as glutenins and are encoded by genes located on R chromosomes. The term 'secaloglutenin' referred to the polymeric storage proteins of triticale; HMW- and LMW-GS encoded by 1A and 1B chromosomes of wheat, HMW-, LMW-SS and 75K γ-secalin encoded by 1R and 2R chromosome, respectively (Pattison et al., 2014). In general, triticale grains have a protein content similar or slightly higher than wheat and lower than rye, an amino acid composition very close to wheat but with higher amount of lysine although it remains the limiting amino acid. Different authors reported higher amounts of albumins and globulins in triticale than wheat (Jonnala et al., 2010a; Pruska-Kędzior et al., 2017). Navarro-Contreras et al. (2014) quantified different protein fractions in complete and substituted triticales finding higher values of albumins and globulins in triticale cultivars (42.7% and 24.2%, respectively) compared to both wheat (30.1% and 16.2%) and rye (11.3% and 8.2%), and lower values of glutenin and secalins in both complete (9.3%) and substituted (7.1%) genotypes. Complete triticales are characterized by higher number of albumins but lower polymeric proteins than the substituted ones, likely due to the absence of the D-genome chromosomes. The lower content of gluten proteins accounts for the lower proportion of protein in the endosperm compared to wheat (Fraś et al., 2016; Pattison et al., 2014). Flour protein content and quality are reliable predictors of the end-use aptitude. Narrow genetic diversity and the lack of selection pressure for protein content and high-quality alleles constrain gluten strength of modern triticale varieties.

3.1.4. Lipids, vitamins and micronutrients

The content of lipids and total polyphenols of triticale is on average similar compared to wheat, whereas ash is present in higher amounts (Aprodu and Banu, 2017). Lipids are abundant in the germ of triticale, therefore their content decreases after milling as well as mineral content mostly present in the bran. The lipid content reported in literature ranged from 0.8 to 1.9% after milling (Fraś et al., 2016; Langó et al., 2017; Watanabe et al., 2019). The level of polyphenols in triticale (65–250 mg/100g) is similar to that reported in wheat or slightly higher, but still lower than rye (Aprodu and Banu, 2017; Fraś et al., 2016; Jonnala et al., 2010b). The polyphenols are found mostly in the bound form with lignin and polysaccharides (89%–98%) and are primarily

located in the bran. Ferulic acid is the predominant phenolic acid found in triticale, accounting for about 90% of the total polyphenols and its content in triticale bran is higher with respect to rye and wheat bran. The average content of total polyphenols and in particular the higher content of ferulic acid, along with a larger proportion of IDF, determine superior antioxidant properties of triticale wholemeal flour compared to wheat (Aprodu and Banu, 2017). The ash content is on average higher in triticale than wheat (1.2–2.3%), in both grain and flour (Fraś et al., 2016; Langó et al., 2017; Sirat et al., 2022; Watanabe et al., 2019). In general, the vitamin and mineral content of triticale refined flour is similar to that of wheat or slightly lower but almost twice that of rye (Agil and Hosseinian, 2014). Interestingly, vitamin E content is higher in triticale than wheat and triticale absorbs much more selenium from soil than wheat. Although these substances represent the smallest portion of seed constituents, they have a high nutritional value and affect the end use quality of triticale flours.

3.2. Parameters affecting technological and rheological properties

Triticale flour and dough are characterized by inferior technological and rheological properties compared to wheat, although wide variations in rheological properties of triticale varieties are reported.

In fact, Farinograph, Mixograph and Alveograph tests showed lower rheological proprieties of triticale dough compared to wheat dough (Aprodu and Banu, 2017; Navarro-Contreras et al., 2014; Pruska-Kędzior et al., 2017; Salmanowicz et al., 2013).

Slight differences in the chemical composition of flour between triticale and wheat, as substantially described before for protein, starch and fiber, strongly impact some parameters essential for the production of high-quality dough. Triticale flour shows low falling number, high water absorption, low milling yield and SDS-sedimentation values. Milling yield is a drawback in triticale use for food production. Dennett and Trethowan (2013) reported a decrease in the milling yield of triticale between 7.1% and 10.1% compared to wheat and a negative correlation with tempering moisture. The moisture content can affect viscoelastic behavior and flour yield; the optimal moisture content for conditioning should be deeply evaluated in triticale because the chemical composition of grains influencing biophysical properties differ among triticale, wheat and rye (Escalante-Aburto et al., 2023). Grain hardness plays a predominant role in milling yield, which is also negatively affected by grain morphology defects, ash content, late maturity amylase and grain composition (Jonnala et al., 2010a, 2010b; Pasha et al., 2010). The water absorption capacity is an important parameter of flour end-use quality because it determines baking absorption, dough strength and therefore it is highly correlated with the quality of baked foods. Chavoushi et al. (2022) reported water absorption values for triticale flours ranged from 60.1% to 87.5%, whose mean is higher than bread wheat but lower compared to rye and durum wheat, which could be explained by higher protein and dietary fiber contents.

