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Variation in gluten quality parameters of spring wheat varieties of different origin grown in contrasting environments

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ABSTRACT

The aim of this study was to investigate variation in protein content and gluten viscoelastic properties in wheat genotypes grown in two mega-environments of contrasting climates: the southeast of Norway and Minnesota, USA. Twelve spring wheat varieties, nine from Norway and three HRS from Minnesota, were grown in field experiments at different locations in Norway and Minnesota during 2009–2011. The results showed higher protein content but lower TW and TKW when plants were grown in Minnesota, while the gluten quality measured as Rmax showed large variation between locations in both mega-environments. On average, Rmax of the samples grown in Minnesota was higher than those grown in Norway, but some locations in Norway had similar Rmax values to locations in Minnesota. The data showed inconsistent relationship between the temperature during grain filling and Rmax. Our results suggest that the weakening effect of low temperatures on gluten reported in this study are caused by other environmental factors that relate to low temperatures. The variety Berserk showed higher stability in Rmax as it obtained higher values in the environments in Norway that gave very weak gluten for other varieties.

1. Introduction

Environmental factors that affect grain development in wheat may also have implications for the functionality of the gluten proteins that eventually will affect the end-use quality. Studies have documented that environmental variations in gluten quality can be large, and this represents a great challenge for the milling and baking industry. Comprehensive knowledge exists on the variability of gluten proteins, their inheritance and influence on gluten functional properties. In contrast, the impacts of environmental factors and their interactions with genotype affecting gluten quality are still only scarcely understood.

Gluten quality is determined by the viscoelastic properties of the dough, which are mainly related to the ratio of monomeric to polymeric proteins (Uthayakumaran et al., 2000) and to the proportion of glutenin aggregates above a certain molecular weight (Southan and MacRitchie, 1999). The fraction of large and unextractable glutenin aggregates, known as SDS-unextractable polymeric proteins (UPP), are found to correlate strongly with dough elasticity (Gupta et al., 1993). Large variation in gluten viscoelastic properties is found between varieties. In particular, the genes encoding the HMW glutenin subunits are known to affect the degree of polymerisation of the glutenins, causing differences in baking quality between varieties (see Shewry et al., 1992 for review).

Variation in protein content and gluten quality caused by the environment (E), the genotypes (G) and the G*E interaction have

Abbrevations: ANOVA, Analysis of Variance; Ext, Extensibility measured by the Kieffer Extensibility Rig; FN, Falling Number; GMP, Glutenin MacroPolymers; HMW-GS, High Molecular Weight Glutenin Subunits; HRS, Hard Red Spring; LSD, Least Significant Difference; NIR, Near InfraRed; PC, Principal Component; PCA, Principal Component Analysis; Rmax, Resistance to extension measured by the Kieffer Extensibility Rig; SDS, Sodium Dodecyl Sulphate Sedimentation Volume; TKW, Thousand Kernel Weight; TW, Test Weight; UPP, SDS-Unextractable Polymeric Proteins.

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been reported in many studies (see Finlay et al., 2007 for overview). In most of these studies gluten quality was analysed by rheological methods or by baking tests, and large variation in gluten quality due to both E, G, and G*E have been documented. In several studies, E is shown to be the main cause of variation in wheat quality, whereas the variation caused by G*E was of less importance (Finlay et al., 2007). The temperature during grain filling is among the environmental factors found to affect gluten quality. In Scandinavia, weaker gluten quality is reported in the seasons having cooler and wetter weather (Johansson and Svensson, 1998; Moldestad et al., 2011; Uhlen et al., 2004). Moldestad et al. (2011) found the temperature during grain filling to be the weather parameter that was most strongly associated with gluten quality, and reported lower resistance to stretching of the gluten dough when the mean daily temperature drops below 17–18 °C. Several researchers have performed experiments in controlled climate chambers and analysed gluten quality and composition (Johansson et al., 2005; Malik et al., 2013, 2011; Randall and Moss, 1990; Uhlen et al., 1998). Some of these studies showed effects on gluten polymer structure and found increased UPP with increasing temperature (Malik et al., 2013, 2011; Uhlen et al., 1998), whereas in other studies, no consistent differences were reported (Johansson et al., 2005). Recently, Moldestad et al. (2014) investigated the effects of temperature during grain filling on gluten quality in growth tunnels where a temperature gradient was established in the longitudinal direction, and found increased UPP and gluten strength with increasing temperatures. However, another study performed in tunnels mimicking cool/wet and warm/dry growth conditions (Georget et al., 2008) could not document differences in gluten quality due to these weather conditions. Thus, contrasting results may reflect complex relationships between the growth temperature and the gluten quality. In a recent review, Johansson et al. (2013) suggests how several environmental factors such as temperature, nutrient availability and the duration of grain filling may involve a number of interacting biochemical mechanisms of relevance for the gluten polymer structure. Still, there are needs for further confirmation of the effects on gluten quality of suggested environmental factors as well as an increased understanding of their mechanisms.

