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Environment and Genotype Effects on the Content of Dietary Fiber and Its Components in Wheat in the HEALTHGRAIN Diversity Screen†

Kurt Gebruers,*,§ Emmie Dornez,§ Zoltan Bedõ,# Mariann Rakszegi,# Anna Frás,⊥ Danuta Boros,⊥ Christophe M. Courtin,§ and Jan A. Delcour§

§Laboratory of Food Chemistry and Biochemistry and Leuven Food Science and Nutrition Research Centre (LFoRCe), Katholieke Universiteit Leuven, Kasteelpark Arenberg 20, Box 2463, 3001 Leuven, Belgium, #Agricultural Research Institute of the Hungarian Academy of Sciences, P.O. Box 19, 2462 Martonvásár, Hungary, and ⊥Laboratory of Quality Evaluation of Plant Materials, Institute of Plant Breeding and Acclimatization, PL-057870 Radzikow, Poland

Within the HEALTHGRAIN diversity screen, the variability of the contents of dietary fiber (DF) and components thereof was studied in wheat. Furthermore, the contribution of genotype and environment to this variability was estimated. The levels of total DF (TDF), total nonstarch polysaccharide (TOTNSP), water-extractable nonstarch polysaccharide (WENSP), total arabinoxylan (TOTAX), lignin, and β-glucan in whole meal, flour, and/or bran varied ∼1.8-fold. The highest variability was observed for the water-extractable arabinoxylan (WEAX) level in flour and bran (∼3.7-fold). Genotype and environment contributed to a similar extent to the variability in TDF, TOTNSP, and TOTAX content in wheat. The observed relatively high impact of genotype−environment interaction suggests that the levels of these constituents are weak breeding parameters. The WENSP level is a more stable parameter as the effect of the interaction term was much less than the impact of genotype. For TOTAX and WEAX in flour, WEAX in bran, β-glucan in whole meal, and extract viscosity, wheat genotype determined ∼50% or higher of the variation observed, whereas the impact of the genotype−environment interaction was relatively low. These findings suggest that the health-related and technological functionality of wheat can be directed to a certain extent by selection of appropriate wheat varieties.

KEYWORDS: Wheat; dietary fiber; nonstarch polysaccharides; arabinoxylan; β-glucan; lignin; viscosity

INTRODUCTION

Wheat (*Triticum aestivum* L.) is one of the most important cereals cultivated worldwide (*1*) and is responsible for a large part of the calories, nutrients, and dietary fiber (DF) in the Western human diet. DF is one of the most important groups of cereal constituents to which a health-promoting functionality has been ascribed. The definition of DF has been recently revised within the European Union (EU) (*2*). Increased DF consumption may lower the risk of occurrence of a number of bowel diseases (*3*). Insoluble DF particularly lowers transit time and augments fecal bulk, defecation frequency (*3*), and binding/discharge of carcinogens (*4*). Fermentable soluble DF results in lower colonic pH and has a positive impact on the composition and number of microorganisms in the gut. Colonic fermentation of DF yields short-chain fatty acids in favor of bowel health (*4*). In particular, soluble DF has the good property of reducing the risk for coronary heart disease and type II diabetes (*4*, *5*).

The most important wheat DF components are the nonstarch polysaccharides (NSP) arabinoxylan (AX), mixed-linkage (1→3),(1→4)-β-D-glucan (β-glucan), and cellulose and the nonpolysaccharide compound lignin, which are all cell wall components. AX consists of a xylan main chain that is mainly substituted with α-L-arabinofuranosyl moieties and, in the case of bran AX, also with (4-*O*-methyl)glucuronic acid moieties. The arabinofuranosyl moieties can be substituted with ferulic or coumaric acid (*6*, *7*). β-Glucan is a linear homopolymer arranged in blocks of consecutive β-(1→4)-linked D-glucose residues separated by single β-(1→3)-linkages (*8*). Like β-glucan, cellulose is a homopolymer of glucose, but all residues are linked by β-(1→4)-linkages (*9*). Lignin is a nonpolysaccharide cell wall substance that is mainly derived from three monolignols (*p*-coumaryl, coniferyl, and synapyl alcohols) polymerized into cell wall-reinforcing biopolymers (*10*).

In particular, β-glucan has well-recognized health benefits (*11*), supported by health claims for barley and oat products. Although AX has also been shown to have health-promoting properties (*12*, *13*), the relative performance of these two DF components has not yet been fully assessed. In wheat and products derived thereof, AX is quantitatively the most important DF.

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*Corresponding author [telephone +32 (0) 16 32 16 34; fax +32 (0) 16 32 19 97; e-mail kurt.gebruers@biw.kuleuven.be].

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Some DF components, in particular AX, have a great impact on wheat technological functionality in, for example, breadmaking (*6*), gluten−starch separation (*14*), and animal feeds (*15*) because of their specific physicochemical properties.

The present study aims at assessing the impact of genotype and environment on the content of total DF (TDF) and its components in wheat through an elaborate field experiment. A strong influence of genotype may allow breeders to develop stable varieties with higher or lower levels of DF components depending on nutritional and/or technological needs. Variability in the nutritional and technological functionality of wheat raw materials is one of the biggest concerns of manufacturers of wheat-derived food and feed products. This study was performed within the EU FP6 HEALTHGRAIN program focusing on improving the well-being of consumers by reducing risks of metabolic diseases by increasing the consumption of wholegrain products (*16*). It was part of the diversity screen within the program in which, on the one hand, the ranges of variation of the levels of DF and health-related phytochemicals in cereals were determined (*17*) and, on the other hand, the contributions of genotype and environment to these variabilities were estimated (*18*).

MATERIALS AND METHODS

Chemicals and Reagents. All chemicals and reagents were of at least analytical grade and obtained from a number of sources including Sigma-Aldrich (Buchs, Switzerland), VWR International (Leuven, Belgium), and Acros (Geel, Belgium). The Mixed-Linkage β-Glucan Assay Kit (K-BGLU) was from Megazyme (Bray, Ireland).