Triticale dough shows high viscosity, low elongation and flexibility, low mixing parameters, shorter development time, reduced dough strength, a greater degree of dough softening, and inferior loaf volume compared to wheat. Development and stability times of doughs obtained from triticale flours are dramatically shorter compared to those of wheat, and dough weakening much higher. Interestingly, substituted types show longer dough development time than complete types (Chavoushi et al., 2022). This finding suggests that triticale possesses weak gluten that determines low tolerance value to the mixing action resulting in limited plasticity of dough (Aprodu and Banu, 2017; Navarro-Contreras et al., 2014; Pruska-Kędzior et al., 2017; Salmanowicz et al., 2013).

The ash content mostly influences the color of milling products (brightness, redness and yellowness values) (Aprodu and Banu, 2017). Triticale flour, especially whole meal flour, has a higher content of ash causing darker color of end products than wheat.

In general, substituted types perform better than complete types in bread-making tests, mostly due to contribution of D-genome that led to an increase of total polymeric protein. Because triticale does not make dough with acceptable quality on its own, it is often blended with other cereals to produce foods such as bread and pasta (Aprodu et al., 2019; Fraś et al., 2018, 2021; Kaszuba et al., 2021; Tohver et al., 2000). The poor technological properties along with the soft kernel texture, make triticale more suitable for the production of biscuits and cakes than bread or leavened products.

3.2.1. Gluten

Many flour properties are highly correlated with protein content and quality. After milling triticale retains a lower content of protein compared to wheat due to the high amount of proteins in the aleurone layer and pericarp. Although triticale grain protein amount is higher than wheat, the gluten content is lower and of poor quality. In triticale gluten is weak, and its content is generally lower than bread wheat, resulting in lower gluten index, SDS-sedimentation value and reduced mixing time (Erekul and Kohn, 2006; Pattison et al., 2014; Salmanowicz et al., 2013; Watanabe et al., 2019). Triticale gluten is composed of HMW and LMW proteins derived from both wheat and rye and small quantities of gliadins. Not only the quantity of proteins, especially gluten proteins, influences the rheological and technological value of doughs but also the quality determined by the allelic composition of gliadins and glutenins (Salmanowicz et al., 2013). Glutenins encoded on 1A and 1B chromosomes seem to contribute much more to the gluten quality than those encoded on 1R. The strongest effect is given by HMW of the 1B chromosome, especially by 7 + 8 and 6 + 8 subunits. Some authors have found that the different HMW-GS/SS and LMW-GS/SS combinations among triticale genotypes determine substantial changes in baking quality. The HMW subunits 2*, encoded on the 1A chromosome, and subunits 7 + 26 or 7 + 19 of the 1B chromosome represent the best combination of alleles in triticale, reported by Tohver et al. (2005). No positive effect has been attributed to glutenins encoded by 1R loci. Other proteins become part of the gluten matrix and contribute to a lesser extent to the visco-elastic properties, especially LMW-GS/SS accounting from 20% to 60% of total gluten proteins, and a small part of gliadins, especially α/β- and γ- (Pruska-Kędzior et al., 2017). Triticale grains contain a greater proportion of ω-gliadins in comparison with the α/β-gliadins that do not participate in the formation of the gluten polymer (Salmanowicz and Nowak, 2009).

The inferior rheological properties of triticale doughs are often attributed to HMW- and LMW-SS. In addition, the absence of HMW- and LMW-GS encoded by genes at the D-genome loci severely affect the formation of strong gluten network. It has already been proven that the introgression of *HMW-GS* genes from 1D chromosomes improves bread-making quality. The introgression of *1D* loci encoding HMW and LMW results in a significant and positive effect on dough characteristics. Salmanowicz et al. (2013) showed an increase in protein and gluten content, sedimentation value and water absorption capacity in hexaploid triticale lines containing the A^m genome from *Triticum monococcum* ssp. *monococcum* and a 1D(1A) chromosome substitution. The rheological properties were also affected, in particular dough extensibility and degree of softening, showing an appreciable increase in dough-mixing properties. The increase of those parameters is mainly due to the increase of polymeric protein amounts and to the positive effect on gluten polymer of HMW-GS encoded by 1D (specifically 5 + 10 subunits) and by $1A^m$ chromosomes. A series of cytogenetically engineered 1R chromosomes carrying gluten loci from bread wheat 1D chromosome and without HMW-GS, γ- and ω-gliadin loci from 1R were produced by Lukaszewski (2006) and analyzed for their end-use quality (Martinek et al., 2008). Presto is considered a good bread making triticale variety because it carries glutenin alleles from wheat (2*/7 + 26) with a positive effect on bread making quality (Tohver et al., 2005) and therefore was used to introduce the new engineered 1R chromosomes. Presto translocation lines showed improved quality traits such as higher SDS sedimentation value, gluten index and water absorption, along with