It is generally experienced that higher protein content as well as stronger gluten quality is obtained for spring wheat from the USA compared to wheat grown in Western Europe. The different weather conditions in these regions are believed to be a main factor causing these quality differences. However, few investigations have tried to compare the impacts of different weather conditions in such mega-environments to gluten quality parameters. The present study characterizes gluten from a set of twelve wheat varieties from Norway and Minnesota, USA grown in field trials at different locations in both countries. The aim was to 1) reveal the effects of different climates on gluten quality, 2) compare the gluten quality potential of the Norwegian varieties with the expected superior North American Hard Red Spring (HRS) wheat varieties, and 3) explore the possibility of using varieties of genetically strong gluten to obtain satisfactory quality in regions with a cooler and wetter climate.

2. Materials and methods

2.1. Field experiments

Twelve spring wheat varieties, including nine varieties adapted to Norwegian/Scandinavian growth conditions and three HRS varieties from Minnesota, USA (Supplementary Table 1), were grown in field trials at several locations during the seasons 2009–2011. All varieties possessed strong gluten and the high molecular weight glutenin subunits (HMW-GS) 5 + 10 encoded by *Glu-D1*. The varieties from Minnesota were selected to be representatives for the HRS quality. The field trials were located at four research farms in the southeast of Norway and were run from 2009 to 2011, at Vollebekk (59.660468, 10.781989), Bjørke (60.80276, 11.20403), Rød (59.34387, 10.89505) and Apelsvoll (60.70024, 10.86952), and at three locations in Minnesota, USA in 2011, at St. Paul (44.98958, 93.17923), Crookston (47.818558, 96.613451) and Morris (45.592758, 95.873911). A replicated complete block design with two replicates was used. The amount of fertiliser used at sowing was optimised for each location. The varieties from Minnesota were very susceptible to lodging when grown in Norway, and they were supported by nylon nettings stretched across the plots to avoid this. The experiments in Norway were treated with fungicides sufficient to control diseases with the potential to destroy grain quality.

The phenological development stages heading (Zadoks 49) and yellow ripeness were recorded for each plot at Vollebekk and Apelsvoll, whereas the phenological data was estimated based on calculations of day-degrees for the locations Bjørke and Rød. Heading (Zadoks 49) was recorded in the experiments in Minnesota. Weather data was collected from weather stations located close to the fields. Mean daily temperatures and sum of precipitation during the grain filling period was calculated for each location. Supplementary Table 2 summarises sowing dates, dates for heading and yellow ripening and the weather parameters for all environments.

The experiments were harvested plot-wise with an experimental plot combine. Samples were dried below 15% moisture and cleaned. The experiments at Rød, Bjørke and Apelsvoll in 2011 suffered from severe sprouting, and were excluded from further analyses.

2.2. Physical grain analyses and milling

Thousand kernel weight (TKW) and test weight (TW) were determined for all samples. Wholemeal flour was milled on a Laboratory Mill 3100 (Perten Instruments AB, Huddinge, Sweden) using a screen of 0.8 mm. Samples of 50 g were milled from each variety and replicated for all locations.

2.3. Analyses of whole-meal flour

Falling Number (FN) was determined for all samples using a Falling Number 1800 (Perten Instruments AB, Huddinge, Sweden). Sodium dodecyl sulphate sedimentation volume (SDS) was determined according to the AACC method 56–70 (AACC 2000). Protein content was determined by near infrared (NIR) reflectance spectroscopy using a Perten Inframatic 9200 (Perten Instruments AB, Huddinge, Sweden).

