

Significance of *Aegilops tauschii* Glutenin Genes on Breadmaking Properties of Wheat

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ABSTRACT

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The contribution of the diploid wild wheat species *Aegilops tauschii* (DD) to breadmaking quality was studied using synthetic hexaploid wheats (AABBDD) derived from a common *Triticum turgidum* var. *durum* (AABB) and three *A. tauschii* parental lines. Prolamin alleles of the *T. durum* and *A. tauschii* parents are additively expressed in the synthetic hexaploids.

Bread loaf volumes (BV) assessed by micro-rapid-mix-test (MRMT) and rheological parameters: gluten index (GI), maximum resistance (RE), SDS-sedimentation (SDSS), dough surface, and other quality characteristics clearly indicate that BV and other breadmaking properties in hexaploids are significantly influenced by glutenin genes of the *A. tauschii* species.

Wheat (*Triticum* spp.) is one of the most important food crops worldwide. Total wheat production in 2000 was approximately 580 million tons (FAO 2000). All cultivated species of wheat belong to the genus *Triticum* which is divided into the groups einkorn, emmer, and dinkel. Einkorn wheats possess a basic diploid chromosome number of $2n = 14$ and contributed the A-genome of *Triticum*. Emmer wheats are allotetraploids (AABB-genome; $2n = 28$), and dinkel wheats (AABBDD) are allohexaploids with a chromosome number of $2n = 42$. The modern bread wheat (*Triticum aestivum* L.) belongs to the dinkel group.

The center of the origin of the *Triticum* species is southwestern Asia. The geographical center of diploid and tetraploid wheats is called the “fertile crescent” extending from the Mediterranean north-eastern coast, southern Anatolia to the Euphrates-Tigris plain. The Asian goatgrass (*Aegilops tauschii* Coss.), a further wild ancestor of bread wheat and donor of the D-genome, is mainly found in an area extending from northeastern Syria, Iran, Iraq, Transcaucasia to the western slopes of the Himalayas into China (Kimber and Feldman 1987; Dvorak et al 1998).

Genetic evidence showed that bread wheat originated by the hybridization of tetraploid *T. turgidum* ssp. *dicoccum* (cultivated emmer) and *A. tauschii* ssp. *strangulata* which occurs in Armenia and the southwestern coastal area of the Caspian Sea (Dvorak et al 1998). For three decades *A. tauschii* has been considered the main contributor to breadmaking properties of common wheat (Kerber et al 1969; Branlard and Dardevet 1985; Dong et al 1991). Due to the D-genome, hexaploid wheat is unique in its ability to form dough with an elastic gluten network that allows the entrapment of carbon dioxide released by yeast during fermentation. The expanding gluten network gives a light porous structure that is fixed by baking. The dough mixing properties of flour and their suitability for breadmaking are largely determined by the quality and quantity of wheat gluten proteins classified into monomer gliadins and polymer glutenins. The gliadins are viscous and provide extensibility, whereas glutenins impart elasticity to a bread dough (Payne 1987). Glutenins are composed of high molecular weight glutenin subunits (HMW-GS) with molecular masses of $\leq 65\text{--}90 \times 10^3$ and of low molecular weight glutenin subunits (LMW-GS) with M_r of $30\text{--}45 \times 10^3$. The strength of gluten was highly correlated with the type and the amount of the HMW-GS present in high M_r polymers (Field et al 1983; Wieser et al 1993).

The HMW-GS are encoded by genes at three loci in the *T. aestivum* genome, *Glu-A1*, *Glu-B1*, and *Glu-D1* located on chromosomes 1A, 1B, and 1D, respectively (Payne et al 1987). Each locus shows allelic variation and the corresponding protein subunits can be separated by SDS-PAGE. More than 20 different high M_r subunits have been characterized. Among these subunits are the so called x- and y- types, according to their electrophoretic mobility and their primary structures; two are encoded at the locus on chromosome 1D and chromosome 1B, respectively, and none or one on chromosome 1A (Shewry and Tatham 1997). Two allelic pairs of 1D subunits occur widely in common wheat cultivars: 1Dx2+1Dy12 and 1Dx5+1Dy10.