an increase in the dough development time and stability and a substantial improvement of the degree of dough softening. Jonnala et al. (2010b) used Presto translocation lines (Lukaszewski, 2006) to transfer translocated segments in three different triticale genotypes and evaluate the effect of those translocations on bread-making quality of derived doughs. They produced three sets of HMW combinations in each genotype introducing 1R.1D and 1A.1D translocations, in which the D chromosome segment carried the HMW subunits 2 + 12 or 5 + 10. The lines containing the 1A.1D translocation with 5 + 10 subunits showed the highest values of UPP (unextractable polymeric protein directly correlated with glutenin content), extensibility and mixograph dough development time among triticale translocation lines and a lower gliadin/glutenin ratio resulting in greater strength of dough. In wheat 2 + 12 subunits are associated with poor bread-making quality, whereas their introduction in triticale increases gluten strength and elasticity, even though to a lesser extent in comparison with 5 + 10 subunits. This type of translocation or other types affecting 'secaloglutenin' composition might be exploited to improve poor quality parameters of triticale dough, but they require further investigations to overcome the decline in agronomic performance traits caused by such translocations.

3.2.2. Kernel texture

Kernel texture is an important factor affecting end-use quality of flours and is used for the classification of wheat in relation to the intended use of end-products. Proteins originally named 'friabilins' determine the hardness degree of the grain endosperm (Morris, 2002). These proteins are associated with starch granules and prevent the formation of complexes between granules and gluten proteins (Pasha et al., 2010; Quayson et al., 2018). Puroindoline a (PINA) and puroindoline b (PINB) are the major friabilin proteins found in wheat, that act together in the determination of grain hardness. Puroindolines in triticale are known as secaloindolines (SINA and SINB) as they are encoded by the R genome. Ramirez et al. (2003) found friabilin proteins on starch granules in all eight triticale lines investigated with varying degree of hardness. Li et al. (2006) have shown a clear difference in starch-associated friabilin between hard and soft secondary hexaploid triticale lines indicating that friabilin is directly involved in the formation of grain texture. Otherwise, not all the secaloindolines are associated with starch granules and participate in determining grain hardness. Therefore, significant changes in grain hardness are associated with the secaloindolines ability of forming complexes with starch, polar lipids and other proteins rather than their total amount (Li et al., 2006; Salmanowicz, 2010). Most of the bread wheats are defined as soft, but when at least one of the PIN proteins is absent or mutated the texture of the endosperm is hard (Bhave and Morris, 2008). On the contrary, durum genotypes are defined as very hard because they do not contain puroindolines. The larger part of triticale cultivars is soft in texture mostly due to the presence of secaloindolines encoded by R genome of rye (Li et al., 2006; Liu et al., 2017).

Kernel texture mainly influences water absorption, milling yield, and milling quality, determining flour particle size and damaged starch proportion. Low milling yields are mostly caused by the extra soft kernel texture of triticale grains. Many other factors, such as protein content, polar lipids on starch granules, different types of pentosans and lipoxygenase activity may influence grain texture. Furthermore, lipid transfer proteins and α-amylase inhibitors show structural characteristics similar to puroindoline-like proteins, suggesting a potential involvement in determining grain hardness through the interaction with PIN/SIN proteins and the other seed storage proteins, as well as with starch granules (Gasparis et al., 2017; Li et al., 2006).

3.2.3. Starch, fiber and ash

Starch composition, in terms of molecular weights, amylose content, particle size distribution, and thermal and pasting properties affect rheological properties of dough. Starches with higher molecular mass require higher temperatures for gelatinization causing changes in viscoelastic properties. The distribution of A- and B-type granules affect pasting values measured by RVA (Makowska et al., 2014). Triticale exhibits a greater proportion of large A-type granules that decrease water adsorption leading to less elastic and cohesive doughs. Milling causes high levels of damaged starch, that increase the water absorption capacity of flours and produce substantial changes in the viscosity of paste. Damaged starch is more easily hydrolyzed by α-amylase and therefore decreases the water retention capacity, negatively altering dough extensibility and development time (Aprodu and Banu, 2017; Chavoushi et al., 2022; Makowska et al., 2014). The starch composition in terms of amylose/amylopectin ratio also contributes to the technological properties, affecting retro-gradation rate, volume and porosity of dough.

The higher levels of fiber in triticale whole meal and refined flours than wheat increase the water absorption capacity. Furthermore, non-starch polysaccharides, especially arabinoxylans, connect to gluten polymers enhancing water retention capacity, viscosity of dough and therefore leading to superior rheological properties and the slowdown of the processes of products staling (Langó et al., 2018b). High ash content in flour is negatively associated with milling yield or can indicate bran contamination of flour, which leads to darker color dough.