2.4. Gluten micro-extension test

Gluten micro-extension tests were performed as described by Moldestad et al. (2011) using the SMS/Kieffer Dough and Gluten Extensibility Rig (Kieffer et al., 1998) for the TA.XT *plus* Texture Analyser (Stable Micro Systems, Godalming, UK). Gluten was prepared from wholemeal in a Glutomatic 2100 (Perten Instruments AB, Huddinge, Sweden) by using a 2% NaCl solution to remove salt soluble components. The dough was mixed for 1 min before 10 min of washing. To remove starch and bran particles, two different filters were used in the process. An 88 μm sieve was changed after 2 min and replaced by an 840 μm sieve. To remove excess water, the gluten dough was centrifuged in a custom-made centrifuge mould at 3000 g for 10 min at 20 °C (Beckmann TJ-25 (Rotor TS-5.1–500). Subsequently, it was pressed in the standard Teflon mould and

rested for 45 min at 30 °C before analysis with the Kieffer-rig. The parameters resistance to extension (Rmax) and extensibility (Ext) were recorded from the extensograms according to Kieffer et al. (1998). The analysis was performed only on samples having a falling number above 200.

2.5. Statistical analysis

ANOVA was performed on combined data from all years and locations using the GLM procedure in Minitab 16 (Minitab Ltd., Coventry, UK). All field trials (location*year) were considered different environments, and included in ANOVA as a random variable. The model Response = environment + variety + environment*variety was used. Tukey test was used for comparisons of the means, and $LSD_{95\%}$ values were calculated. Principal component analysis (PCA), which is a multivariate approach designed for multicorrelated data, was carried out using The Unscrambler v 10 Z.1 (CAMO Software AS, Oslo, Norway) on the quality data from the grain, flour and gluten dough analysis. This method is meant to give an overview of the data, to reveal which properties are related, and to find the properties most important in distinguishing between samples (Martens and Martens, 2001). Finlay–Wilkinnson regressions (Finlay and Wilkinnson, 1963) for the Rmax were calculated for the varieties against the environment (location*year) mean.

3. Results

The PCA score plot (Fig. 1A) shows how the different years and locations differ from each other in quality. The first two principal components explain 61% (PC1 explained 38%, PC2 explained 23%) of the variation in the dataset analysed. There is a clear difference between the locations in Minnesota compared to the locations in Norway. The loading plot (Fig. 1B) shows that the protein content, TKW and FN span out the variation in the data set along the first principal component. Ext and Rmax span out the variation along the second principal component. Hence, the viscoelastic properties of gluten measured by the Kieffer-Rig varied independently of the protein content. The samples from Minnesota had lower TKWs compared to the samples from Norway. Within the locations in Minnesota, the samples from St. Paul differ from the two other locations by having higher Rmax and lower protein content. The samples from Vollebekk, Norway in 2011 differ from the other samples grown in Norway by having higher Rmax.

The locations in Minnesota had mean daily temperatures of 21.5–24.2 °C during grain filling, whereas this varied from 14.3 to 16.9 °C for the Norwegian locations (Supplementary Table 2). The accumulated precipitation during grain filling was low in Crookston with only 57 mm. Frequent precipitation during grain filling was seen in the locations in Norway and at Morris, and total precipitation for the period varied between 143 mm (Bjørke 2010) to 264 mm (Apelsvoll 2010). At St. Paul, 118 mm of a total precipitation during grain filling of 253 mm was recorded in one day, approximately mid-way in the grain filling period.

The environment averages for the quality parameters are shown in Table 1. The samples harvested in the Minnesota locations had higher protein contents, lower TKWs and TWs, and higher FNs than the samples harvested in Norway. The gluten quality, measured by SDS, Rmax and Ext, showed overlapping location means between the environments in Minnesota and in Norway. The highest Rmax was obtained in the samples from St. Paul, which also had the lowest extensibility. Large variation in Rmax was found between the locations in both mega-environments. Among the Norwegian locations, Bjørke in 2009 had very low Rmax, while Vollebekk in 2011 had high Rmax. Among locations in Minnesota, St.Paul obtained high Rmax values whereas lower values were found at Croockstone and Morris.