Wheat Samples. *Wheat Varieties and Growing Sites*. Table 1 of the Supporting Information gives an overview of all samples analyzed in this study, the country in which they were grown, and the year of harvest. The sample set included 24 winter wheat and 2 spring wheat varieties, which were selected from a pool of 153 wheat lines on the basis of their DF and phytochemical content as described by Ward et al. (*17*). The selected varieties were grown at a site in Martonvásár, Hungary, during three successive growing seasons [2004−2005 (harvest on July 20), 2005−2006 (harvest on July 18), and 2006−2007 (harvest on July 5)] and in one season (2006−2007) at three additional sites across Europe, that is, Clermont Ferrand (France, harvest on July 13), Saxham [United Kingdom (U.K.), harvest on August 22], and Choryn (Poland, harvest on July 20) except for the varieties Crousty and Tiger, which were not sown in Hungary in 2004, and the varieties Chinese Spring and Cadenza, which were not sown in Poland in 2006 (*18*). All wheat varieties were grown in two replicate blocks. The plots were 2.5 m long, with six rows spaced at a distance of 20 cm, and were treated appropriately with herbicide, insecticide, and fungicide. Edge effects were negligible because the size of the plots was 2.5 m^2, the plots were surrounded by other plots (distance between the plots was 40 cm), and after harvest for each plot the material was bulked to ensure homogeneity of the samples. Because of the wide variation in weather conditions and locations across Europe (*18*), these samples provide an ideal opportunity to study the contribution of genotype, environment, and genotype−environment interaction to the total variation in the levels of DF and components thereof in wheat.

Weather Conditions during Wheat Growth. (*a*) *Temperature*. After sowing, the average temperature in autumn was highest in France in 2006 (11 °C) and lowest in Hungary in 2004 and 2005 (6 °C). The latter temperature was comparable to that in Poland in 2006 (7 °C). For all trials, the coldest periods of the winter were the end of December, the end of January, and the beginning of February. On average, the coldest winters occurred in Hungary in the years 2004−2006 (0 to −1 °C). The United Kingdom and France (2006−2007) had the mildest winters (on average 6−7 °C). The average temperature in spring was highest in Hungary in 2007 (16 °C) and lowest in the United Kingdom (12 °C) and Poland (13 °C) in 2007. The temperatures generally increased from April until July. In 2007, June was warmest in Hungary (23 °C) and coldest in the United Kingdom (15 °C).

(*b*) *Rainfall*. During autumn there was quite a lot of rainfall in Hungary in 2004 and in Poland and the United Kingdom in 2006 (∼17 mm/10 days). The lowest amount of rainfall was measured in Hungary in 2006 (∼6 mm/10 days). In the winter (2006−2007) especially Poland and the United Kingdom dealt with a lot of precipitation (∼20 mm/10 days), whereas the winters in Hungary in 2004−2005 and 2006−2007 and in France in 2006−2007 were relatively dry (∼10 mm/10 days). Spring was very wet in Hungary in 2005 and in the United Kingdom in 2007 (23 mm/10 days). This season was driest in Poland in 2007 (9 mm/10 days). In May 2007, there was a high amount of precipitation in Hungary (27 mm/10 days) and the United Kingdom (42 mm/10 days), whereas June 2007 was rainy in France (27 mm/10 days) and the United Kingdom (37 mm/10 days). The total amounts of precipitation in Hungary and France during the entire growing season (2006−2007) were similar and relatively low (∼315 mm). Comparable and intermediate amounts were noted for Hungary in 2004−2005 and 2005−2006 and for Poland (2006−2007) (∼426 mm). The total precipitation was highest in the United Kingdom (2006−2007) (∼689 mm).

Sample Preparation. Wheat grain was conditioned to 15.5% moisture content and was subsequently ground with a Perten Laboratory mill 3100 (Perten Instruments AB, Huddinge, Sweden), to yield whole meal passing through a 0.5 mm sieve, or milled with a Chopin CD1 Laboratory mill (Chopin Technologies, Villeneuve-la-Garenne, France) to produce white flour, shorts, and bran. All samples were stored in sealed plastic bags in the dark at −20 °C until analyzed.

Determination of Dietary Fiber Content. The TDF content was determined with the Uppsala method (AACC 32-25; AOAC 994.13) (*19*−*22*), which includes quantification of NSP by gas chromatography, uronic acid residues by a colorimetric assay, and Klason lignin by a gravimetric assay (*23*). The method allows assessment of total (TOT) and water-extractable (WE)NSP content (*21*). TDF and NSP were only analyzed in whole meal of the wheat samples harvested in 2007 at the four different growing sites. The data obtained with the Uppsala method also allowed estimation of the TOTAX levels in these whole meal samples. The coefficient of variation for the analysis of TDF, NSP, and TOTAX in whole meal was typically 4% for triplicate measurements.

Total (TOT) and water-extractable (WE)AX levels in flour and bran were determined by gas chromatography of alditol acetates as described by Gebruers et al. (*23*). The coefficient of variation was typically 3% for triplicate analysis of samples.

β-Glucan levels were determined in whole meal with the Megazyme Mixed-Linkage β-Glucan Assay Kit according to the streamlined method (*24*), which is consistent with methods AACC 32-23 (*20*), AOAC 995.16 (*19*), and ICC 166 (*25*). All β-glucan measurements were performed in duplicate. The experimental error was below 5% deviation of the mean value. The AX levels in flour and bran and the β-glucan and Klason lignin levels in whole meal were measured for all harvested wheat samples.

All values are expressed on a dry matter (dm) basis. Moisture contents were measured according to AACC method 44-15A (*20*).

Determination of Water Extract Viscosity. The viscosities of whole meal aqueous extracts were analyzed as described by Gebruers et al. (*23*). Viscosity measurements were carried out in duplicate, and results are expressed in mP·s.

Statistical Analysis. Two types of analyses were conducted to investigate the impact of environment and genotype on the variability of the levels of TDF and components thereof in whole meal, flour, and/or bran and on the variability of whole meal extract viscosity.

In a first analysis, the emphasis was on detecting significant differences between environments. To this end, a one-way ANOVA was performed to assess the effect of environment (including location and harvest year) on the levels of TDF and DF components in wheat whole meal, flour, and/or bran and on whole meal extract viscosity. A Tukey test with a 5% family significance level was used to evaluate significant differences. Box plots were drawn in Excel (Microsoft).