3.2.4. Late maturity α-amylase and pre-harvest sprouting

High levels of α-amylase during the grain ripening stage, responsible for starch degradation, may induce grain quality defects, namely late maturity amylase (LMA) and pre-harvest sprouting (PHS). Amylases are synthesized in the scutellum, firstly, and later in the aleurone layer, when the germination is initiated as a result of imbibition of seeds with water, and finally transported into the endosperm for degrading of polysaccharides, providing energy for embryo development (Mares and Mrva, 2014). PHS causes the germination of grains while they are still on the spike, in the absence of water imbibition, whereas LMA is due to the synthesis of α-amylase during the final ripening stages of grain development, that may result in high enzymatic activity during kneading. Both PHS and LMA are correlated with low Hagberg falling number (FN), which is considered an indicator of the amount of sprout damage caused by enzyme activity (α-amylase). α-amylases cause a reduction in the viscosity of dough due to the digestion of the starch during the kneading. Methods for determining pasting properties of starch viscosity tests (Rapid Visco Analyzer, Alveograh, Mixograph) are also used for the determination of α-amylase activity. The decrease of the viscosity, as determined by low FN, is caused by α-amylase activity impacting on the functional properties of starch. Maximum viscosity of triticales refined flours, reported by Navarro-Contreras et al. (2014), was drastically reduced compared to wheat and rye flour. High quality wheat possesses FN values between 250 and 350, whereas too low of values indicate poor end-use quality correlated with a reduction of loaf height, volume and texture and sometimes determine the declassification from bread wheat to wheat for other uses, mostly for animal feed. Following the same rating scale, triticale flour shows too low values to be classified as bread making flour.

The range of FN in triticale is quite broad but on average less than half of wheat (Dennett and Trethowan, 2013; Erekul and Kohn, 2006; Salmanowicz et al., 2013; Watanabe et al., 2019). Low FN is common in both rye and triticale (Mares and Mrva, 2014). Several factors, in addition to α-amylase activity, can affect FN, especially impacting on the viscosity of the dough. Dennett et al. (2009) found a correlation between fiber content and FN in triticale. The action of enzymes that degrade dietary fiber can have a role in the reduction of viscosity. Also, the polymeric to monomeric gluten protein ratio impact on the firmness of the dough and can influence FN (Chavoushi et al., 2022). For these reasons FN in triticale should not be used in the same way as wheat.

Most likely, wheat genotypes with reduced α-amylase activity were selected unconsciously in wheat through breeding selection for dwarf stature, because QTLs associated with LMA are co-located with some *Rht* genes encoding DELLA proteins which inhibit downstream signaling of

gibberellin and reduce LMA expression. Even if the mechanisms involving gibberellins in the activation of α-amylases is still not well understood, this explains the high α-amylase content in triticale probably due to a poor breeding selection for those characters (Cannon et al., 2022; Derkx et al., 2021).

3.3. Genetic control of grain quality

3.3.1. Starch and dietary fiber

The starch biosynthesis pathway is highly conserved among cereal species. ADP-glucose pyrophosphorylase (AGPase) is the first enzyme acting in the starch biosynthesis pathway, producing ADP-glucose. Starch synthase (SS) enzymes catalyze the polymerization of glucose units from ADP-glucose onto a preexisting glucan chain. In the endosperm, amylose is synthesized by granule bond starch synthase I (GBSS-I), encoded by the *Waxy* (*Wx*) genes, through α-(1,4) linkages, whereas amylopectin is synthesized by four SS isoforms, namely SS-I, SS-II, SS-III and SS-IV. Starch-branching enzymes (SBE) and starch-debranching enzymes (DBE) also participate in the synthesis of amylopectin; two SBEs isoforms exist in cereals (SBE-I, SBEIIa and SBEIIb), which are responsible for the branched structure generating α- (1,6) linkages, and two starch DBEs, isoamylase and pullulanase, hydrolyze α- (1,6) glycosidic linkages, removing branches formed at improper positions (Huang et al., 2021). In wheat, *Wx* genes are located on the short arm of the chromosomes 7A (*Wx-A1* locus), 7D (*Wx-D1* locus), and on the long arm of the chromosome 4A (*Wx-B1* locus). Three homologous *SSII* genes are located on the short arm of the chromosome group 7 (Huang et al., 2021). In hexaploid triticales gene *loci* located on A and B genomes are present along with rye orthologs.

Li et al. (2010) studied the spatio-temporal pattern of starch synthesis and accumulation during kernel development of triticale. At the early stages (3–15 dpa), starch accumulates in the pericarp layer, then from 6 to 9 dpa until maturity the endosperm becomes the main storage tissue of starch granules, reaching the maximum synthesis accumulation rates between 15 and 21 dpa. Carbohydrate synthesis and accumulation start at the early stage of kernel development, increasing rapidly to the medium stage and decreasing slightly at the later stages. Cornejo-Ramírez et al. (2016) compared starch synthesis in substituted and complete triticales. Complete triticales contained a higher amount of starch at the end of the kernel development compared to substituted genotypes, but the latter accumulated more starch faster than complete types during early stages of development. High temperatures during kernel development negatively impact the starch synthesis and accumulation. Probably, the more tolerant complete triticales accumulate greater amounts of starch than the less tolerant substituted types, in which one or more R chromosomes were replaced. No more specific genetic investigation has been done to study the behavior of triticale in starch synthesis and accumulation that may result from the interaction of two different chromosome sets from wheat and rye.

