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The effect of weather conditions from heading to harvest on gluten quality of spring wheat – A study of historical data 2005–2022

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ABSTRACT

The gluten-viscoelastic properties are essential for breadmaking quality and are affected by both genotypes and environments, such as weather conditions. However, it is still not clear how weather conditions cause variation in gluten quality and at which stage of the grain filling they are critical. The aim of the study was to explore the relationship between weather parameters during grain filling and the viscoelastic properties of gluten.

The gluten of spring wheat varieties grown over 17 seasons, resulting in a total of 70 different environments, was analyzed with the Kieffer extensibility rig. The variation in viscoelastic properties of gluten was mainly explained by environment, followed by genotype, while the genotype*environment interaction was small. The results also indicated that the periods around heading and physical maturity were the most critical when weather conditions affected the gluten quality. Our results also revealed that factors other than weather conditions are responsible for the variation in gluten quality.

1. Introduction

Gluten quality varies largely depending on both genotype and environment. Much research is performed on the genotypic variation in gluten quality, which is primarily determined by genes for gluten protein composition (Shewry et al., 1992). Although the composition, structure, and functionality of gluten proteins have been widely studied for more than a hundred years, our understanding of fundamental aspects is still incomplete, as reviewed by Shewry and Belton (2024).

The viscoelastic properties of gluten make wheat suitable to produce a range of baked products. The viscoelasticity of the wheat dough is primarily affected by gluten proteins, consisting of the monomeric gliadins and the polymeric glutenins forming the gluten network during dough mixing. Polymeric glutenins confer elasticity to the dough, primarily dependent on their state of polymerization affected by genes, in particular those encoding the high molecular weight-glutenin subunits (HMW-GS) (Gupta et al., 1993; Payne, 1987; Shewry et al., 1992). It is shown that the assembly of glutenin polymers takes place extensively in the later part of grain filling towards physiological maturity and continues further during the desiccation phase (Carceller and Aussenac, 1999; Koga et al., 2017; Shewry et al., 2009). Environmental factors have been reported to affect the size distribution of glutenin polymers (Branlard et al., 2020; Koga et al., 2020; Malik et al., 2013), presumably in a complex manner that is not completely understood.

The breadmaking quality of wheat is often measured by standard rheological methods, such as farinograph, extensograph, and alveograph, as well as baking tests. However, these measurements are adapted to refined flour, require a relatively large amount of samples and are time-consuming. As an alternative to the standard extensograph, the small-scale Kieffer extensibility rig (Kieffer et al., 1998) was adopted. The method is faster than the standard extensograph method, requires less flour sample and can measure dough and gluten prepared from refined- and whole-meal flour. Several studies have found the Kieffer extensibility rig to be reliable for testing dough viscoelasticity (Nash et al., 2006; Caffe-Treml et al., 2011; Tronsmo et al., 2003). Although not high throughput, it has been used to evaluate breeders' samples or samples from multi-environment field trials. Tronsmo et al. (2003) compared uniaxial extensions of dough and gluten by using the

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Kieffer extensibility rig. They found that the gluten measurements were superior for investigating the actual gluten functionality compared to dough measurements, as the effect of protein content (%P) could be ignored.

As the baking industry has become increasingly automated worldwide, both the milling and baking industries require stable and high-quality wheat to fulfil requirements for breadmaking. Among breadmaking quality parameters, gluten quality is highly important for the baking industry. Gluten quality, however, largely varies depending on environmental factors (Johansson and Svensson, 1998; Branlard et al., 2020, 2023; Mkhabela et al., 2018; Moldestad et al., 2011). Factors such as temperature, rainfall, nutrient availability and fungal diseases are found to affect the quality of gluten in wheat (Johansson and Svensson 1998, Mkhabela et al., 2018, Malik et al., 2013, Moldestad et al., 2011; Uhlen et al., 2015 showed that wheat produced in high-latitude areas has large variations in gluten quality, e.g. when testing the same varieties in multi-environment field trials. Similarly, Johansson and Svensson, 1998 observed that low temperatures during grain filling caused poor gluten quality under Nordic weather conditions. Moldestad et al. (2011) found weaker gluten when the temperature during grain filling was low under Norwegian weather conditions, presumably due to the combined effect of temperature and rain. In Norway, wheat plants are often subjected to decreasing temperatures as the maturation proceeds, and grain maturation and harvest could suffer from wet conditions. The results from previous studies indicate that Norwegian weather conditions greatly affect variability in gluten quality. However, Koga and co-workers could not find a negative effect of low temperature (13 °C) during grain filling on gluten functionality when wheat was grown under controlled climates (Koga et al., 2015). On the other hand, Koga et al. (2020) observed that frequent rain during grain desiccation had a negative effect on the assembly of glutenin polymers in the field, suggesting it caused reduced gluten quality. However, it has not yet been established which environmental factors cause a detrimental effect on the gluten quality and which stage of the grain filling is critical for such an event. Moreover, there is scarce knowledge about whether some varieties will have more stable quality under variable environmental conditions. Such knowledge allows breeders to develop varieties with increased stability in gluten quality.

This study, therefore, aims to document the variations in gluten viscoelasticity due to varieties, environments, and their interaction using multi-environmental trials from 17 seasons. Moreover, the study explores the relationship between weather parameters and gluten functionality.