Recent genetic studies with near-isogenic lines showed significant associations between *Glu-D1* subunits 1Dx5+1Dy10 with greater gluten viscoelasticity and strong dough characteristics (Popineau et al 1994; Redaelli et al 1997). Also, in U.S. common wheats, the HMW-GS 5+10 at the *Glu-D1* locus had the largest positive effect on dough mixing traits (Dong et al 1991). Most of the Canadian Western Red Spring wheats possess the HMW-GS 5+10 (Bushuk 1998). In Germany, among the 11 bread wheat cultivars belonging to the best baking quality group elite of the National List of Commercial Cultivars (BSA 1999), nine cultivars reveal the HMW-GS 5+10 subunits. This subunit combination has been correlated with good breadmaking quality parameters in commercial bread wheat cultivars grown in Germany (Wieser and Zimmermann 2000), Great Britain (Payne et al 1987), Norway (Uhlen 1990), Syria (MirAli et al 1999), and the United States (Dong et al 1991) indicating the significance of this allele combination at the *Glu-D1* locus.

The influence of *A. tauschii* HMW-GS on breadmaking quality parameters was studied by developing synthetic hexaploid wheat lines (AABBDD, $2n = 6x = 42$) through crosses of the tetraploid *T. turgidum* with diploid *A. tauschii* (Lagudah et al 1987; Peña et al 1995). These studies showed a positive contribution of the newly introduced HMW-GS 5+12 and 5+10 in synthetic hexaploids on certain rheological characteristics. However, the influence of the newly added *Glu-D1* alleles could not be clearly established due to differential contribution of the *Glu-B1* and *Glu-B3* loci from *T. turgidum* (Peña et al 1995).

The present study reports the breadmaking potential of the diploid *A. tauschii* species and demonstrates the significance of its prolamin alleles on quality characteristics of hexaploid derivatives developed from crosses between three *A. tauschii* accessions and a common *T. turgidum* var. *durum* parent.

MATERIALS AND METHODS

Breeding

The diploid *A. tauschii* accessions TD12, TD26, and TD190 were kindly provided by J. Jahier, Le Rheu, France; W. Lange, Wageningen, The Netherlands; and E. R. Kerber, Winnipeg, Canada, respectively. The *T. turgidum* var. *durum* cv. Maroccos 182 was

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obtained from A. Zeven, Wageningen, The Netherlands. The synthetic wheat amphiploids were developed by crossing *T. turgidum* cv. Maroccos 182 with *A. tauschii* accessions TD12, TD26, and TD190, respectively. Embryos of the hybrids were rescued on artificial growth medium according to the method of Kasha (1974). The chromosome complement of the sterile F₁ hybrid was doubled with colchicine following the technique described by Metz et al (1988).

Preliminary seed increase of F₃ to F₅ synthetic hexaploid plants and *A. tauschii* lines were conducted under glasshouse conditions. The *T. turgidum* (TT89) and the synthetic wheat lines XX202, XX227, and XX229 were grown further in a randomized block at Weißenstephan in 1997 under the same conditions.

Cultivar Monopol (MON), a German elite bread wheat, harvest 1998, was used for comparison.

Flour and Gluten Testing

Gliadin analysis was performed on single grain using 70% ethanol extraction and A-PAGE, whereas reduced glutenins were visualized by SDS-PAGE according to the methods described by Jackson et al (1996). HMW-GS were numbered according to Payne and Lawrence (1983), while allele designation of LMW-GS and gliadins followed the nomenclature of Jackson et al (1996).

The kernels were milled to flours with ash contents of 0.55% using a Quadruplex mill (Brabender). Falling numbers were set to 250 sec by addition of malt flour. Flour (10 g, water content 14%), 0.2 g of NaCl, and 5.6 mL of distilled water giving dough consistencies of 500–600 BU were mixed at 22°C in a micro-farinograph (Brabender) with a 10-g sigma-kneader at 60 rpm for 2 min.

To isolate gluten, dough was washed for 5 min with 2% NaCl solution in a Glutomatic instrument (Perten Instruments, Sweden). After centrifugation (22°C, 2,000 × g, 5 min), the amount of wet and freeze-dried gluten was determined gravimetrically.

Extension tests on gluten were conducted according to Kieffer et al (1981). Centrifuged wet gluten was pressed into a Teflon-coated mold and measured after resting for 40 min at 22°C with the SMS/Kieffer Dough and Gluten Extensibility Rig on the texture analyzer TA-XT2 (Stable Micro Systems, Surrey, GB). Maximum resistance (RE) and the extensibility (EX) were measured. Gluten

index (GI) was determined according to the methods described by Perten (1989), and Nilsson and von Koenigsmark (1994). SDS sedimentation test was conducted according to Method 151 (ICC 1994).