Table 2 shows the yield and quality parameters for the two groups of varieties, the Norwegian varieties and the HRS varieties, when grown both in Norway and Minnesota. The grain development was good for both variety groups when grown in Norway, as seen from the high TWs and TKWs. All varieties produced smaller grains in the Minnesota environments, but the difference for the HRS varieties was only half compared to the reduction in TKW for the Norwegian varieties when grown in Minnesota. While the TWs for the HRS varieties were about the same when grown in Norway or Minnesota, the Norwegian varieties had very low TWs when grown in Minnesota. Thus, the HRS varieties produced somewhat larger and well-filled grains in Norway compared to when grown in Minnesota, while the Norwegian varieties produced small and shrivelled grains when grown in Minnesota compared to when they were grown in Norway. Mean grain yield for the HRS varieties was slightly, but not significantly higher when grown in Norway compared to when grown in Minnesota. The Norwegian varieties out yielded the HRS varieties when grown in Norway, and vice versa. Low TKWs could explain most of the yield decreases of the Norwegian varieties compared to the HRSs when grown in

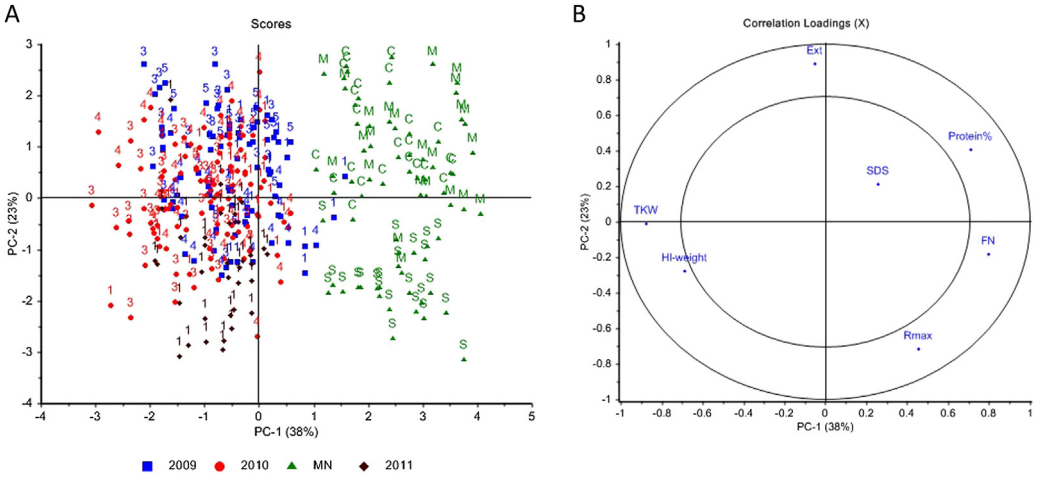

Fig. 1. Biplots of the scores (A) and loadings (B) for PC1 and PC2 from the PCA analysis. The growth seasons in Norway are visualised by different colors and the locations by numbers (1 = Vollebekk, 3 = Bjørke, 4 = Rød, 5 = Apelsvoll). The locations in Minnesota 2011 are visualized by letters (S = St. Paul, C = Crookstone, M = Morris). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Quality analyses of grain, flour and gluten dough obtained at the 11 locations, average of varieties and replicates.

		TW, Kg/hl[1]	TKW, g[1]	FN, s	Protein, %[2]	SDS, ml	Rmax, N	Ext, mm
Norway	Vollebekk 2009	75.1	36.2	316	13.7	77	0.60	116.9
	Bjørke 2009	79.0	34.8	293	12.3	78	0.41	148.4
	Rød 2009	80.2	35.3	307	15.1	73	0.68	123.4
	Apelsvoll 2009	77.5	36.2	238	14.7	89	0.57	135.2
	Vollebekk 2010	75.5	36.7	204	13.6	76	0.54	101.8
	Bjørke 2010	82.5	38.5	267	13.0	77	0.58	111.8
	Rød 2010	79.9	39.7	256	14.5	81	0.75	122.0
	Vollebekk 2011	80.4	37.6	262	12.3	80	0.92	101.5
Minnesota	Morris 2011	73.3	25.3	415	17.5	81	0.68	131.0
	St. Paul 2011	75.4	25.8	440	15.0	71	1.00	95.2
	Crookston 2011	75.5	26.9	399	17.1	85	0.71	141.5
	$LSD_{95\%}$	1.5	2.5	97	0.6	3.5	0.1	12.6
	P value	>0.0001	>0.0001	>0.0001	>0.0001	>0.0001	>0.0001	>0.0001

[1] Given as is.
[2] Given on dry weight basis.