2. Material and methods

2.1. Field trials and plant material

This study is based on the results from the yearly quality assessments of the new harvest of Norwegian spring wheat between 2005 and 2022. The predominant market varieties for each season were grown with two replicates, laid out with a block design with varieties randomized within each replicate. In total, twelve varieties were included throughout the research period. All varieties possess the HMW-GS 1Dx5+1Dy10, indicating strong wheat (Payne, 1987). Among the varieties used in this study, Bastian, Mirakel and Betong are characterized as the strongest and Caress as the weakest according to the Norwegian classification system. Two of the varieties, Bjarne and Zebra, were included at all locations throughout the research period. The field trials were conducted at three to five locations at farmers' fields and at research farms at the Norwegian Institute of Bioeconomy Research (NIBIO) in collaboration with the Norwegian Agricultural Advisory Services each season. All fields are located within the wheat-production areas in Norway. The varieties and locations were not fixed and changed between seasons. An overview of the locations and plant material is given in Supplementary Table S1. Management practices were optimized for the individual location according to sowing time, fertilization, weed control, and harvest time. Generally, 100–180 kg nitrogen (N)/ha was applied according to the expected yield, pre-crop and soil organic matter. Split fertilization was applied where 90–110 kg N/ha was applied in spring and 30–70 kg N/ha between flag leaf development and early booting (Biologische Bundesanstalt, Bundessortenamt und Chemische Industrie, BBCH 37–49). All field trials were treated with fungicides at the heading to control fungal diseases. Grain quantity and moisture content were measured at harvest, and yield (t/ha) was calculated at 15% moisture. Field trials with severe pre-harvest sprouting were not harvested (e.g., 2017 season). Moreover, the samples with a falling number (FN) below 200 were not analyzed for viscoelastic properties because the minimum FN for bread wheat is 200 in Norway, with a few exceptions.

2.2. Weather data

Daily weather data were collected from weather stations near the field locations (Agrometeorology Norway, lmt.nibio.no). The weather data included daily values for rainfall and air temperatures (mean, maximum and minimum), relative humidity (RH), and global solar radiation. Mean temperature and accumulated rain were calculated for the periods: sowing to heading, heading to harvest, and physiological maturity to harvest (Supplementary Table S2).

2.3. Estimation of heading date and physiological maturity

The heading date (BBCH 55) and date for physiological maturity (BBCH 85) were estimated based on the sowing date and the daily mean temperatures for each environment (Supplementary Table S3). The cereal growth simulation model Konor for phenological development (Bleken, 2001) was used with the model parameter values of accumulated temperature sums and the corresponding base temperatures (T_{base}) for the three periods: sowing to emergence, emergence to heading, and heading to physiological maturity. The parameter values of accumulated temperature sum/T_{base} for the three periods were 140/-1.60, 625/1.06, and 423/5.81, respectively (Bleken pers. comm.). The results were compared and evaluated against manual recordings available for at least one of the field trials each year, except for 2005, 2011, and 2022. When the sowing date was missing, it was estimated to be the same as for other nearby trials.

2.4. Milling

Grain samples from each plot were harvested, dried to a moisture content below 15%, cleaned, and milled to whole-meal flour using Falling Number 3100 (Perten Instruments AB, Hägersten, Sweden) with a screen 0.8 mm. 200 g samples were milled for each variety in two replicates.

2.5. Quality analysis

The falling number was analyzed using a Falling Number 8000 (Perten Instruments AB) according to the standard method (ICC-Standard No. 107/1).

Protein content (%P, dry weight basis) was analyzed by NIT using a Foss Infratec™ 1241 Grain Analyzer (FOSS, Hilleroed, Denmark). Sodium dodecyl sulphate (SDS) sedimentation volume test was carried out using the AACC method 56–70 (AACC, 2000) to evaluate gluten quality. Specific sedimentation (SSDS) volume was calculated by the equation (SDS/%P)*10. Gluten viscoelastic properties were analyzed by the Kieffer dough and gluten extensibility rig (Kieffer et al., 1998). Gluten was prepared from 10 g whole-meal flour and 5 ml 2% NaCl in the Glutomatic 2100 (Perten Instruments AB) by using the procedure adapted to whole-meal flour. This implies 1 min of mixing and 10 min of washing with 2% NaCl. To remove starch and bran particles, an 88 μm sieve was used for the first 2 min and then changed to an 840 μm sieve.

The wet gluten was centrifuged at 3000 g, 20 °C for 10 min, pressed into a Teflon mold, and rested at 30 °C for 45 min. The gluten was thereafter stretched by using the SMS/Kieffer Dough and Gluten Extensibility Rig attached to the TA.XT *plus* Texture Analyzer (Stable Micro Systems, Godalming, UK). The maximum resistance to stretching (Rmax, N) and the extensibility (Ext, mm), given as the distance of stretching until rupture, were measured. Three pieces of gluten were prepared from each sample, and the average for Rmax and Ext was calculated.