The micro-rapid-mix-baking test (MRMT) recipe was 10 g of flour, 0.1 g of D-glucose, 0.2 g of coconut fat, 0.7 g of fresh yeast (Uniform GER), 0.4 mg of L-ascorbic acid, and 5.75 mL of distilled water were mixed for 1 min at 220 rpm, proofed at 30°C for 20 min, rounded and shaped to dough balls, then kept at 30°C and 70–80% rh for a further 40 min. Baking was performed at 240°C for 10 min. For MON, dough was mixed as usual at 1,450 rpm (Kieffer et al 1993, 1998).

Nitrogen contents of flour (FN) and dry gluten (GN) were determined by the Dumas method on the protein/nitrogen analyzer FP-328 (Leco Corp. St. Joseph, MI).

Extension tests were performed two to three times (mean coefficient of variation [CV] = ±5%). Protein content and GI were determined two times (CV = ±3.0%). MRMT was performed one time (CV = ±3.0% with commercial bakery flour).

RESULTS

The *Glu-D1* locus of the *A. tauschii* accessions TD12 and TD190 is characterized by the presence of HMW-GS pair 5+10. The *Aegilops* accession TD26, however, possesses three HMW-GS: 2, T1, and T2 (Table I). The subunit T2 has a higher mobility than subunit 12 of *T. aestivum*, whereas the T1 band occurs as a minor band relative to subunits 2 and T2. The duplex and triplex subunit combinations of the *Glu-D1* locus of the *Aegilops* parents are fully expressed in the synthetic hexaploid wheat lines. The synthetic hexaploid lines XX201 and XX229 derived from the cross between *T. durum* TT89 and the *Aegilops* accessions TD12 and TD190 showed HMW-GS N, 7+8, 5+10 at the *Glu-1* loci. The synthetic hexaploid line XX227, the derivative of TT89 and TD26 possesses HMW-GS N, 7+8, 2+T1+T2. Thus, the synthetic lines XX201 and XX229 are related to good breadmaking quality based on these HMW-GS. The LMW-GS and gliadin alleles of the synthetic hexaploids possess the additive combination of the alleles present in the *T. durum* *Glu-A3/Gli-A1*, *Glu-B3/Gli-B1* loci and

TABLE I
High and Low Molecular Weight Glutenin Subunits and Gliadin Allele Compositions of Synthetic Hexaploids (XX) and Parental (TD, TT) Lines

No.	Accession	Identity	Genome	HMW			LMW			Gliadin		
				<i>Glu-A1</i>	<i>Gli-B1</i>	<i>Glu-D1</i>	<i>Glu-A3</i>	<i>Glu-B3</i>	<i>Glu-D3</i>	<i>Gli-A1</i>	<i>Gli-B1</i>	<i>Gli-D1</i>
1	TD12	<i>A. tauschii</i> 33	DD	5+10	c	d
2	TD26	<i>A. tauschii</i> G	DD	2+T1+T2	a	f
3	TD190	<i>A. tauschii</i> RL5671	DD	5+10	c	d
4	TT89	<i>T. durum</i> Maroccos 182	AABB	N	7+8	...	d	a	...	a	g	...
5	XX201	TT89 × TD12	AABBDD	N	7+8	5+10	d	a	c	a	g	d
6	XX227	TT89 × TD26	AABBDD	N	7+8	2+T1+T2	d	a	a	a	g	f
7	XX229	TT89 × TD190	AABBDD	N	7+8	5+10	d	a	c	a	g	d

TABLE II
Nitrogen Determinations, Yield, and Rheological Properties of Gluten and Baking Quality of Flour from Synthetic Hexaploids (XX) and Parental (TD, TT) Lines