Minnesota. In addition, the number of grains produced per m^2 was also reduced when the Norwegian varieties were grown in Minnesota. Higher TKW could not compensate for the lower grain number per m^2 when the HRS varieties were moved from Minnesota to Norway. Protein contents of 12–13%, typical for the Norwegian spring wheat, were achieved for the Norwegian varieties when grown in Norway, whereas higher protein contents were achieved for both groups when grown in Minnesota as well as for the HRS varieties grown in Norway. SDS was higher for the Norwegian varieties than the HRS varieties in both environments. A significant difference, however, was only found for the Norwegian environments. Interestingly, SDS values were similar for the Norwegian varieties between the environments, even though the protein contents were much higher in samples grown in Minnesota. Both the Norwegian varieties and the HRS varieties achieved higher Rmax when grown in Minnesota. The HRS varieties had higher Ext than the Norwegian varieties when grown in Norway, whereas no significant difference was found between the variety groups when grown in Minnesota.

For both mega-environments, highly significant differences in the gluten quality parameters Rmax and SDS were found for variety ($p < 0.001$) and for the variety*environment interaction ($p < 0.001$). Ext varied less between varieties and significant differences were found only for the Norwegian environments. Table 3 shows the variety means of Rmax, Ext and SDS from both mega-environments. When grown in Minnesota, the varieties Bastian, Bajass-5, Bjarne and Quarna obtained Rmax values similar to Sabin, the strongest of the HRS varieties when grown in this mega-environment, whereas Zebra and Demonstrant showed lower values. In the Norwegian environments, Bajass-5 and Berserk obtained the highest Rmax values, and were significantly higher than the HRS varieties Sabin and Tom. Demonstrant, Bjarne and Bastian had similar Rmax values to Sabin, whereas Zebra had lower values. Highly significant differences between varieties were found for SDS for both mega-environments ($p < 0.001$), and high values were found for Bastian, Berserk, Bajass-5 and Bjarne.

Highly significant environment*variety interactions were found for Rmax, both within environments in Norway and Minnesota, as well as in the combined analyses. To explore differences between varieties in the stability of the gluten quality across environments, regressions between Rmax of the variety and the Rmax field experiment mean were calculated (Fig. 2). The calculations showed that the Norwegian variety Berserk differed from the other varieties by having higher Rmax in the environments where the Rmax means were low, giving a low b-value of the linear regression equation for Berserk.

4. Discussion

By including varieties from Minnesota in Norwegian field trials, and vice versa, challenges might appear due to lack of agronomic adaptation. Registrations in the field trials in Norway showed that the varieties from Minnesota were quite similar to the Norwegian varieties in phenological development. Both heading dates and dates for yellow ripeness were within the range of the Norwegian varieties. Varietal differences in disease resistance to prevalent pathogens in the two mega environments was expected, but disease infestations were avoided as fungicides were applied in the Norwegian experiments. At the sites in Minnesota, no severe disease infestations were established in 2011. An obvious difference between the variety groups was the long and weak straw of the varieties from Minnesota when grown in Norway. Severe lodging was however prevented by supporting the HRS plots with nylon nettings.

Table 2
Yield and quality parameters presented as averages of Norwegian (N) varieties grown in Norway (N), HRS varieties grown in Norway, Norwegian varieties grown in Minnesota (MN) and HRS varieties grown in Minnesota. Different letters given after the means indicate significant differences at the P < 0.05 according to Tukey's test.

	TW, kg/hl[1]	TKW, g[1]	Yield, kg/ha[2]	No. grain/m^2	FN, s	Protein, %[3]	SDS, ml	Rmax, N	Ext, mm
N varieties in N (n = 110)	79.4 a	36.4 a	5353 a	14832 a	305 b	12.8 b	81.4 a	0.616 b	126.7 b
HRS varieties in N (n = 28)	79.7 a	37.4 a	3680 b	9944 c	247 c	17.0 a	73.3 b	0.523 b	139.2 a
N varieties in MN (n = 48)	73.2 b	24.4 c	2748 c	11272 bc	423 a	16.4 a	81.2 a	0.778 a	125.3 b
HRS varieties in MN (n = 12)	79.9 a	31.5 b	4027 b	12994 ab	436 a	17.2 a	76.3 ab	0.843 a	120.2 b
p-value	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.011

[1] Give as is.
[2] Given as 15% moisture.
[3] Given on dry weight basis.

Table 3
Protein content, Rmax, Ext and SDS of the varieties grown in Norway (N) and in Minnesota (MN).