The aim of the second analysis was to quantify the contributions of environment, genotype, and their interaction to the total variance in the levels of TDF and DF components and in extract viscosity. Therefore, environment, genotype, and their interaction were considered as random factors in a random effects model. A likelihood ratio test was used to identify the significant sources of variance (*26*). Maximum likelihood was used for model selection, whereas restricted maximum likelihood was used to estimate the variance components. The analysis was performed for the different locations and harvest years separately and for the combination of the four locations (one year)

Table 1. Range and Average Value for the Levels of Different Cereal Constituents and Quality Parameters for All Wheat Samples Analyzed from Different Harvest Years and Locations

	range	average
TDF whole meal[a] (% of dm)	9.6−14.4	11.7
TOTNSP whole meal[a] (% of dm)	7.8−11.4	9.5
WENSP whole meal[a] (% of dm)	1.25−2.25	1.67
TOTAX whole meal[a] (% of dm)	4.4−6.9	5.8
TOTAX flour (% of dm)	1.31−2.73	1.99
TOTAX bran (% of dm)	12.1−22.6	17.3
WEAX flour (% of dm)	0.24−1.03	0.54
WEAX bran (% of dm)	0.27−0.92	0.44
lignin whole meal (% of dm)	1.40−3.05	2.07
β-glucan whole meal (% of dm)	0.46−0.95	0.66
viscosity (mP·s)	1.29−4.19	2.19
starch whole meal[b] (% of dm)	55.4−67.5	61.5
protein whole meal[b] (% of dm)	11.4−19.8	14.8
ash whole meal[b] (% of dm)	1.42−2.25	1.81
flour yield[b] (%)	27.7−63.4	46.3
xylanase flour[c] (XU/g of dm)	0.01−0.35	0.07
bran yield[b] (%)	20.5−42.4	24.9
xylanase bran[c] (XU/g of dm)	0.09−3.23	0.55
hardness index[b]	3.5−89.2	48.3
thousand kernel weight[b] (g)	27.0−60.0	41.0

[a] Only samples from different locations harvested in 2007 were analyzed. [b] Based on data from Rakszegi et al. (*27*) and unpublished data. [c] Based on data from Gebruers et al. (*28*).

and three harvest years (one location), being considered as six different environments.

To study the linear correlations between different parameters, a multivariate analysis of variance was performed. Hereby, environment was considered as a discrete covariate. The reported correlations are the partial correlations after correction for the possible effect of environment.

All statistical analyses were performed using Statistical Analysis System software 9.2 (SAS Institute, Cary, NC).

RESULTS AND DISCUSSION

As mentioned above, the contribution of genotype, environment, and their interaction to the variability of the TDF, TOTNSP, WENSP, TOTAX, WEAX, Klason lignin, and β-glucan levels in wheat whole meal, flour, and/or bran and to the variability of whole meal extract viscosity was estimated on the basis of an elaborate genotype−environment study including wheat samples (26 varieties) from six growing trials, that is, from three growing seasons (one location) and four locations (one year). The trials differed considerably in weather conditions (*18*), which are briefly discussed under Materials and Methods. For the most important wheat DF component, that is AX, the contribution of genotype, environment, and their interaction to the variability of the TOTAX and WEAX contents in flour and bran was also estimated.

Total Variation in the Levels of Dietary Fiber and Fiber Components. An overview of all wheat samples analyzed in this study, the country in which they were grown, their year of harvest, their contents of TDF and DF components in whole meal, flour, and/or bran, and their whole meal extract viscosity is provided in the Supporting Information (Table 1). **Table 1** summarizes the ranges of variation of these parameters, the levels of starch, protein, and ash in whole meal (*27*), grain hardness index (*27*), endo-1,4-β-D-xylanase (xylanase) activities in flour and bran (*28*), and flour and bran yields (*27*). For all of these parameters a large variation can be observed that is caused by genetic differences and differences in environmental parameters during growth (climate, location, and agronomical inputs).

The TDF content in the analyzed wheat whole meal samples ranges from 9.6 to 14.4% of dm with a mean value of 11.7 of dm (**Table 1**). On average, about 80% of the TDF in wheat whole meal is NSP, of which approximately 18% is water extractable. AX makes up about 50% of the wheat TDF, whereas lignin and β-glucan are responsible for approximately 18 and 6%, respectively (**Table 1**). The values shown in **Table 1** are relatively common for wheat. Knudsen (*29*) reported average TDF, TOTNSP, TOTAX, Klason lignin, and β-glucan levels in wheat whole meal of 13.8, 11.9, 5.2, 1.9, and 0.8% of dm, respectively. Dusel et al. (*30*) measured TOTNSP levels ranging from 7.5 to 11.5% of whole meal dm (mean = 9.7% of dm). TOTAX concentrations of 5.8−7.6% of grain dm (mean = 6.62% of dm) were documented by Dornez et al. (*31*). Gebruers et al. (*23*) reported lignin levels of 1.40−3.25% of dm (mean = 2.20% of dm), and Dusel et al. (*30*) measured 0.32−1.16% of dm (mean = 0.61% of dm) β-glucan in wheat whole meal. Cellulose, which is not analyzed in this study, makes up approximately 2.0% of dry wheat grain (*29*). It is generally known that AX occurs at higher concentration in bran than in flour (*32*). In flour and bran, on average, comparable WEAX levels were measured (**Table 1**).

The relatively strong variation in whole meal extract viscosity is largely attributed to the variation in WENSP level, WEAX level, in particular (*30*, *33*, *34*). According to earlier studies, WENSP and WEAX constitute 0.93−1.79% of dm (mean = 1.22% of dm) (*35*) and 0.44−0.99% of dm (mean = 0.66% of dm) (*31*), respectively, of wheat whole meal, which is comparable with data from this study (**Table 1**).