2.6. Statistical analysis

Analysis of variance (ANOVA) was performed using Minitab® 21.3.1 (Minitab, 2022). Each field trial within each season was treated as one environment. ANOVA with a general linear model was performed to investigate the effect of genotype (G), environment (E), and their interaction (G*E) on Rmax and Ext, following the equation:

$$Y_{ijm} = \mu + G_i + E_j + GE_{ij} + R(E)_{jm} + \varepsilon_{ijm}$$

where Y_{ijm} is the value of a trait measured for genotype i, in replicate m and in environment j, μ is the overall mean, G_i is the effect of the variety i, E_j is the effect of environment j, GE_{ij} is the effect of the interaction between variety i and environment j, $R(E)_{jm}$ is the effect of replicate m nested in environment j, and ε_{ijm} is the residual effect for the variety i in replicate m in environment j. Replicate and environment were considered as random factors, and variety was considered a fixed factor in this model. This was done for selected time periods where the same varieties were included over more than two seasons. Additional ANOVA was conducted to analyze the effect of G, E, and G*E on %P, Rmax, and Ext individually within each season. Significance was assumed at $p < 0.05$. Pearson correlation coefficient was used to determine the linear relationships between the quality measurements using Minitab®. The impact of the weather was assessed by multiple linear regression analysis. The period from heading to harvest was divided into eleven segments to investigate the impact of weather at the different periods (Supplementary Fig. S1). Each segment partially overlaps with the previous and subsequent periods. Total rain and averages of the other weather parameters (mean, maximum and minimum temperatures, RH, global solar radiation) and their interactions were calculated for these periods and used in the multiple linear regression analyses, both for all varieties combined and separately for each variety. For the significant variables, interactions (e.g. temperature × rain) and quadratic terms (e.g. temperature^2) were also included. The regression analysis on all the combined varieties was done using weather parameters with and without variety information, including interaction terms between variety and weather parameters. The regression analysis was conducted with MATLAB 2023b (The MathWorks, Inc., Natick, MA, USA).

3. Results

3.1. Variation in temperature and rainfall between environments

For the period between heading and harvest, the mean temperature ranged from 13.6 °C to 19.8 °C between seasons, and the accumulated rain varied from 50 mm for the dryest season to 330 mm for the wettest season (Table 1). Lower temperatures (<16 °C) were observed in 2007–2013, 2015, 2016 and 2020, and wetter seasons (>200 mm) in 2007–2012, 2015, 2016 and 2019. Accumulated rainfall and mean temperature for each season gave an indication that in seasons with high amounts of rainfall (>200 mm) and low mean temperatures (<16 °C), the gluten strength (Rmax) is weaker than for seasons with a lower amount of rainfall (<200 mm) and higher mean temperatures (>16 °C) (Table 1).

3.2. Variation in gluten quality parameters

The variations in %P, Rmax, and Ext between and within seasons are shown in Fig. 1. Yearly mean %P varied from 10.8% in 2015 to 15.3% in 2006 (Table 1). An ANOVA within seasons showed that E was a significant factor in twelve out of 17 seasons and was the largest source of variation for %P. On the other hand, significant differences for G occurred in nine out of 17 seasons, and the contribution was small (Fig. 1a–Supplementary Table S5).

Large variations in Rmax were observed both between and within seasons, and mean Rmax varied from 0.39 N in 2009 to 0.74 N in 2021 (Table 1). Mean Rmax was low (<0.60 N) in seasons 2007–2012, 2015 and 2016 (Table 1). Seven environments (out of 70) had very weak gluten quality expressed as mean Rmax values lower than 0.4 N, which included environments from seasons 2007, 2009, 2012, 2015, 2016, and 2018 (Supplementary Table S4). Except for 2016, variations in Rmax were prominent for the same seasons. An ANOVA showed that E was the greatest source of variation for Rmax; G also had a large impact on variation in some seasons, while G*E interaction was less important (Supplementary Table S6). Thus, the environment was the main

Table 1

Number of trials and varieties, accumulated rain (Acc. rain, mm), and mean daily temperature (MD Temp, °C) for the periods sowing to heading, heading to physiological maturity (PM), and PM to harvest, average yield (t/ha), protein content (%P, %), falling number (FN, sec), specific SDS sedimentation volume (SSDS, ml), and mean values for maximum resistance to stretching (Rmax, N) and extensibility (Ext, mm) of gluten analyzed with Kieffer extensibility rig for seasons 2005 to 2022.

Season	No. trials	No. variety	Sowing – heading		Heading – PM		PM – Harvest		Yield (t/ha)	%P (%)	FN (sec)	SSDS (ml)	Rmax (N)	Ext (mm)
			Acc. rain (mm)	MD Temp. (°C)	Acc. rain (mm)	MD Temp. (°C)	Acc. rain (mm)	MD Temp. (°C)						
2005	5	4	157	11.6	113	16.9	45	15.6	7.0	13.4	349	65	0.70	115
2006	4	4	108	13.6	52	18.7	82	16.6	5.1	15.3	269	61	0.66	121
2007	5	4	184	11.9	190	15.2	44	14.8	5.5	13.5	271	63	0.45	170
2008	2	2	96	12.8	170	16.3	63	13.9	6.3	12.6	314	66	0.45	162
2009	3	2	105	12.7	200	15.9	97	14.7	5.3	12.7	256	69	0.39	141
2010	4	3	123	12.0	143	16.5	80	14.5	6.6	13.3	338	67	0.49	139
2011	2	5	218	12.6	169	16.3	117	14.3	5.9	13.1	257	M.d.	0.54	122
2012	4	5	184	12.0	186	14.7	42	12.6	5.9	12.9	321	M.d.	0.50	137
2013	5	6	173	14.5	87	16.7	61	13.2	6.1	11.9	352	63	0.72	123
2014	4	6	103	12.6	72	18.3	109	15.9	5.8	14.0	240	M.d.	0.61	128
2015	4	6	198	10.9	154	15.2	177	14.1	6.6	10.8	214	67	0.57	124
2016	5	6	130	13.3	148	15.6	58	15.1	5.4	12.4	283	62	0.50	140
2018	5	6	47	16.9	12	20.2	38	19.3	3.6	14.9	408	53	0.66	133
2019	5	6	203	12.4	72	17.2	128	15.2	5.1	12.2	245	68	0.66	142
2020	4	6	99	11.6	135	15.3	39	15.7	5.9	12.5	349	64	0.63	140
2021	4	6	154	11.8	75	18.5	65	15.5	6.2	13.5	296	61	0.74	139
2022	4	6	107	12.6	84	16.7	36	16.1	6.3	14.0	342	63	0.67	133

M.d.: Missing data.