		Protein content (%)		Rmax (N)		Ext (mm)		SDS (ml)	
		N	MN	N	MN	N	MN	N	MN
Norwegian	Basjass-5	12.7	16.3	0.76	0.99	113	111	91	88
	Bastian	12.9	16.2	0.59	0.86	137	128	86	86
	Berserk	12.2	16.8	0.79	0.74	110	127	81	90
	Bjarne	12.1	16.1	0.61	0.87	108	116	78	86
	Demonstrant	11.1	15.8	0.61	0.63	109	128	65	73
	Quarna	13.2	17.7	0.66	0.93	127	114	82	77
	Zebra	11.5	15.3	0.47	0.63	121	134	67	69
HRS	Sabin	14.1	17.0	0.70	0.89	124	115	68	71
	Tom	14.9	17.4	0.49	0.80	140	126	70	82
	$LSD_{95\%}$	0.5	1.2	0.05	0.21	13	22	3	4

The Norwegian varieties out-yielded the HRS varieties when grown in Norway, as well as the HRS varieties out-yielded the Norwegian ones when grown in Minnesota. These results could be expected due to their adaptation to the local environment. Nevertheless, normal grain development of HRS varieties was observed when they were grown in Norway whereas the Norwegian varieties had improper grain filling when they were grown in Minnesota (as both TKWs and TWs were considerably low). Mean day temperature during grain filling in Minnesota was 4.5–7.5 °C higher than the highest temperature recorded during grain filling among the Norwegian environments. It is previously reported that higher temperatures during grain filling reduce grain weight by shortening the duration of grain filling (Sofield et al., 1977). Since starch is a major storage component of endosperm, reduction in starch accumulation as is observed at higher temperatures (Hurkman et al., 2003; Altenback et al., 2003) attribute to lower grain weight when grown at higher temperatures. Increased temperatures are found to influence the accumulation of proteins less (Altenback et al., 2003; DuPont et al., 2006), thus the protein content is expected to increase due to decreased dry matter at higher temperatures. Hence, differences in grain weight and protein content between the two mega-environments were considered to relate to temperature differences between the two. However, the poorer grain filling of the Norwegian varieties when grown in Minnesota compared to the local HRS varieties indicate a poorer adaptation to high temperatures during grain filling.

It is well known that HRS wheat varieties from USA possess high gluten strength and are among the stronger wheats worldwide. The present results showed, however, that the Norwegian varieties Bajass-5, Berserk, Bastian and Bjarne had similar or even slightly higher Rmax values compared to the best HRS variety Sabin when grown in Minnesota and Norway, respectively. Bastian was released in Norway in 1989 as a strong gluten cultivar, and was a result of a long-term breeding strategy to improve bread-making quality of Norwegian wheats. The cultivars Bjarne, Berserk and Bajass-5 are all progenies from crosses with Bastian. Our results revealed that these Norwegian varieties possess high genetic potential to produce wheat with strong gluten similar to the HRS varieties when grown in an optimal environment. All varieties included in this study were having HMW-GS alleles giving high gluten scores according to Payne et al. (1984), including the 5 + 10 subunit encoded by the Glu-1D loci. Hence, the results further suggest that these varieties might have differences in allelic composition of other gluten proteins (LMW-GS and gliadins) giving high gluten strength. Hence, further studies should be conducted to explore the genetic background of these varieties.

The results from this study showed that the Rmax of the varieties was highly dependent on environmental conditions. Although Norwegian varieties were obviously adapted to the Norwegian environment as higher TKWs and yield were observed when they were grown in Norway, the gluten quality was generally stronger when they were grown in Minnesota. The HRS varieties dealt with the Norwegian environment better than vice versa as TKWs, TWs