No.	Accession	FN (%)	WG (g) ⁻¹	DG (g) ⁻¹	GN (%)	GI	RE (mN)	EX (mm)	SDSS (mL)	DS	BV (mL) ⁻³
1	TD 12	3.09	5.6	1.84	13.6	53	415	170	76	n	60.9
2	TD 26	3.18	6.0	2.20	10.9	34	75	250	58	s	41.2
3	TD 190	3.24	5.1	2.17	11.7	49	230	154	72	n-s	53.2
4	TT 89	2.72	4.9	1.64	12.6	15	120	140	38	n	41.2
5	XX 201	2.87	5.3	1.72	12.4	51	456	148	81	n	60.2
6	XX 227	3.34	6.1	2.12	11.4	28	86	230	53	s	38.5
7	XX 229	3.38	6.4	2.13	12.9	36	277	190	76	n	58.0
	MON	2.28	3.1	1.05	14.7	95	731	114	...	n	51.6

^a FN = crude flour nitrogen content; WG = wet gluten content in 10 g of flour (14% humidity); DG = dry gluten content in 10 g of flour (14% humidity); GN = dry gluten nitrogen content; GI = gluten index; RE = maximum resistance of gluten; EX = extensibility of gluten; SDSS = SDS sedimentation value; BV = bread loaf volume; DS = dough surface after first dough rest (n = normal dry, s = sticky); BV = bread volume (mL) with 10g of flour

the *Glu-D3/Gli-D1* locus of the respective *Aegilops* parental lines. The synthetic hexaploids XX201 and XX229 possess alleles c and d, while XX227 reveals alleles a and f, transmitted by the diploid *Aegilops* parents at the *Glu-D3* and *Gli-D1* loci, respectively.

The results of protein-nitrogen determinations, gluten extension, and MRMT baking tests are shown in Table II. Due to the limited available quantity of flour, dough farinograms and dough extensigrams according to the ICC methods could not be performed. Because RE of dough and gluten determined by microextensibility tests have been highly correlated to each other and to the baking performance (Kieffer et al 1998), only the gluten and baking results were considered. In accordance with these findings, high correlations can be seen between the products of RE × DG or RE × GN and the BV for the hexaploids and the parental lines ($r^2 = 0.97$ resp 0.96). The following method was adopted to prepare doughs from *Aegilops*, *T. durum* and synthetic hexaploids flour because of the wide range of properties and the limited amount of flour. Water was added to *T. durum* (TT89) flour in the 10-g sigma kneader of the farinograph until the dough consistency was suitable for baking as determined by sensory tests. Water addition was then kept constant for all MRMT. Because the doughs of the flours containing the HMW-GS, 2+T1+T2 in the accession TD26 and its synthetic hexaploid derivative line XX227 were rather sticky, the mixing speed for the MRMT was reduced from 1,450 rpm (Kieffer et al 1993) to 220 rpm so as not to exceed the dough temperature of 26–28°C at the end of mixing.

Table II shows that the values for flour nitrogen (FN), wet (WG), and dry gluten (DG) content are rather high as well for the hexaploids as for the parental lines when compared with normal bread flour like MON, a German elite wheat. The flour of *T. durum* accession TT89 had the lowest FN and the lowest wet and dry gluten

(DG) contents among the parental lines. The gluten extensigram (Fig. 1) showed a convex curve, resembling extensigrams of poor quality wheat flour dough (Kieffer et al 1998). This is a sign of higher plasticity and lower elastic properties compared with wheat gluten of MON. The dough surface after the first dough rest was not sticky or wet. The baking volume was low, the crumb was regular with very fine pores. The shape of the bread was somewhat flat but still normal (Fig. 2).

Flour yields of the *A. tauschii* lines were very low compared with the *durum* and synthetic wheat lines. The FN and GN values of the three *Aegilops* accessions were higher than those of the *T. durum* line. The accessions TD12 and TD190 possessing HMW-GS 5+10 at the *Glu-D1* locus contained elastic gluten of medium and low firmness (RE), respectively, and showed normal to good extensibility (EX) compared to MON and other bread wheat cultivars (Kieffer et al 1998). Baking volumes of both lines were high and the loaf form was good (Fig. 2). The crumb was less fine and less regular than for the *T. durum* line TT89. The dough surface of TD12 was dry and normal, however, that of TD190 was a little bit sticky.

The accession TD26 with HMW-GS 2+T1+T2 showed the poorest gluten quality among the three *Aegilops* lines as seen from the RE and EX values (Table II). The extensigram (Fig. 1) resembled that of poor quality spelt wheat (Buss 1997). The amount of WG was higher than that of TD12 or TD190, but the nitrogen content of the dried gluten was lower. The BV of TD26 was low (44.9 mL), the crumb structure rather compact, and the dough was very sticky and wet.