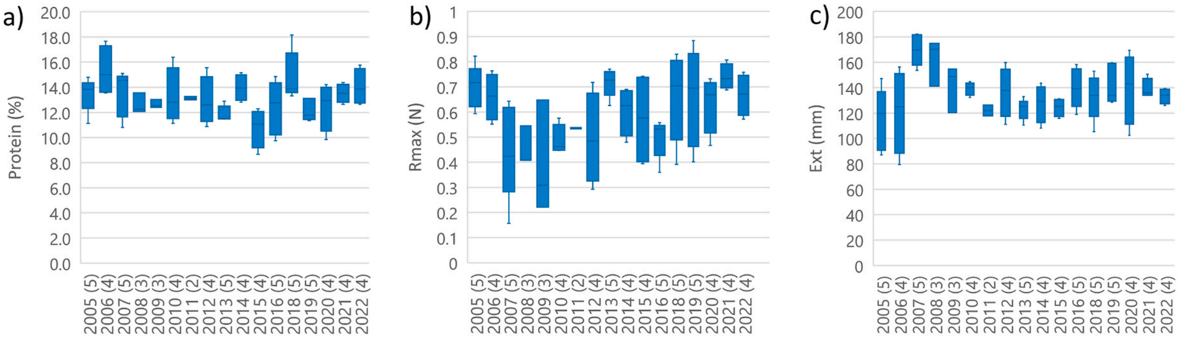

Fig. 1. Box plot of a) protein content (Protein, %), b) maximum resistance to stretching (Rmax, N) and c) extensibility (Ext, mm) of gluten measured by Kieffer extensibility rig for seasons 2005–2022. Data are based on the mean over all varieties, locations, and replicates in the given seasons. The number of locations within each season is given in parentheses. The median is marked by the line.

contributor to variation in Rmax. This was also confirmed by a high and positive correlation between the mean Rmax for Bjarne and Zebra, included in all seasons, and the mean Rmax for all varieties for each environment ($r = 0.92$, $p < 0.001$, Supplementary Fig. S2).

Mean Ext varied from 115 mm in 2005 to 170 mm in 2007 (Table 1). Variation was also observed for Ext between seasons and within seasons, but to a lesser extent than for Rmax. Still, in seasons 2005, 2006, and 2020, variation in Ext between locations was larger than for other seasons (Fig. 1c). An ANOVA revealed that E was the greatest source of variation, while the variation caused by G*E was low for Ext (Supplementary Table S7). There was a negative correlation between Rmax and Ext ($r = -0.539$, $p < 0.001$), while there was no correlation between Rmax and %P when the whole dataset was included (Supplementary Fig. S3). Within seasons, the correlations between Rmax and %P were non-significant or weak negative except for four seasons (2007, 2014, 2015, 2018) with relatively stronger negative correlations (Supplementary Table S8). Likewise, no correlation was found between Ext and %P when including the whole dataset (Supplementary Fig. S3), while within seasons, the correlations between Ext and %P were non-significant or weak positive except for four seasons (2007, 2012, 2016, and 2020) with relatively stronger positive correlations (Supplementary Table S8).

As SDS is affected by %P, the Pearson correlations between SSDS and Rmax, as well as SSDS and Ext, were calculated. When the whole dataset was included, no correlation was found (Supplementary Fig. S3). Within seasons, however, the results showed positive and significant correlations ($p < 0.01$) between SSDS and Rmax in ten out of 14 seasons. Relatively strong correlations ($r > 0.6$) were found in 2008, 2015, 2018, 2021 and 2022. There was no correlation between SSDS and Ext when the whole dataset was included, while they were negatively correlated in nine out of 14 seasons and were relatively strong ($r > 0.6$) in the seasons 2008, 2010, 2020, and 2021 (Supplementary Fig. S3 and Supplementary Tabel S8).

3.3. *Variation in gluten quality for genotypes*

To investigate the performance of the varieties, the field trials were grouped into six classes according to environments giving low, medium, and high Rmax. The mean Rmax value of Bjarne and Zebra from each field trial was used for this classification and each class was defined as follows: class 1 Rmax <0.31 N, class 2 Rmax = 0.31–0.41 N, class 3 Rmax = 0.41–0.55 N, class 4 Rmax = 0.55–0.65 N, class 5 Rmax = 0.65–0.75 N and class 6 Rmax >0.75 N. Field trials containing less than three varieties and varieties included in less than four seasons were excluded, giving a total of 62 field trials and eight varieties. All varieties were included in all classes except for classes 1 and 6. Mean Rmax and Ext for each variety within classes were calculated (Fig. 2). As seen from Fig. 2a–h, Rmax increased from class 1 to 6 for all varieties except Demonstrant, which had the highest Rmax in class 4. Hence, the varieties responded relatively similarly to environments. Notably, the elastic property of the varieties Berserk, Demonstrant, and Mirakel had relatively higher values for the classes of low Rmax (classes 1 and 2). Berserk and Mirakel are known to have a very strong gluten quality among the Norwegian spring wheat. The Ext showed a decreasing trend as the Rmax increased; however, there were some different responses among the varieties. Ext values for Caress were higher than for the other varieties in classes 5 and 6, and Ext for Krabat varied less between classes with mean values between 124 and 142 mm. When grown in environments giving high Rmax values (class 5 and 6), varieties are expected to have a potential Rmax value. When the varieties were compared within class 5, Caress was the weakest variety, with the lowest Rmax and the highest extensibility (Fig. 2 i). Other varieties overlapped in both Rmax and extensibility, with Berserk having the highest and Zebra having the lowest average Rmax. The results indicate relatively similar viscoelastic properties of gluten among these varieties when the growing environment is favorable.