Genotype and Environment Effects. *Whole Meal.* (*a*) *TDF, TOTNSP, and TOTAX.* The wheat samples harvested on the different growing sites in 2007 show on average significant differences in TDF (**Figure 1A**), TOTNSP (**Figure 1B**), and TOTAX (**Figure 1D**) content. Although the weather conditions in 2007 on the sites in Hungary (warm and dry) and the United Kingdom (cold and wet) were extremely different, the wheat samples from both sites, in particular, those from Hungary, tend to have high levels of these components. The wheat samples grown in France and Poland tend to have on average low but comparable TDF, TOTNSP, and TOTAX levels. The French site received more precipitation than the Polish site from wheat heading to harvest [204 mm and 101 mm, respectively (*18*)]. Hence, the relationship between weather conditions during growth and DF content is not straightforward and probably also other factors play a role, for example, agronomical input and soil type (*18*). Also, others reported that environment has an impact on DF content. Dusel et al. (*30*) noted significantly higher DF levels for samples grown under cold and wet conditions compared to samples cultivated under warmer and drier conditions, whereas Kim et al. (*36*) reported a negative relationship between annual rainfall and acid detergent fiber content. Choct et al. (*35*) saw that TOTNSP content in wheat is significantly affected by climatic conditions. In addition, Li et al. (*37*) observed a significant impact of the amount of rainfall on the level of TOTAX in hard winter wheat whole meal. They noted the lowest TOTAX levels for the dry locations and the highest levels for the higher rainfall environments. In contrast, Coles et al. (*38*) found a decrease in wheat TOTAX level with increasing water supply, whereas Dornez et al. (*31*) measured comparable TOTAX levels in wheat samples from different years that strongly differed in amount of precipitation. Hansen et al. (*39*) described a significant impact of environment on the TDF, TOTNSP, and TOTAX levels in rye, and Saastamoinen et al. (*40*) observed an increase in rye TOTAX level with increasing water supply.

Genotype and environment each explain approximately 30% of the variability of TDF, TOTNSP, and TOTAX content in wheat whole meal. Around 20% of the variation in the levels of these constituents is attributed to the interaction between genotype

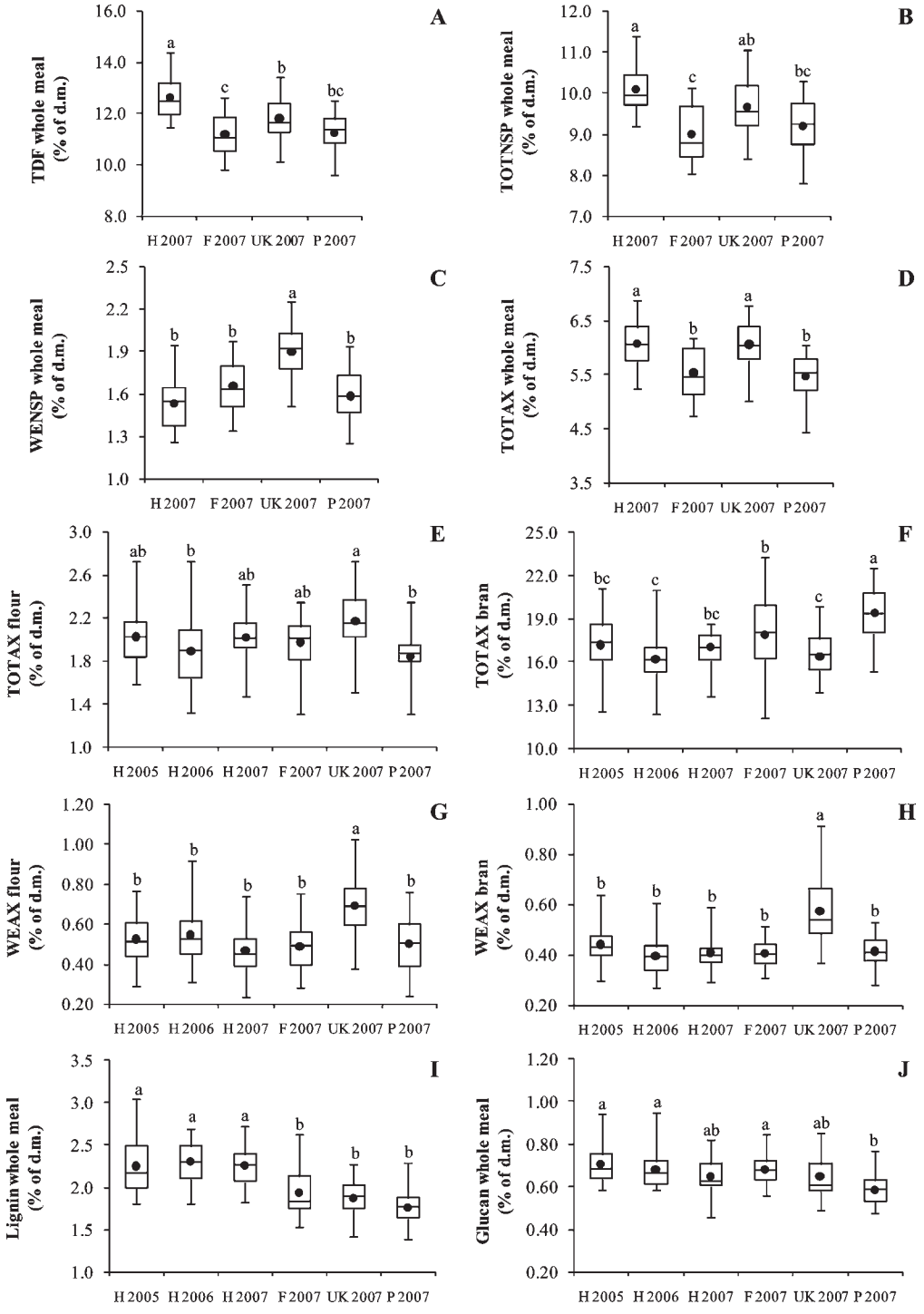

Figure 1. Box plot representation of the variability of TDF (**A**), TOTNSP (**B**), WENSP (**C**), TOTAX (**D**), lignin (**I**), and β-glucan (**J**) levels in whole meal and of TOTAX (**E**, **F**) and WEAX (**G**, **H**) levels in flour (**E**, **G**) and bran (**F**, **H**) of wheat grown at different sites (H, Hungary; F, France; UK, United Kingdom; P, Poland) and from different harvest years (2005, 2006, and 2007). The medians are indicated by horizontal lines in the boxes and the average values by black dots. Averages indicated by different letters are significantly different from each other ($P < 0.05$).