The flours of the synthetic hexaploid wheats had similar FN, WG, and DG characteristics as their respective *A. tauschii* parents, with the values for XX201 being somewhat lower than for XX227

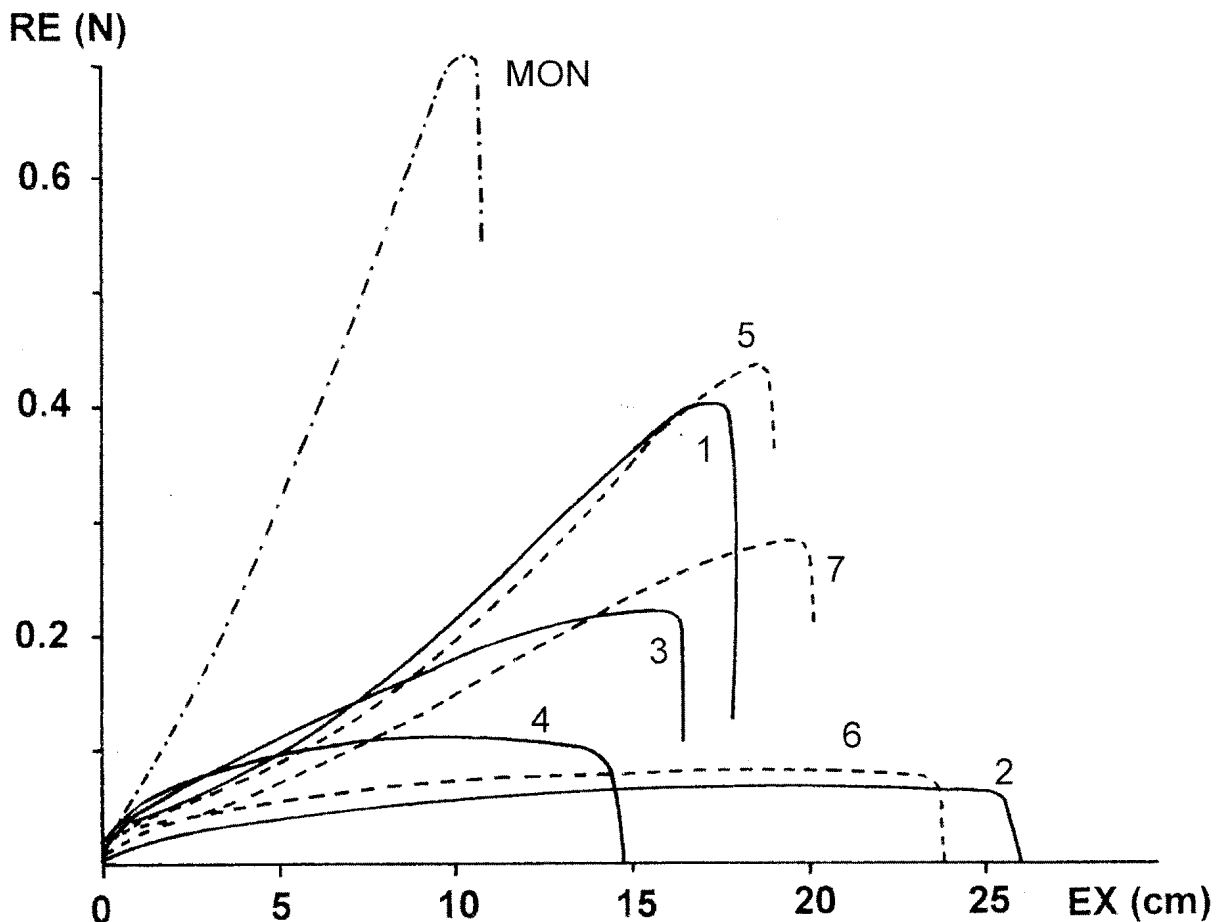


Fig. 1. Microextension tests with hydrated gluten. Solid lines: parental *Aegilops* TD lines TD12 (1), TD26 (2), TD190 (3) and *T. durum* TT89 line (4); dashed lines: synthetic hexaploid wheats XX201 (5), XX227 (6) and XX229 (7); Cultivar Monopol (MON) used for comparison.

and XX229. Furthermore, the extensigrams and baking volumes of the synthetic hexaploids were almost identical with those of the *Aegilops* parents involved in their development (Fig. 1). Compared with MON, the dough of XX227 was sticky and wet, which was similar to the properties observed in the parental line TD26. The crumb was fine and compact.