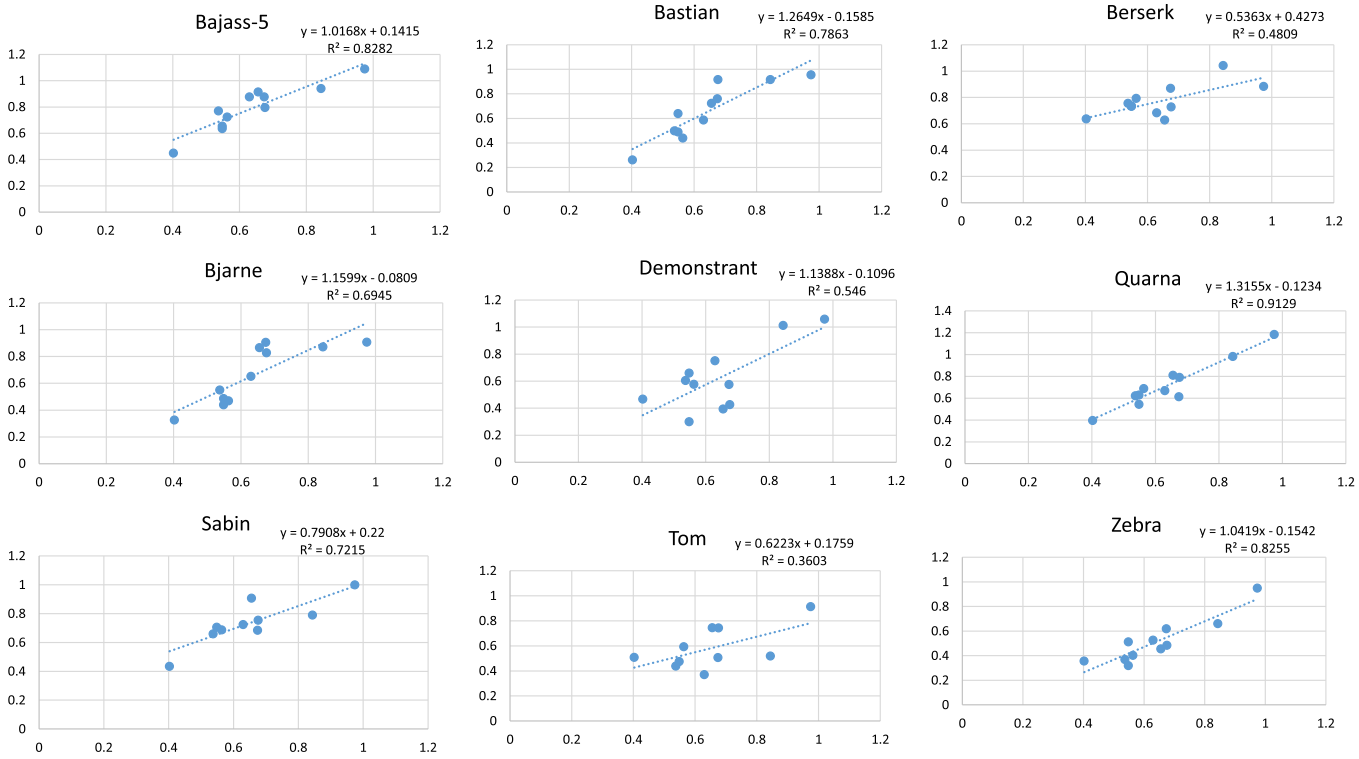

Fig. 2. Plot of Rmax for the actual variety against the Rmax location mean for Norwegian and HRS varieties.

and yield were similar to values obtained from the Minnesota environment, while gluten quality was negatively influenced by the Norwegian environment. These results may partly agree with other investigations showing increased gluten strength with increasing temperatures (Johansson and Svensson, 1998; Malik et al., 2013, 2011; Moldestad et al., 2011; Randall and Moss, 1990; Uhlen et al., 2004). In the present study, the highest Rmax values were obtained at St. Paul, the location with the highest temperature during grain filling. Similar and even lower Rmax levels were however found for the environments Morris and Crookston in Minnesota to some of the environments in Norway, having considerably lower temperatures during grain filling. Furthermore, Rmax for Bjørke in 2009 was much lower than that for Apelsvoll in 2009, even though both locations had approximately equally low temperature and high precipitation during grain filling. Hence, consistent relationships between the weather parameters and gluten quality could not be revealed. Obviously, other factors than the recorded weather parameters are causing the large variation in Rmax.

The results obtained in this study are similar to those reported by Moldestad et al. (2011) in finding very low Rmax values in some Norwegian environments subjected to lower temperature and high precipitation during grain filling. For these environments, the low Rmax values were not reflected in a lower SDS. The SDS location means varied less, whereas a consistent variation between varieties was found. The SDS measures differences linked to solubility properties of the gluten proteins in flours, whereas the Kieffer extensibility test measures the viscoelastic properties of gluten after mixing and resting. As shown by Weegels et al. (1996), changes in the glutenin aggregates occur during mixing which can be observed as an increase in their extractability and a decrease in amount of glutenin macropolymers (GMP). This is followed by an increase in GMP during resting, indicating that a re-assembly of the glutenin aggregates occur in this phase. Thus, SDS and Rmax measures different properties of the proteins as they occur in flours or in a rested dough, respectively. In general, positive relationships are found between the amount of GMP in the flour (affecting SDS) and the amount of GMP in a rested dough (affecting Rmax). The apparent discrepancy between SDS and Rmax seen in this study can indicate that some environmental factors linked to the locations having low Rmax values may hinder a normal re-assembly of the gluten network during resting.