The synthesis of non-starch polysaccharides or dietary fiber in triticale is more complex and even less investigated. Recent advances have been made in wheat and rye regarding genes encoding enzymes involved in the synthesis of dietary fiber, especially arabinoxylans and α-glucans (Kozlova et al., 2022). Large gene families control the synthesis of these polysaccharides encoding glycosyltransferase (GT), cellulose synthase (Ces) and cellulose-synthase-like enzymes (Csl). Kozlova et al. (2022) identified *GT*, *Ces* and *Csl* genes in rye distributed on several chromosomes, mostly located on chromosomes of groups 2, 5 and 6. In triticale, the substitution of chromosomes 5R and 6R with 5D and 6D resulted in a reduction of soluble dietary fibre amount (Boros et al., 2002). The synthesis of polysaccharides is controlled by gene super families and therefore, they need to be deeply investigated to elucidate those mechanisms that could be controlled by the breeders in order to regulate carbohydrates and dietary fibre content.

3.3.2. Glutenin

The main constituents of endosperm proteins in wheat, the storage proteins gliadins and glutenin, are encoded by genes at *Gli* and *Glu* loci of 1A, 1B, 1D, 6A, 6B and 6D chromosomes. In rye, gliadins and glutenin orthologs are located on chromosomes 1R and 2R. The hexaploid triticale encodes three sets of HMW-GS/SS from 1A, 1B and 1R chromosome, two sets of LMW-GS/SS from 1A to 1B chromosomes and 75 γ-secalin from the 2R chromosome. Secalins are encoded by genes located at four chromosomal loci on 1R and 2R chromosomes (Li et al., 2021). *Sec-1* locus, also known as *Gli-R1,* located on the long arm of chromosome 1R, contains two clusters of genes encoding γ- and ω-secalins. *Sec-2*, also known as *Gli-R2*, located on the short arm of chromosome 2R, contains three genes encoding 75K γ-secalins, whose orthologs are not known in wheat. *Sec-3,* also known as *Glu-R1,* located on the short arm of chromosome 1R, contains two genes encoding one y- and one x-type HMW-SS (HMW-1Rx and HMW-1Ry). *Sec-4,* also known as *Gli-R3*, mapped between *Glu-R1* and *Gli-R1 loci,* has two genes encoding for γ- and ω-secalins (Igrejas et al., 1999). No orthologs of the wheat *LMW* and *α-gliadins* genes were found in rye chromosomes so far (Li et al., 2021).

Genetic variability at *Glu-1*, *Gli-2* and *Gli-1/Glu-3* loci in triticale cultivars around the world were reported (Amiour et al., 2002a, 2002b; Kozub et al., 2007; Makarska et al., 2008; Salmanowicz and Nowak, 2009; Vyhnánek et al., 2013) (Table 2). Pattison et al. (2014) reported a reduced variability in HMW subunits profiles of different Australian triticale cultivars. The most common alleles at *Glu-B1* and *Glu-R1* loci were *Glu-B1f* (13 + 16) and *Glu-R1c* ($6^r + 13^r$ subunits), respectively. On the other hand, Amiour et al. (2002b) investigated allelic variability at *Glu-1, Glu-3* and *Gli-R2* loci finding 40 different alleles in 134 cultivars grown in Europe (Table 2). In a complementary study, they analyzed about one thousand triticale seeds derived from ten crosses by SDS-page and observed high polymorphism of storage proteins in hexaploid triticale. The most frequent allele at the *Glu-B1* locus was *Glu-B1b* (encoding subunits 7 + 8), at the *Glu-R1* locus were *Glu-R1a* and *Glu-R1c* and at the *Glu-A1* was *Glu-A1b* (encoding subunit 2*). Furthermore, four alleles at the *Gli-R2* locus, five allelic forms of LMW-subunits at *Glu-A3* locus and seven at *Glu-B3* locus were observed. Salmanowicz and Dylewicz (2007) identified 11 *Glu-1* alleles in 46 Polish cultivars, in particular three alleles at *Glu-A1* and eight alleles at *Glu-B1*. Vyhnánek et al. (2013) identified, in 15 triticale 1R.1D substituted genotypes, three and five alleles at *Glu-A1* and *Glu-B1* loci, respectively. These results indicate a high polymorphism at glutenin loci on 1B chromosome followed by the *Glu-R1* locus. The *Glu-A1* locus showed only three allelic variants, as reported in wheat.