3.4. *Variation in gluten resistance due to G, E, and G*E*

Because varieties included in this study changed from season to season, it was not suitable to study the effect of G, E, and G*E on the viscoelastic properties of gluten for the whole data set. Therefore, the experimental seasons were grouped into four time periods, with chosen varieties grown in all environments within each period. The percentage adjusted mean square of G, E, and G*E was calculated for each period and shown in Table 2. The results revealed that gluten strength and elasticity are both affected by G and E factors (Table 2). The environment was the predominant source of variation in Rmax for the periods 2005–2007, 2014–2016, and 2005–2022, while G caused the greatest variance in the period 2018–2022. The G*E effects were consistently small, explaining lower than 8% of the total variance in Rmax. The environment was the greatest source of variation for Ext in the periods 2005–2007 and 2014–2016, while G caused the greatest variance in the periods 2018–2022 and 2005–2022. The G*E effects for Ext were also consistently small, explaining lower than 6% of the total variance.

3.5. *Effect of temperature, rainfall, and relative humidity on Rmax*

When data from Bjarne and Zebra were used to investigate the effect of weather parameters on Rmax, only total rainfall, average temperature and RH were found to be significant. For both varieties, temperature and rain had the greatest impact on Rmax in the period between heading and physiological maturity. Linear models for rain and temperature explained 10–20% of the variation in Rmax for both Bjarne and Zebra up until and including physiological maturity (Fig. 3). From heading to and including physiological maturity, the R^2 values were similar between the linear models with and without interaction and quadratic terms. After physiological maturity, the R^2 value for the linear model without