One such factor could be infestations by *Fusarium* species (spp.), as it is reported that proteases from *Fusarium* spp. in infected grains have the ability to degrade gluten proteins (Gartner et al., 2008; Nightingale et al., 1999; Wang et al., 2005). Several *Fusarium* spp. are commonly infecting Norwegian wheat fields (Bernhoft et al., 2013), and the infestation was prevalent during the seasons 2009–2011. Koga et al. (2012) reported severe gluten protein degradation in winter wheat from Norwegian fields in 2011 having extremely low Rmax values. The proteases derived from *Fusarium* spp. was suggested as the most plausible explanation for protein degradation in their study. Hence, infestations by *Fusarium* spp. could be one likely explanation for the extremely low Rmax values found in some environments in Norway. More research is however needed to unravel the possible negative consequences of *Fusarium* infestation on the gluten quality. Furthermore, these results suggested that mechanisms affecting both synthesis and polymerisation of gluten proteins during grain development as well as those factors that might cause deleterious gluten protein degradation needs to be considered to understand environmental impacts on gluten quality.

Significant environment*variety interactions were found for Rmax. For the Norwegian environments, these were mainly caused by different ranking of the varieties in environments resulting in low Rmax values compared to environments resulting in moderate and high Rmax values. The variety Berserk differed from the others by having high Rmax values also in the environments with low Rmax mean. This was also seen from the lower b-value of the Finlay–Wilkinson regression, indicating a higher stability in gluten strength across environments. These results are in line with others who have reported variation in stability among varieties in breadmaking or gluten quality, as measured by either baking tests or other gluten quality tests (Johansson et al., 1999). However, the genetic basis for the variation in stability of the different quality parameters is scarcely understood. Also in this investigation, more research is needed, both to confirm an increased tolerance in Berserk towards environments, causing a weaker gluten, and to unravel the genetic mechanisms. If confirmed in new experiments, Berserk may represent a very important genetic source in breeding for both increased stability of increased gluten strength, which is of overall importance for the baking industry.

The results from the present study revealed that relationships between environmental factors and gluten quality were complex. The temperature during grain filling affected grain weight and protein concentration. Although higher Rmax means were obtained in Minnesota, no consistent effects of temperatures on the viscoelastic property of gluten were documented. This result may be in line with those of Johansson et al. (2013), who recently concluded that the temperature is not among the most important factor affecting the polymerisation of gluten proteins during grain filling. Instead, they proposed that short cultivar-determined plant development times give weak or unstable gluten. These relationships could not be confirmed in this study as the early maturing variety Bastian as well as the newer varieties originated from crosses with Bastian were having the higher Rmax values. Our results suggests that the most important factors to obtain superior gluten quality is the genetic background providing strong gluten as well as the ability to exhibit stable gluten quality over diverse environments. Berserk was identified as one promising candidate showing both strong gluten and more stable gluten when grown in different environments. Further detailed studies are needed to unravel genetic factors associated with the stability of gluten quality.

5. Conclusions

The main differences in quality traits between samples grown in Norway and Minnesota were found for protein content, TKW and TW, whereas for Rmax, large variation in Rmax was found between locations within both mega-environments. Wheat grown in Minnesota appeared to have stronger gluten quality, however consistent relationships between Rmax on gluten and the temperature during grain filling could not be documented. The results suggest that the weakening effect of low temperatures, as found at some locations in Norway, are caused by other environmental factors that relate to lower temperatures.

Our study revealed that Norwegian varieties possess high potential to produce wheat with strong gluten, and that wheat of strong gluten quality can be produced in cooler climates as experienced in Norway. The variety Berserk showed higher stability in Rmax as it obtained higher values in the environments with low average Rmax. Berserk may represent a very important genetic source in breeding for both increased stability of increased gluten strength, which is of overall importance for the baking industry.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jcs.2015.01.004.

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