Allelic variation at *Glu-1* and *Sec-3* loci strongly determines bread making quality, defining gluten strength and dough elasticity. In particular, the *Sec-1* locus on the 1R short arm negatively affects end-use quality. Therefore, triticale substituted types with the introgression of glutenin loci from 1D chromosome and with the elimination of secalin loci were produced with the aim to improve end-use quality (Budak et al., 2004; Jonnala et al., 2010b; Rabiza-Swider et al., 2010; Salmanowicz et al., 2013). Lukaszewski and Curtis (1992, 1994) cytogenetically engineered 1R chromosome to remove *Sec-1* and *Sec-3* loci and to introduce *Glu-D1* and *Gli-D1/Glu-D3* loci; The *Glu-D1d* allele (5 + 10 subunits) was introduced on the long arm of 1R, replacing *Sec-3*, and encodes HMW-GS 5 + 10. The *Gli-D1/Glu-D3* locus replaced the *Sec-1* locus on the 1R short arm and encoded LMW-GS. Later, three classes of translocation chromosomes were generated in the cultivar Presto and named Valdy, FC and RM (Lukaszewski, 2003). All those chromosomes maintain the *Sec-2* locus on 2R chromosome, encoding 75K γ-secalins. The same types of translocations were also produced on chromosome 1A in cultivar Presto. Rabiza-Swider et al. (2010) introduced translocated chromosomes from Presto (Valdy, FC and RM) to a range of hexaploid triticale cultivars, to determine their transmission rate. Triticale with high gluten strength may be obtained both introducing genes from relatives and other species or selecting parents with high quality gluten alleles.

Table 2
Allelic composition of major glutenin (*Glu-A1*, *Glu-B1*, *Glu-R1*, *Glu-D1*, *Glu-A3*, *Glu-B3*) and gliadin (*Gli-A1*, *Gli-B1*, *Gli-R2*) loci reported in literature.

Locus	Type	Allele	Subunits	References
Glu-A1	HMW	a	1	Amiour, Bouguennec et al., 2002;
		b	2*	Amiour, Dardevet et al., 2002; Ewa
		c	null	Makarska et al., 2008; Igrejas et al. (1999); Kozub et al. (2007); Salmanowicz and Dylewicz (2007); Tohver et al. (2005); Vyhnánek et al. (2013)
			2 + 12 (D)	Jonnala et al. (2010b)
			5 + 10 (D)	
			5.2m + 14m (A^m)	Salmanowicz et al. (2013)
			2 + 12	Jonnala et al. (2010b); Lafferty and
			5 + 10	Lelley (2001)
Glu-B1	HMW	a	7	Pattison et al. (2014); Amiour, Bouguennec et al., 2002; Amiour, Dardevet et al., 2002
		b	7 + 8	Pattison et al. (2014); Igrejas et al. (1999); Amiour, Bouguennec et al., 2002; Amiour, Dardevet et al., 2002; Makarska et al. (2008); Kozub et al. (2007); Jonnala et al. (2010b)
		c	7 + 9	Pattison et al. (2014); Makarska et al. (2008); Amiour, Dardevet et al., 2002
		d	6 + 8	Tohver et al. (2005); Igrejas et al. (1999); Amiour, Bouguennec et al., 2002; Amiour, Dardevet et al., 2002; Makarska et al. (2008)
		e	20	Amiour, Bouguennec et al., 2002
		f	13 + 16	Pattison et al. (2014); Tohver et al. (2005); Igrejas et al. (1999); Amiour, Bouguennec et al., 2002; Amiour, Dardevet et al., 2002; Jonnala et al. (2010b); Kozub et al. (2007)
		p	23 + 18	Pattison et al. (2014); Igrejas et al. (1999); Amiour et al., 2002
		av/r	7 + 18	Pattison et al. (2014); Amiour, Bouguennec et al., 2002; Amiour, Dardevet et al., 2002
			7 + 19	Tohver et al. (2005)
			7 + 26	Tohver et al. (2005); Makarska et al. (2008)
		ac	6.8	Igrejas et al. (1999)
		s	6.8 + 20	Amiour, Bouguennec et al., 2002; Amiour, Dardevet et al., 2002
			6.8 + 20*	Salmanowicz et al. (2013)
			6 + 8* (6 + 8)	Salmanowicz et al., 2007
		al	7 + 8*	Salmanowicz et al., 2007; Vyhnánek
		ak	7* +8*(7 + 8)	et al., 2013
		as	7 + 18*	
		aw	7 + 20	Samanowicz et al., 2007
		az	7 + 20*	Salmanowicz et al., 2007; Vyhnánek et al., 2013
		u	7* +8	Salmanowicz et al., 2007
			7 + 25	Makarska et al. (2008)
			6 + 7 + 8	
		p/IV	23 + 18	Amiour, Bouguennec et al., 2002
			2 + 12	Lafferty and Lelley (2001)
			5 + 10	
Glu-R1 (Sec-3)	HMW	c	$6^r + 13^r$	Pattison et al. (2014); Igrejas et al. (1999); Amiour et al., 2002
		d	$2^r + 9^r$	Amiour, Bouguennec et al., 2002; Amiour, Dardevet et al., 2002
		a	$1^r + 4^r$	Amiour, Dardevet et al., 2002
			6^r	Igrejas et al. (1999)
		e	6.5^r	Igrejas et al. (1999); Amiour, Bouguennec et al., 2002; Amiour, Dardevet et al., 2002
		b	$2^r + 6.5^r$	Amiour, Bouguennec et al., 2002; Amiour, Dardevet et al., 2002
		g	5.8^r	Pattison et al. (2014)
			$2^r + 5.3^r$	Salmanowicz et al. (2013)
		f	$0.8^r + 6^r$	Amiour, Bouguennec et al., 2002
			2 + 12 (D)	Lafferty and Lelley (2001)
			5 + 10 (D)	Lafferty and Lelley (2001); Jonnala et al. (2010b)
Glu-D1	HMW	d	5 + 10	Pattison et al. (2014); Salmanowicz et al. (2013); Vyhnánek et al., 2013
		a	2 + 12	Lafferty and Lelley (2001)
Gli-R2 (Sec-2)	75K γ-sec	a	d1	Pattison et al. (2014); Igrejas et al. (1999); Amiour et al., 2002, 2002b
		d	null	Igrejas et al. (1999); Amiour et al., 2002; Pattison et al. (2014)
		b	d2	Amiour, Bouguennec et al., 2002; Amiour, Dardevet et al., 2002
		e	t2	Amiour, Bouguennec et al., 2002
		c	t1	Pattison et al. (2014); Igrejas et al. (1999); Amiour et al., 2002, 2002b
Glu-A3	LMW	a		Amiour, Bouguennec et al., 2002; Amiour, Dardevet et al., 2002; Igrejas et al. (1999)
		d		Amiour, Bouguennec et al., 2002
		d'		
		e		
		f		
		h	null	Igrejas et al. (1999)
Glu-B3	LMW	b		Amiour, Bouguennec et al., 2002;
		b'		Amiour, Dardevet et al., 2002; Igrejas et al. (1999);
		d		Amiour, Bouguennec et al., 2002;
		h		Amiour, Dardevet et al., 2002
		h'		Amiour, Bouguennec et al., 2002
		i		Amiour, Bouguennec et al., 2002;
		i'		Amiour, Dardevet et al., 2002
		j		
		k		
Gli-A1	γ-, ω-	p		Kozub et al. (2007)
		a		
		c		Igrejas et al. (1999)
		e		
		o		Kozub et al. (2007)
Gli-B1	γ-, ω-	d		
		d		Igrejas et al. (1999)
		h		Kozub et al. (2007)