and environment (**Table 2**). The contribution of this interaction term is relatively close to that of genotype, which suggests that the TDF, TOTNSP, and TOTAX contents in wheat whole meal are rather weak breeding parameters. The correlation between the levels of TDF, TOTNSP, and TOTAX in grain from different growing sites is often weak and in some cases even not significant (**Table 3**), which also suggests rather low contribution of genotype to the variability and limited stability of these parameters for breeders. Nevertheless, some wheat varieties tend to have consistently high (Rialto and Campari) or low (Isengrain, Crousty, and San-Pastore) TDF, TOTNSP, and TOTAX levels (**Table 4**). In line with our results, Dornez et al. (*31*) and Li et al. (*37*) reported a low impact of genotype on TOTAX level. Whereas the former group did not observe an effect of weather, the latter group observed a strong impact of environment. Dornez et al. (*31*) attributed about one-third of the variation in TOTAX level to the interaction between genotype and environment, and about half of the variation remained unexplained by their random effects model. In addition, Andersson et al. (*41*) did not find a relationship between TOTNSP level in wheat grain and wheat variety. For rye, Hansen

et al. (*39*) measured a generally higher yearly variation in TDF, TOTNSP, and TOTAX level than the variation due to genotype.

(*b*) *WENSP and Viscosity*. The average WENSP content is highest in the U.K. samples (**Figure 1C**). The cold and wet weather conditions, as they occurred in the United Kingdom from May until July in 2007, are known to favor preharvest sprouting and microbial growth, which tend to increase the level of hydrolytic enzymes that may result in NSP solubilization and, related herewith, increased WENSP levels. In analogy with amylases, increased activities of endogenous cereal β-glucanase (*42*) and xylanase (*31*) have been observed as a result of preharvest sprouting. Dornez et al. (*31*) also observed a drastic increase in microbial xylanase activity as a result of raw weather conditions. The occurrence of higher xylanase activities in the present U.K. samples compared to the samples of the other growing trials is described by Gebruers et al. (*28*). Concomitant with elevated endogenous and microbial xylanase activities in wheat grown under moist and relatively warm conditions in the weeks before harvest, Dornez et al. (*31*) noted increased WEAX levels. In addition, Kim et al. (*36*) described a positive relationship between the annual rainfall and WENSP level. In contrast, Li et al. (*37*) reported for hard winter wheat higher WEAX levels for dry, lower yielding locations and lower levels for higher rainfall, higher yielding environments.

Together with the elevated WENSP levels in the U.K. whole meal samples, extracts of these samples are on average more viscous than those from other sites, which are on average comparable (results not shown). According to Dusel et al. (*30*), whole meal extract viscosity is positively correlated with the amount of precipitation during the growing period and the level of soluble pentosan. They emphasize the importance of molecular weight of the soluble pentosan, which may be different for samples from different sites, in determining viscosity.

Approximately 36% of the variability of WENSP level can be explained by genotype, whetrsd environment accounts for approximately 44% of the variability (**Table 2**). The higher contribution of environment is probably caused by the relatively cold and extreme wet weather conditions that occurred in the United Kingdom and resulted in increased polysaccharide hydrolase activities and NSP solubilization as discussed above. The contribution of genotype−environment interaction to the total variation is low compared to the impact of genotype, suggesting that WENSP level is a relatively stable breeding parameter (**Table 2**). This is supported by the significant correlation between the WENSP levels in wheat from different locations (**Table 3**). The wheat varieties Valoris and San-Pastore consistently have high and low WENSP levels, respectively, when grown on the four different sites in 2007 (**Table 4**). Results of earlier analogous studies focusing on the WEAX fraction of the NSP in wheat whole meal are very diverse. Whereas Dornez et al. (*31*) found that most of the variability of WEAX level was caused by genetic differences between varieties, Li et al. (*37*) attributed most of it to the variation of environmental parameters.

Extract viscosity is strongly determined by genotype [55−70% (**Table 2**)] and much less by environment and genotype−environment interaction. Correlation analysis revealed a strong relationship between extract viscosity and the level of WENSP and WEAX (see below). In line with the important genotype effect, the extract viscosities of samples from different locations are strongly correlated (**Table 3**). The whole meal extracts from the varieties Lynx and Rialto typically have high viscosities, whereas those from Crousty and Isengrain always are low in viscosity. Oury et al. (*43*) equally reported that viscosity largely depends on genotype and is a stable quality trait. According to their results the interaction between genotype and environment does not contribute significantly to the variability of viscosity, which is in agreement with the relatively low values obtained here (**Table 2**). Other studies show that wheat (*30*) and rye (*44*) whole meal extract viscosities are also significantly influenced by the temperature and precipitation after heading.

(*c*) *Lignin*. The lignin levels are on average comparable between the Hungarian samples harvested in different years and between the samples from the other sites. The mean lignin levels in the former samples are significantly higher than those in the latter samples (**Figure 1I**). With the present experimental setup, the contribution of genotype to the total variability in lignin content is lower than the contribution of the interaction between genotype and environment. This is typical for unstable breeding parameters. Lignin content is mostly determined by environmental factors when all trials (45%) or only the different growing locations (41%) are taken into account, whereas for the Hungarian field trials the impact of environment is negligible (**Table 2**). The relatively high value for the genotype−environment interaction

Table 2. Contribution of Genotype (G), Environment (E), and the Interaction Term between Genotype and Environment (G × E) to the Variation of the Levels of TDF and Components Thereof in Wheat and Wheat Whole Meal Extract Viscosity[a]

	total				harvest year				location			
	G	E	G × E	R	G	E	G × E	R	G	E	G × E	R
TDF whole meal	nd	nd	nd	nd	nd	nd	nd	nd	29	28	23	10
TOTNSP whole meal	nd	nd	nd	nd	nd	nd	nd	nd	32	32	20	16
WENSP whole meal	nd	nd	nd	nd	nd	nd	nd	nd	36	44	10	10
TOTAX whole meal	nd	nd	nd	nd	nd	nd	nd	nd	32	32	20	16
TOTAX flour	68	17	12	3	80	7	9	4	62	23	13	2
TOTAX bran	32	30	21	17	46	12	22	20	30	33	20	17
WEAX flour	60	26	14	0	77	9	13	1	52	36	12	0
WEAX bran	47	39	14	0	82	6	11	1	37	48	15	0
lignin whole meal	22	45	30	3	35	2	57	6	20	41	34	5
β-glucan whole meal	52	19	27	2	56	8	34	2	55	20	23	2
viscosity	55	27	18	0	70	10	20	0	62	22	16	0

[a] The contributions to the total variation and variations observed between different harvest years and different locations are presented. The residual variation (R) that cannot be explained by G, E, or G × E is also shown. nd = not determined (only the samples of harvest year 2007 were analyzed).