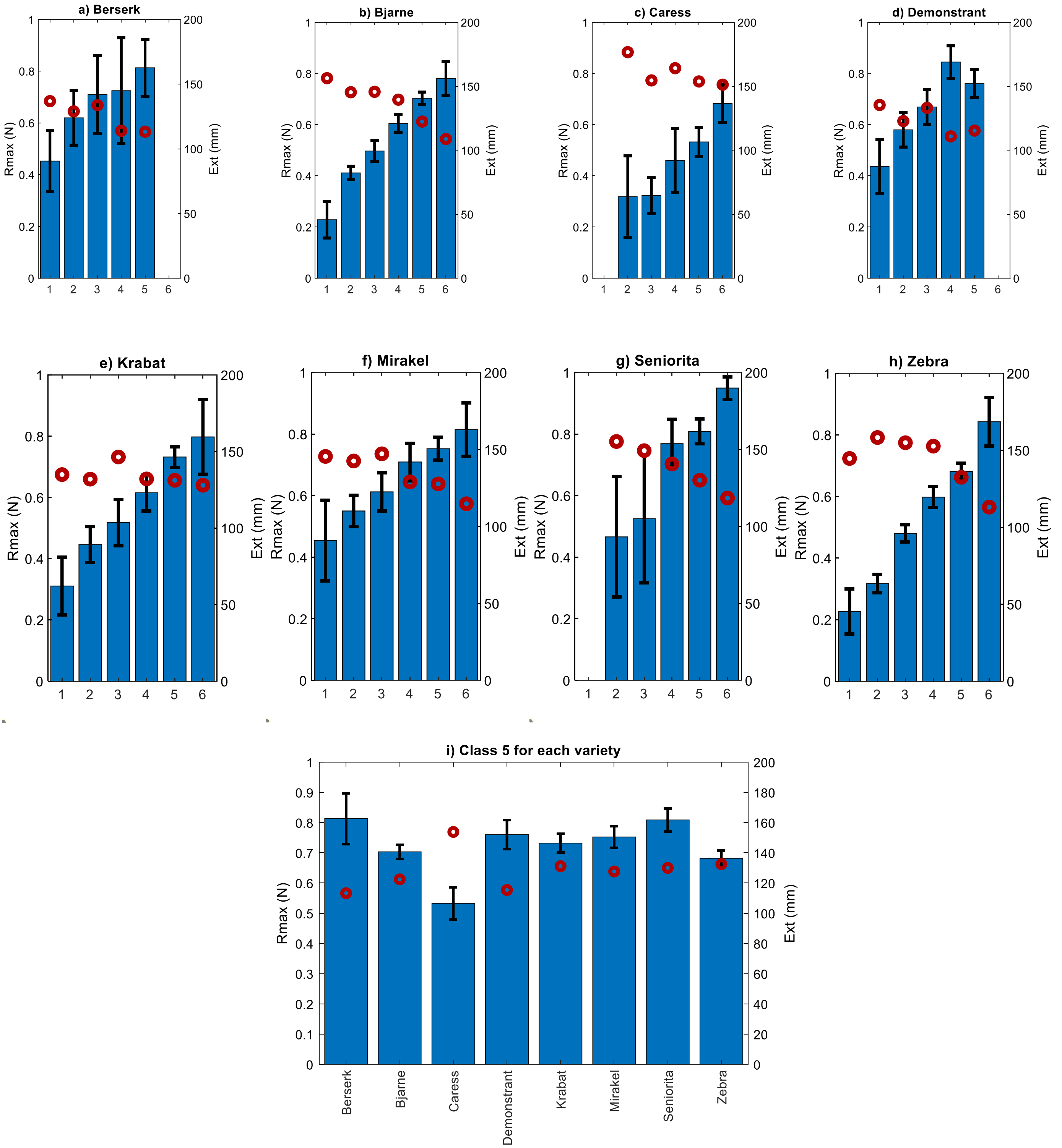

Fig. 2. Means of Rmax (bars) and Ext (dots) of a) Berserk, b) Bjarne, c) Caress, d) Demonstrant, e) Krabat, f) Mirakel, g) Seniorita and h) Zebra for six classes (1–6). Classes were defined according to the mean Rmax of Zebra and Bjarne as follows: class 1 Rmax <0.31 N, class 2 Rmax = 0.31–0.41 N, class 3 Rmax = 0.41–0.55 N, class 4 Rmax = 0.55–0.65 N, class 5 Rmax = 0.65–0.75 N and class 6 Rmax >0.75 N, and i) mean Rmax (bars) and Ext (dots) of each variety in class 5.

interaction or quadratic terms decreased, while it remained high for the more complex models, especially for Bjarne. When modelling with weather data for the whole period from heading to harvest, the linear models explained 29% and 32%, respectively. The models for Bjarne and Zebra improved with interaction terms explaining 49% and 47%, and further to 52% and 61%, respectively, when including quadratic terms.

When all varieties and all time periods were included in a single linear model, it explained 26% of the Rmax variation. The explained variance increased to 41% with interaction terms and to 53% when quadratic terms were also included. When the information about varieties was included, it explained another 15% variation for every model. However, adding the interaction between variety and average temperature and rain increased the explained variation by only 1–2%. The relatively low explained variance indicated that the weather parameters

Table 2
Variance components based on ANOVA showing the percentage of variation in the mean sum of squares linked to genotype, environment, and their interaction for maximum resistance to stretching (Rmax, N) and extensibility (Ext, mm) for different time periods. Degrees of freedom (df), % mean sum of square (%MSS), genotype (G), environment (E) and replicates (R). (R(E)): biological replicate nested in the environment, %MMS: % adjusted mean square.

	2005–2007			2014–2016			2018–2022			2005–2022		
Varieties	Avle, Bastian, Bjarne, Zebra			Bjarne, Demonstrant, Krabat, Mirakel, Rabagast, Zebra			Bjarne, Caress, Mirakel, Seniorita, Zebra			Bjarne, Zebra		
	df	%MSS Rmax	%MSS Ext	df	%MSS Rmax	%MSS Ext	df	%MSS Rmax	%MSS Ext	df	%MSS Rmax	%MSS Ext
G	3	21*	21**	5	37***	25**	4	68***	60***	1	12 NS	80***
E	13	70***	71***	12	56***	60***	21	28***	35***	67	73***	16***
G*E	39	5***	4**	60	4***	6**	84	2***	2 NS	67	8***	1 NS
R(E)	14	2 NS	2 NS	13	2*	6*	22	1*	1 NS	67	3 NS	2 NS
Error	38	2	2	60	1	3	88	1	2	60	4	1

NS = Not significant, * = < 0.05, ** = < 0.01, *** = <0.001 level of significance.

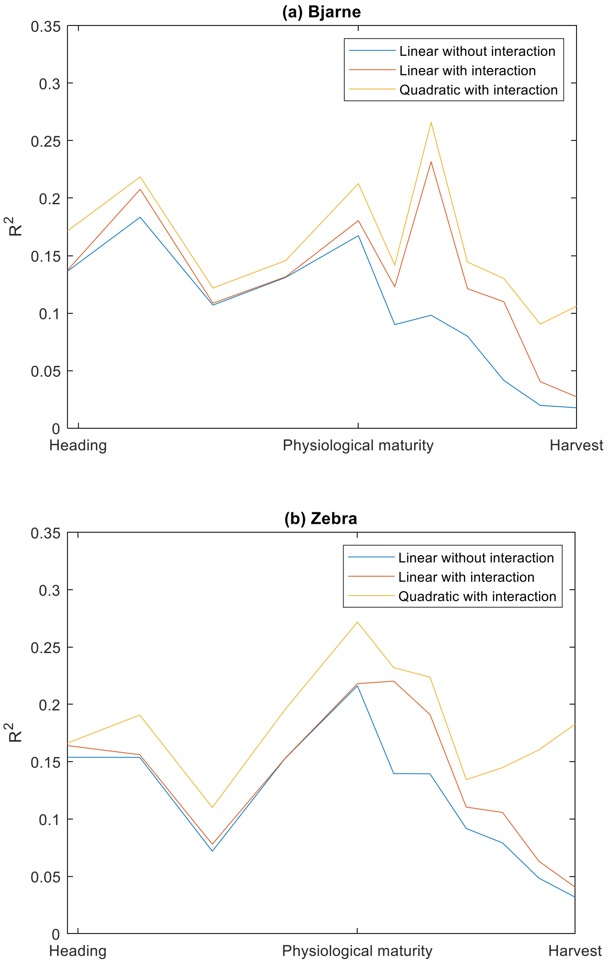

Fig. 3. The R^2 values for linear and quadratic models based on average temperature and total rainfall in time periods between heading and harvesting for a) Bjarne and b) Zebra without and with the interaction of temperature and rain (blue and red line, respectively), as well as a quadratic model with interaction (yellow line). Time points for heading, physiological maturity, and harvest are labelled on the x-axis (the timeline is shown in more detail in Supplementary Fig. S1). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

had a higher impact on Rmax than variety. The high level of explained variance from the variety compared to the variety-weather interaction terms indicates that while potential Rmax for the varieties differs, their changes related to weather conditions are comparable.