3.3.3. Secaloindolines

The genetic control of grain texture in wheat is mainly attributed to two (isoforms) puroindoline genes, *Pina* and *Pinb* that are located at the *Hardness locus* (*Ha*) on chromosome 5D in bread wheat, and therefore absent in tetraploid wheat. (Bhave and Morris, 2008). *Puroindoline-like* genes were identified in rye on chromosome 5R and referred to as *secaloindoline* (*Sina* and *Sinb*). Triticale grains have generally soft kernel texture although a range of variance was found among triticale genotypes. In particular, primary triticale mostly shows soft texture and secondary or substituted types have a wider range of hardness (Salmanowicz, 2010). Li et al. (2006) found two *Sina* allele and three *Sinb* allele (Table 3) in 171 hexaploid triticale genotypes from CIMMYT showing a broad variation for grain hardness. Liu et al. (2017) analyzed 60 primary hexaploid and octoploid triticales from CIMMYT for kernel hardness and identified the allelic variance of *Sin* genes at a molecular level (Table 3); Eight allelic combinations of *Sin* alleles were identified (Table 3). Recently, new *Sina* and *Sinb* alleles were identified in hexaploid triticales from Czech Republic, but their effect on grain hardness was not evaluated (Kselíková et al., 2020). To date, further investigations are required to define an association between specific *Sin* alleles and variance of grain hardness in triticale.

Not all the mutations affecting *Sin* genes determine changes in grain texture. Other factors can play a role in the determination of the

Table 3
Sina and *Sinb* alleles reported in literature.

Locus	Allele	References
Sina-R1	a	Gasparis et al. (2013); Li et al. (2006); Liu et al. (2017)
	b	Li et al., 2006
	c	
	d	Liu et al. (2017)
	e	
	f	
	h	Kselíková et al. (2020)
Sinb-R1	a	Li et al., 2006
	b	Gasparis et al. (2013); Li et al. (2006); Liu et al. (2017)
	c	Li et al., 2006; Liu et al. (2017)
	d	Liu et al. (2017)
	e	
	f	
	h	Kselíková et al. (2020)