Table 3. Pearson's Correlation Coefficients for the Levels of TDF and Components Thereof in Whole Meal and Whole Meal Extract Viscosities of Wheat Grown at Different Locations in 2006−2007[a]

	France−U.K.[b]	France−Poland[c]	France−Hungary[b]	U.K.−Poland[c]	U.K.−Hungary[b]	Poland−Hungary[c]
TDF	0.67***	0.45*	0.27	0.70***	0.45*	0.71***
TOTNSP	0.59**	0.51*	0.38*	0.72***	0.43*	0.76***
WENSP	0.79***	0.78***	0.76***	0.80***	0.68***	0.64***
TOTAX	0.60**	0.51*	0.38	0.78***	0.57**	0.78***
lignin	0.60**	0.13	0.01	0.44*	0.49*	0.52**
β-glucan	0.75***	0.75***	0.65***	0.82***	0.61***	0.58**
viscosity	0.81***	0.96***	0.80***	0.81***	0.83***	0.85***

[a] *, P value < 0.05; **, P value < 0.01; ***, P value < 0.001. [b] Number of varieties included in the analysis (n) = 26. [c] Number of varieties included in the analysis (n) = 24.

Table 4. Wheat Varieties and Their Frequency of Occurrence in the Top Five and Bottom Five of the List of Varieties Ordered from High to Low Level of TDF, TOTNSP, WENSP, TOT-AX, WE-AX, Lignin, β-Glucan, and Extract Viscosity[a]

	TDF whole meal		TOTNSP whole meal		WENSP whole meal		TOTAX whole meal		TOTAX flour		TOTAX bran	
	variety	frequency	variety	frequency	variety	frequency	variety	frequency	variety	frequency	variety	frequency
top 5	Rialto	4/4	Rialto	4/4	Valoris	4/4	Rialto	4/4	Campari	6/6	Gloria	5/6
	Campari	3/4	Campari	3/4	Gloria	3/4	Campari	3/4	Lynx	6/6	MV-Emese	5/6
	Lynx	3/4	Herzog	3/4	Campari	2/4	Herzog	3/4	Rialto	6/6	Spartanka	4/6
	Atlas-66	2/4	Atlas-66	2/4	Herzog	2/4	Lynx	3/4	Cadenza	5/5	Tiger	3/5
	Herzog	2/4	Malacca	2/4	Lynx	2/4	Atlas-66	2/4	CF99105	4/6	Herzog	3/6
	Malacca	2/4	Maris-Huntsman	2/4	Rialto	2/4	Malacca	2/4			Lynx	3/6
bottom 5	Isengrain	4/4	Crousty	4/4	San-Pastore	4/4	Crousty	4/4	Isengrain	6/6	Cadenza	5/5
	San-Pastore	4/4	Isengrain	4/4	Crousty	3/4	Isengrain	4/4	Crousty	5/5	Disponent	5/6
	Avalon	2/4	San-Pastore	4/4	Estica	3/4	Tremie	3/4	Claire	5/6	Tremie	4/6
	Crousty	2/4	Avalon	2/4	Riband	3/4	San-Pastore	2/4	San-Pastore	5/6	Claire	3/6
			Tremie	2/4	Tiger	3/4	Spartanka	2/4	Atlas-66	4/6	Isengrain	3/6
					Claire	2/4			Riband	3/6		
					Isengrain	2/4						

	WEAX flour		WEAX bran		lignin whole meal		β-glucan whole meal		viscosity	
	variety	frequency	variety	frequency	variety	frequency	variety	frequency	variety	frequency
top 5	Lynx	6/6	Campari	6/6	Malacca	5/6	Atlas-66	6/6	Lynx	6/6
	Rialto	6/6	Lynx	6/6	Lynx	4/6	Isengrain	6/6	Rialto	6/6
	Valoris	6/6	Rialto	6/6	Estica	3/6	Obriy	5/6	Valoris	5/6
			Maris-Huntsman	4/6	Tommi	3/6	Spartanka	4/6	Campari	4/6
			Valoris	3/6			Gloria	3/6	CF99105	4/6
							Malacca	3/6	Tremie	3/6
bottom 5	Isengrain	6/6	Isengrain	6/6	San-Pastore	5/6	CF99105	5/6	Crousty	5/5
	Crousty	5/5	San-Pastore	6/6	Isengrain	4/6	Lynx	5/6	Isengrain	6/6
	Claire	5/6	Crousty	5/5	Disponent	3/6	Riband	4/6	San-Pastore	6/6
	San-Pastore	5/6	Chinese Spring	3/5	Gloria	3/6			Claire	5/6
	Estica	3/6	Estica	3/6					Riband	3/6
	Tommi	3/6								

[a] Frequencies are expressed as (times of occurrence of a variety in the top or bottom 5)/(the number of field trials in which the variety has been analyzed). Only varieties with frequencies of 3/6, 2/4, or higher are presented.

term suggests that the wheat varieties show different responses to differences in environmental stimuli, that is, that both genetic predisposition and certain environmental conditions are needed to obtain increased/decreased lignin levels. The weak effect of genotype on lignin content is also reflected by the weak correlations, or even the absence of correlation, between data from different trials (**Table 3**). However, the varieties Malacca and San-Pastore contain in most cases high and low lignin levels, respectively (**Table 4**). In contrast to our results, a large impact of genotype and a minor, or even no, impact of genotype−environment interaction on lignin content have been described for oat and switchgrass (*45*, *46*).