While temperature had a positive and rain had a negative impact on Rmax, RH had a more complex impact on Rmax, presumably because the RH is largely dependent on temperature and rain (Supplementary Fig. S4). When the RH was added to the linear models, it had no impact. On the other hand, when it was added to the model as interaction terms with temperature and rain, it had a similar impact on Rmax as the quadratic terms. When RH was added to the quadratic model, the impact was smaller.

To illustrate the effect of weather, the mean Rmax was calculated for different weather combinations (Table 3). High and low levels of the weather parameters were defined as values above and below the median for each parameter. In general, temperature had a higher impact, with decreased temperatures potentially decreasing Rmax. On the other hand, the effect of rain and RH on Rmax was more complex. At high temperatures, high RH tended to lower Rmax regardless of rain, while at low temperatures, a large amount of rain tended to lower Rmax, especially when RH was high.

4. Discussion

4.1. *Variation in gluten quality*

The analyzed wheat material comprises samples from field trials from 17 seasons (2005–2022), resulting in a total of 70 environments. The results showed that there was a large variation in the viscoelastic properties of gluten in these samples. The variations presumably relate to the Norwegian climate, which is characterized by relatively cool and decreasing temperatures between heading and harvest, combined with highly variable rainfall both in intensity and frequency. Overall, the results showed a large variation in the elastic property (Rmax) of gluten between seasons but also within a season between different fields. Less variation was found in gluten viscosity (Ext). Moreover, there was an inverse relationship between elastic and viscose properties. These results are in line with previous observations by others who show that environmental factors have a large effect on the viscoelastic properties of gluten (Caffe-Treml et al., 2011; Nightingale et al., 1999; Koga et al., 2015; Uhlen et al., 2015). Negative correlations between Rmax and %P and positive correlations between Ext and %P were also found for some seasons. It has been shown previously that increased nitrogen fertilization and a late nitrogen application increase the %P and gliadin/glutenin ratio (see Wieser et al., 2022 for review). The correlations between Rmax, Ext, and %P observed in our study align with their observations, leading to slightly weaker gluten with increased extensibility in samples from the environments with increased %P.

4.2. *G, E, and G*E effect on gluten quality*

Environment and G affected gluten quality differently in the time periods that were investigated. Environmental factors accounted for most of the variation in Rmax in the seasons 2005 to 2007 and 2014 to

Table 3

Mean Rmax for Bjarne and Zebra, and the confidence intervals for the means, that were grown under different weather combinations when physiological maturity was reached for the period 2005–2022. The high and low levels of rain, temperature, and humidity are defined as above and below the median for each parameter, which is 54.6 mm, 16.2 °C, and 77%, respectively. The number of samples in each category is presented in parentheses. For example, the 14 samples of Bjarne that were grown with high levels of rain, temperature, and humidity had an average Rmax of 0.58.

		Temperature high		Temperature low		Mean	
		Bjarne	Zebra	Bjarne	Zebra	Bjarne	Zebra
Rain high	Humidity high	0.58 ± 0.06 (14)	0.59 ± 0.08 (14)	0.47 ± 0.06 (33)	0.43 ± 0.06 (37)	0.50 ± 0.05	0.48 ± 0.05
	Humidity low	0.66 ± 0.06 (9)	0.68 ± 0.07 (9)	0.50 ± 0.11 (12)	0.49 ± 0.11 (12)	0.57 ± 0.08	0.57 ± 0.08
Rain low	Humidity high	0.58 ± 0.12 (12)	0.59 ± 0.11 (12)	0.56 ± 0.12 (10)	0.54 ± 0.12 (9)	0.57 ± 0.08	0.57 ± 0.08
	Humidity low	0.67 ± 0.05 (25)	0.66 ± 0.06 (25)	0.56 ± 0.09 (10)	0.52 ± 0.15 (10)	0.64 ± 0.05	0.62 ± 0.06
	Mean	0.63 ± 0.04	0.63 ± 0.04	0.50 ± 0.04	0.47 ± 0.04		

2016. This stood in contrast to the period 2018 to 2022, when G accounted for most of the variation in Rmax. While both E and G were important factors for gluten quality, their interaction effect on gluten quality was small for all periods.

The large effect of E on Rmax could be associated with environments giving low (Rmax <0.5 N) and, in some cases, very low Rmax values (Rmax <0.4 N), causing large in-season variation. For these field trials, low Rmax and high Ext values were measured for most varieties and replicates within the experimental field. A subset of the data (2005–2008) in this study was investigated earlier by Moldestad et al. (2011), which included some of the samples with very low Rmax. The authors suggested that the degradation of proteins by endogenous or exogenous enzymes is a reason for weak gluten. Koga et al. (2015) investigated samples of winter wheat from field trials having either normal or very weak gluten and discussed the degradation of gluten proteins by fungal proteases as a possible explanation for weakened gluten. This hypothesis was strengthened by the findings of Koga et al. (2019), which showed that some *Fusarium* spp. secreted proteases that degraded gluten proteins. Aamot et al. (2020) also analyzed the subset of the samples from 2011 to 2014 in this study and found a relationship between low Rmax and high fungal DNA derived from fungi within the Fusarium Head Blight (FHB) complex. It can be speculated that low Rmax values in some of the samples were related to fungal infection, as the incidence of fungal infection increases under frequent rain or high RH conditions.