hardness. Li et al. (2006) found hard and soft triticale genotypes with different allele compositions, assuming that specific alleles play different roles in the determination of grain hardness. Interestingly, Nirmal et al. (2016) conducted an RNA-Seq analysis of 33 diverse wheat genotypes with hard and soft grain texture. In conclusion, they supposed that hardness might be associated with differences in the expression of *Pin* and other genes more than mutations in *Pin* coding sequence. They also found some hard genotypes showing the wild-type *Pina* and *Pinb* alleles. In these genotypes the *Pinb* expression level was higher compared to *Pina* level. These findings highlight that PINA and PINB act together and probably PINA stabilize PINB in the formation of starch-associated friabilin. Furthermore, a deep investigation of regulatory sequences at *Sin* loci and the relative gene expression is required to correlate genetic variation to grain hardness because no data were published in this regard so far. No additional genes related to grain hardness have been identified and validated in wheat or triticale so far, but several QTLs, dispersed over multiple chromosomes, have been found to be associated with grain hardness in wheat (Aoun et al., 2021; Boehm, Jr. et al., 2018; Kumar et al., 2019). However, Kiseleva et al. (2020) conducted a genome-wide association study on a panel of Russian wheat varieties and found significant SNPs associated with grain hardness. They found several genes on 5B, 7B, and 7D chromosomes showing a good expression correlation to *Pin* genes. Genes involved in the metabolism of galactolipids and carbohydrates as well as in plant grain defense mechanism were identified. Polar lipids and galactolipids regulate the insertion, structure and orientation of PIN proteins in the lipid layer surrounding the starch-protein matrix. Defensins demonstrate a structure closely related to PIN proteins and a great co-expression with the *Pin* genes. They could be located in the protein-lipid matrix surrounding starch granules of endosperm, along with puroindolines.

In general, genotypes with *null puroindolines* allele might result in hard grain texture thus mutations in *Sin* genes producing gene knockouts could be exploited to induce harder texture in triticale, making it more suitable for baking process. To date no knock-out mutations of *Sin* genes have been found in triticale genotypes.

3.3.4. *LMA*

The synthesis of α-amylase is primarily controlled by the *α-Amylase1* (*α-Amy1*) genes located on the group 6 chromosomes, which specifically encode high pI isoforms (Mares and Mrva, 2014). Recently, Mieog et al. (2017) found a new gene, *Amy-4*, potentially involved in the development of LMA phenotypes. Furthermore, LMA seems to be controlled also by two major QTLs located on chromosomes 3B and 7B, that are independently effective and additive (Derkx et al., 2021). The 7B QTL has been mapped to a single gene, namely *LMA-1*, encoding an ent-copalyl diphosphate synthase, involved in gibberellin biosynthesis. The functional form of this gene leads to LMA phenotypes, whereas loss of function mutations produces LMA-resistant genotypes. Many other factors, besides genetic control, can impact LMA. Environmental factors, such as temperature shocks around 25–30 days post-anthesis, can trigger LMA phenotypes. On the other side, dwarfing genes (*Rht1*, *Rht2*, *Rht3*) confer insensitivity to gibberellin, reducing the expression of LMA. A specific genetic investigation of LMA mechanisms in triticale is still lack.

4. Conclusion

Triticale is regarded as potential food crop for human consumption, but the rheological and technological properties required for the end-use quality are still far from making triticale a suitable cereal for food processing. Due to weak gluten, soft kernel texture and low FN, it is mainly used in food production that does not require high gluten strength and specific visco-elastic properties of dough or not strongly influenced by the enzymatic activity of flour. Besides the use of triticale-wheat blends, acting on the genetic control of the major constituents of the grain, especially starch, protein and dietary fiber, may foster better triticale flour and dough performance. The amount and composition of starch and gluten proteins have a great effect on viscoelastic properties of doughs and therefore can be manipulated to increase pasting behavior and gluten strength. Lower milling yield, particle size and water absorption may be improved controlling secaloindoline genes and other factors involved in kernel texture.

To develop a crop that would be competitive with other cereals, end-use quality is one of the major concerns to be addressed. However, the utilization of triticale flours in food production, even if limited by poor end-use quality, is gained by the nutritional value conferred by a more balanced amino-acid composition and higher content of protein and health promoting compounds compared to wheat, such as dietary fiber and polyphenols. Furthermore, it demonstrates high hardiness therefore would increase the cereal world production, especially under poor and stress growth conditions.

The narrow genetic variability of triticale constitutes an obstacle to the breeding of quality characters. In that respect, the constitution of new hybrids or crossing triticale genotypes with relative species, exploiting primary and secondary gene pools, and the use of gene editing tools are needed to broaden available genetic resources. In the perspective of more sustainable agriculture, the environmental adaptation plasticity of triticale with low inputs and its end-use versatility, could be exploited and improved to face the demand of health benefits foods and the need to growth cereals in marginal lands in order to feed a constantly increasing world population.

Author statement

Francesco Camerlengo: Conceptualization, Investigation, Validation, Writing – original draft. Alecia M. Kiszonas: Validation, Writing – review & editing, Supervision, Resources.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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