(*d*) *β-Glucan*. On average, the β-glucan levels are comparable between the different growing trials, but the Polish samples tend to be somewhat lower in β-glucan (**Figure 1J**). Under the current experimental setup, β-glucan concentration is mainly determined by genotype (**Table 2**). In line herewith, the β-glucan data from different trials correlate very well (**Table 3**). The wheat varieties Atlas-66 and Isengrain contain high β-glucan levels irrespective of the year of harvest and the site where they were grown. The varieties CF99105 and Lynx, on the other hand, mostly contain low β-glucan levels (**Table 4**). Earlier studies revealed a negative relationship between water supply by irrigation and β-glucan level in wheat (*47*). For barley, the opposite has been observed (*38*). Furthermore, Savin et al. (*48*) noted decreased β-glucan levels in grain of heat-stressed barley plants. The present study does not disclose straightforward relationships between water supply, temperature, and β-glucan level as the samples from Hungary and the United Kingdom (2007) have comparable average β-glucan levels, whereas they are grown under highly different temperature and moist conditions.

Flour and Bran. The TOTAX levels in wheat flour and bran vary very strongly (**Figure 1E**,**F**). The average TOTAX level in flour tends to be high in the U.K. samples and low in the Hungarian samples (2006) and the Polish samples (**Figure 1E**). More than 62% of the observed variation in flour TOTAX level can be explained by genetic differences between wheat varieties (**Table 2**), which is reflected by the strong correlations between data from different growing trials (r values = 0.77−0.93; P values < 0.001). When only the Hungarian samples are taken into account, the variation determined by genotype is even 80%. The TOTAX level in bran is much less dictated by genotype compared to the level in flour (**Table 2**) and shows a different profile when the different growing trials are compared, that is, the Polish samples having on average a high and the U.K. and Hungarian (2006) samples a low TOTAX level in the bran (**Figure 1F**). However, note that the contributions of genotype, environment, and their interaction to the variability of the AX levels in flour and bran, as listed in **Table 2**, are apparent values because these may also be influenced by milling parameters, including technical milling parameters, grain hardness, and related herewith flour and bran yield. The varieties Campari, Lynx, Rialto, and Cadenza tend to have a high TOTAX level in the flour, whereas flour of Isengrain, Crousty, Claire, and San-Pastore tends to be poor in TOTAX (**Table 4**). As discussed above, whole meal of Campari and Rialto also has high TDF, TOTNSP, and TOTAX levels, whereas these levels are low in Crousty, Isengain, and San-Pastore whole meal.

As in the case of TOTAX in flour, the WEAX levels in flour and bran are also relatively strongly dictated by genotype. This is most discernible when only the Hungarian samples are included

Table 5. Partial Correlation Coefficients for Different Parameters and for All Wheat Samples from Different Harvest Years and Locations after Elimination of Environmental Effects[a]

	TDF WM[b]	TOTNSP WM[b]	WENSP WM[b]	TOTAX WM[b]	TOTAX flour[c]	TOTAX bran[c]	WEAX flour[c]	WEAX bran[c]	β-glucan WM[c]	lignin WM[c]	viscosity WM[c]	starch WM[c,d]	ash WM[c,d]	flour yield[c,d]	xylanase flour[c,e]	bran yield[c,d]	xylanase bran[c,e]	HI[c,d]
TDF WM		0.97***	0.46***	0.93***	0.50***	0.15	0.49***	0.43***	−0.04	0.72***	0.45***	−0.57***	0.53***	−0.20*	0.24*	0.43***	0.18	0.27**
TOTNSP WM			0.50***	0.95***	0.50***	0.18	0.51***	0.41***	0.00	0.52***	0.43***	−0.54***	0.45***	−0.23*	0.20*	0.41***	0.14	0.28**
WENSP WM				0.56***	0.63***	0.10	0.76***	0.65***	−0.13	0.20*	0.79***	−0.16	0.02	−0.28**	0.16	0.12	0.14	0.28**
TOTAX WM					0.62***	0.18	0.59***	0.52***	−0.18	0.54***	0.54***	−0.51***	0.48***	−0.23*	0.27**	0.39***	0.19	0.28**
TOTAX flour						−0.03	0.62***	0.63***	−0.37***	0.29***	0.62***	−0.22**	0.28***	−0.67***	0.24***	−0.04	0.08	0.63***
TOTAX bran							0.19*	0.12	0.12	0.03	0.05	−0.06	−0.15	0.02	−0.05	−0.33***	0.14	0.04
WEAX flour								0.77***	−0.22**	0.26**	0.83***	−0.29***	0.20*	−0.18*	0.32***	0.08	0.28***	0.12
WEAX bran									−0.46***	0.33***	0.75***	−0.17*	0.30***	−0.18*	0.47***	−0.03	0.48***	0.27***
β-glucan WM										−0.10	−0.28***	−0.01	−0.42***	0.12	−0.25**	0.01	−0.17*	−0.23**
lignin WM											0.29***	−0.45***	0.46***	−0.06	0.11	0.20*	0.17*	0.17*
viscosity WM												−0.19*	0.18*	−0.18*	0.18*	0.08	0.20*	0.19*
starch WM													−0.56***	0.13	0.08	−0.27***	0.07	−0.09
ash WM														−0.04	0.15	0.37***	0.08	0.11
flour yield															−0.11	0.14	0.08	−0.79***
xylanase flour																−0.08	0.65***	0.14
bran yield																	−0.05	−0.31***
xylanase bran																		0.02
HI																		

[a] *, *P* value < 0.05; **, *P* value < 0.01; ***, *P* value < 0.001. WM whole meal; HI, hardness index. [b] Number of samples included in the analysis (*n*) = 102. [c] Number of samples included in the analysis (*n*) = 152. [d] Based on data from Rakszegi et al. (*27*) and unpublished data. [e] Based on data from Gebruers et al. (*28*).

in the genotype−environment study. The variability of WEAX level of the samples from the different growing sites is more determined by environmental parameters (**Figure 1G**,**H**; **Table 2**). As discussed above for WENSP, the foul weather conditions in the United Kingdom are probably at the basis of the increased influence of environment. The varieties Lynx and Rialto typically have high WEAX levels in flour and bran, whereas the flour and bran of Isengrain, Crousty, and San-Pastore contain low WEAX levels. As mentioned earlier, whole meal extracts of these varieties have high and low viscosities, respectively, a trait that is strongly related with WEAX level.