DISCUSSION

Electrophoretic analysis is being used routinely for early-generation selection in wheat breeding programs worldwide and is being credited with success in quality improvements. In order to increase genetic variation for baking quality, many attempts have been made to introduce new sources of genes from *A. tauschii* since the importance of the *Glu-D1* encoded proteins was established (Lagudah et al 1987; Payne et al 1987; Williams et al 1993). The HMW-GS 5+10 in wheat have long been associated with good baking properties (Payne et al 1987; Wieser and Zimmermann 2000). The effect of these subunits was suggested to be due to their greater capacity to form larger sized polymers (Gupta and MacRitchie 1994). The two *A. tauschii* accessions TD12 and TD190 possessing HMW-GS 5+10 used in the present study indeed revealed positive effects on dough characteristics and breadmaking properties of their synthetic hexaploid derivatives.

The HMW-GS 2+T1+T2 found in the *Aegilops* accession TD26 have been previously reported in *A. tauschii* (Lagudah and Halloran 1988; Williams et al 1993) and in derived synthetic hexaploids (Lagudah et al 1987; Peña et al 1995). The indication that HMW-GS 2+T1+T2 is responsible for dough stickiness and, hence, poor breadmaking properties (Lagudah et al 1987) is confirmed in the present study, which shows that the HMW-GS 2+T1+T2 are associated with poor rheological properties and bread loaf volume.

The contribution of prolamin alleles present at the *Glu-3* and *Gli-1* loci to breadmaking properties are not yet fully understood (Gupta et al 1994; Metakovsky et al 1997). In an analysis of 97 wheat cultivars grown in Germany in 1997, wheat cultivars classified as good baking quality 'A' group possessed the allele *Gli-D1d*, which is present in the *Aegilops* accessions TD12 and TD190. Among the glutenin and gliadin loci, alleles at the *Glu-D1* locus are known to determine breadmaking quality (Payne 1987; Gupta et al

1994). Although a total of 14 alleles has been observed at the *Glu-D1* locus in diploid *A. tauschii* (Lagudah and Halloran 1988), only about half have been reported to occur in common wheat (Payne et al 1987). Hence, *A. tauschii* possessing different combinations of HMW-GS should be investigated for enhancing breadmaking properties of *T. aestivum* cultivars.

The low flour protein content of the *T. durum* parent apparently was not expressed in the synthetic hexaploids. However, from the ranking of the protein contents we see that the *Aegilops* lines influence the protein contents of the derived hexaploids. The same is true for the amount of total dried gluten in flour. The FN and especially the amount of gluten proteins are closely related to the water absorption of flour and therefore to the baking quality (Kieffer et al 1998). However, the quality and composition of gluten may exert the most significant influences as large variations of rheological properties will correspondingly produce different baking results.

The most important findings in the present investigations are the striking parallels between the rheological properties of gluten and the bread volumes of the *A. tauschii* parents and the derived synthetic hexaploid wheat lines. GI and RE of the *Aegilops* parents are almost unchanged in the hexaploid derivatives. Moreover, even the forms of the extensigrams retain their shape, therefore, it can be concluded that even the ratios of viscosity to elasticity remain unchanged. The *Aegilops* parent TD26 transmits very sticky and wet dough surface properties fully to XX227, whereas the somewhat wet properties of dough from TD190 are not observed in the resultant synthetic line XX229. Probably the *T. durum* parent without negative dough properties has some influence on surface properties.

CONCLUSIONS

The present results show that the HMW-GS 5+10, in comparison to HMW-GS 2+T1+T2 determined by the *Glu-D1* gene locus of the wild wheat *A. tauschii*, are responsible for good breadmaking properties. The contribution of diploid *Aegilops* to rheological properties of gluten and bread volumes is expressed in the synthetic hexaploid wheat derivatives. The breadmaking qualities in *T. aestivum* will certainly be improved by the incorporation of new prolamin alleles from the diploid *A. tauschii* species.



Fig. 2. Micro-rapid-mix-test (MRMT) bread loaves (left to right, upper row) XX201 (5); XX227 (6); XX229 (7) and Monopol; (left to right, bottom row) TD12 (1); TD26 (2); TD190 (3) and TT89 (4).

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