Partial Correlations between the Levels of Dietary Fiber Components and Other Grain Characteristics. Partial correlation coefficients were calculated between TDF, TOTNSP, WENSP, TOTAX, WEAX, β-glucan, and lignin levels and other parameters, that is, extract viscosity, flour and bran yield, hardness index, starch and ash content (*27*), and xylanase activity (*28*). The effect of environment (harvest year, location) was hereby eliminated to avoid obtaining deceiving correlations (**Table 5**).

As expected, the TDF content in whole meal is strongly correlated with the TOTNSP content, the latter fraction making up the largest part of the former one. The TDF and TOTNSP contents are strongly correlated with the TOTAX content in whole meal, AX being quantitatively the most important DF component in wheat. The correlations of the TDF and TOTNSP levels with the TOTAX level in flour are much weaker and even not significant with the TOTAX level in bran. In contrast to β-glucan, the concentration of lignin is significantly correlated with the TDF, TOTNSP, and TOTAX levels in whole meal. In wheat, β-glucan is a minor DF component, which contributes on average only about 6% to the TDF content.

The level of WENSP in whole meal and the WEAX levels in flour and bran are significantly interrelated. The correlation between the WEAX and WENSP levels can be expected because the former constitutes a large part of the latter. The levels of the water-extractable DF components are strongly correlated with whole meal extract viscosity. After all, as mentioned above, viscosity is strongly determined by these soluble components. The WEAX levels in flour and bran tend to increase with increasing xylanase activities, suggesting some AX solubilization in situ. A similar correlation between WEAX level and xylanase activity in whole meal was reported by Dornez et al. (*31*).

The contents of TDF, TOTNSP, TOTAX, and lignin are negatively correlated with starch content and positively with ash content and bran yield, suggesting that wheat varieties with a higher DF content tend to have a lower caloric value. Similar correlations were noted by Zijlstra et al. (*49*) and Coles et al. (*38*). Zijlstra et al. (*49*) also observed a strong negative correlation between the levels of DF components and digestible energy, which was mainly caused by the negative impact of these components on digestibility rather than differences in starch levels.

The TOTAX content in wheat flour is positively related with kernel hardness, whereas kernel hardness is inversely correlated

with flour yield. The correlation between the latter two parameters is commonly known (*50*). These relationships are probably at the basis of the inverse relation observed between flour TOTAX content and flour yield. For the TOTAX and TOTNSP levels in whole meal and the WEAX level in bran, the correlations with hardness index and flour yield, if these exist, are very weak. Correlations between pentosan (mainly consisting of AX) level and grain texture parameters have been reported before. Hong et al. (*51*) reported for a pool of hard and soft wheat varieties that grain hardness tends to increase with increasing level of pentosan in whole meal flour and that pentosan level, in particular water-extractable and enzyme extractable pentosan level, is positively correlated with whole wheat flour particle size after milling. Bettge and Morris (*50*) observed similar correlations between hardness and different pentosan fractions, but these were not observed when hard and soft wheat samples were studied separately.

Relevance of the Present Findings. From this study, it is obvious that both genotype and environment can affect the levels of DF and its components NSP, AX, lignin, and β-glucan in wheat grain and fractions thereof and can influence wheat whole meal extract viscosity. Because of the importance of these components as DF and for wheat processing functionality, these variations will probably affect the health-related functionality and other quality parameters of wheat-derived products such as bread, especially when whole meal is used.

Wheat generally contributes considerably to the daily DF intake in human diets. The results in **Table 1** suggest that for wheat-derived products a proper choice of wheat variety may result in a nutritionally relevant increase in DF content (up to 1.5-fold). Like the TDF and TOTAX levels, the concentration of WENSP, an important source of soluble DF, varies considerably (1.8-fold difference between highest and lowest value). The level of soluble fiber can be increased in cereal foodstuffs by using polysaccharide hydrolases such as xylanases. Xylanases are nowadays already frequently applied as cereal processing aids (*6*,*52*,*53*). Hence, wheat varieties, rich in DF, have a strong potential for the production of healthy or even health-promoting food products that contain not only a high overall DF content but also increased levels of soluble DF and/or prebiotic oligosaccharides produced by in situ action of enzymes.

From a technological point of view, the variation in DF content in general and AX content in particular is relevant because AX is generally considered to have a significant effect on wheat technological functionality. When the impact of xylanases on AX molecular weight and physicochemical properties is taken into account, it is clear that AX affects the suitability of flours for certain applications. Indeed, leaving other important quality-determining characteristics such as protein content and composition aside, one might suggest that, for example, for good dough and bread characteristics, a high [high molecular weight WEAX]/[TOTAX] ratio is preferable (*6*,*52*), whereas for gluten−starch separation, a high level of both high molecular weight WEAX and water-unextractable AX (WUAX) content is detrimental for gluten agglomeration (*14*, *53*). In practice, xylanases are used in breadmaking and gluten−starch separation to increase this ratio by selectively solubilizing WUAX and to extensively degrade AX to low molecular weight fragments, respectively.

Furthermore, the large variation in extract viscosity observed here (**Table 1**) suggests the occurrence of considerable variation in the feed conversion ratio of wheat-derived feeds because several studies point to a positive relationship between these two parameters (*15*, *54*).

General Conclusion. As the levels of TDF and the main components thereof and extract viscosity are significantly affected by genotype, selection of appropriate wheat varieties can be an important tool to direct the health-related and technological functionality of wheat. However, the possibility to control functionality is limited because the impact of environment and the interaction between genotype and environment is often substantial. In particular, the water-extractable fiber and β-glucan levels, the flour TOTAX level, and viscosity are stable breeding parameters, whereas TDF, TOTNSP, TOTAX, and, especially, lignin came out as weak breeding parameters.

ABBREVIATIONS USED

AX, arabinoxylan; DF, dietary fiber; NSP, nonstarch polysaccharides; TDF, total DF; TOTAX, total AX; TOTNSP, total NSP; WEAX, water-extractable AX; WENSP, water-extractable NSP; WUAX, water-unextractable AX; XU, xylanase unit.

Supporting Information Available: Detailed list of all wheat varieties analyzed, the country in which they were grown, their year of harvest, and their TDF, TOTNSP, WENSP, TOTAX, WEAX, lignin, and β-glucan levels in whole meal, flour, and/or bran. This material is available free of charge via the Internet at http://pubs.acs.org.

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