For the seasons between 2018 and 2022, on the other hand, Rmax values were mostly high, and weather conditions were generally warmer and dryer in the period before and after physiological maturity. In addition, the variety Caress, which possesses weaker gluten than the other varieties, has been included since 2018. Hence, the inclusion of Caress and more favorable weather conditions could have contributed to the higher G effect between 2018 and 2022. G*E interactions were highly significant for Rmax, while it was less significant for Ext, but for both traits, the contribution to variation in MSS was small (2–8%). Uhlen et al. (2015) also found the G*E effect to be highly significant for Rmax under Norwegian climate conditions. This was mainly because the ranking of varieties changed from the environments with low Rmax compared to environments with moderate or high Rmax. Finlay et al., 2007 tested six spring wheat varieties in eleven environments in Canada. They found the environment to be generally the greatest source of variation for wheat yield and quality parameters and genotype to be the second largest source, while G*E contributed less to the variation. Nehe et al. (2019) tested 35 spring wheat varieties in three locations for three years in Turkey and found grain and quality traits to be mostly affected by genotypic factors and secondly by environmental factors, while the interaction effect was found to be small. They found the testing location to be more important than the seasons for the traits tested. Surma et al., 2012 tested 24 varieties of winter wheat at four locations and also found environment and genotype to be the most important factors for variation in grain quality, while the interaction effect was of less importance. The effect of environment in this study was further described by classifying the environments into six classes according to the mean Rmax of Bjarne and Zebra and comparing them with the mean Rmax and Ext of each variety. The varieties responded similarly to environments, giving increasing Rmax from class 1 to 6. On the other hand, the Ext was for most varieties decreasing with increasing Rmax from class 1 to 6, but this differed between the varieties. It is interesting to note that Krabat showed a stable Ext even if Rmax was increasing from slightly below 0.3 N in class 1 to 0.8 N in class 6. Caress showed a similar trend to Krabat, having relatively higher Ext for classes with high Rmax.

The question has been raised whether breeding varieties with stable gluten quality under varying environmental conditions could be possible. However, the results from this study showed small G*E. On the other hand, the experiments comprised a low number of genotypes but with distinct differences in gluten quality according to the Norwegian classification system. Investigating a larger set of genotypes may be necessary to identify germplasm that is more stable in gluten quality. High stability for Ext in Krabat and Caress would be an interesting topic for further investigation.

4.3. Weather conditions and their effects on gluten quality

The data showed that there was a large variation in the elastic property of gluten, largely caused by the environment. Therefore, the effect of weather parameters on Rmax was further investigated. Weather conditions from 2005 to 2022 included both warm and dry seasons like 2006, 2018, and 2021, as well as wet and cold seasons like in 2007, 2012, and 2015. The spring wheat in Norway matures late in the summer and is usually harvested in late August or early September. In the period after physiological maturity, wheat grown in Norway usually experiences decreasing temperatures with high RH during the night and morning, and in some seasons, wheat plants are subjected to frequent rain during this period. Aussenac et al. (2020) tested 130 wheat varieties at six locations in France for three years and found that the accumulation of polymeric proteins was, to a large extent, controlled by the environment during wheat grain development. Moldestad et al. (2011) showed that diurnal temperatures above 18 °C during grain filling had a positive effect on gluten resistance. Similarly, Branlard et al. (2020) found that increasing temperatures during the last month of the wheat resulted in increased molecular weights of glutenin polymers. Furthermore, Koga et al. (2020) showed that an increase in grain moisture content due to rain during the grain desiccation phase caused a decreased size of glutenin polymers under field conditions. The disassembly of glutenin polymers was proposed to be an indirect effect of increased moisture. Earlier studies have shown that the environment, including weather conditions, during grain development and maturation has a large effect on gluten quality.

Because Bjarne and Zebra were included in all environments, regression analysis for the two varieties made it possible to study the whole dataset. The other varieties showed similar behavior, but due to the lower number of samples, only the results from Bjarne and Zebra are shown in the paper. Moreover, the processing of the weather parameters in eleven time periods allowed us to study the impact of weather conditions at different grain development stages from heading to harvest.

The regression analyses showed that temperature and rain were among the weather factors that contributed the most to the variation in gluten strength. By including RH and its interactions with temperature and rain, the model was slightly improved, particularly for Bjarne. However, the inclusion of interaction and quadratic terms was more informative than RH for both Bjarne and Zebra.

The regression analysis indicated that the weather conditions around physiological maturity and around heading were the two most important periods influencing the elastic property of gluten. Around physiological maturity, high RH caused by a high amount of rain at low temperatures tended to decrease gluten strength. The regression analysis also indicated that the weather condition between physiological maturity and harvest affected gluten strength to a lesser degree but in a more complex manner. The material comprises field trials with delayed harvest due to rainy weather, which might lead to a quality loss since grain desiccates during the last period before harvest, and the impact of weather in this period may be related to the assembly of glutenin polymers. Koga et al. (2020) observed that high temperatures with dry conditions during grain desiccation promoted, while wet conditions (e.g., frequent rain) during the same period disrupted the assembly of glutenin polymers in the field condition. Branlard et al. (2020) also found a positive effect of temperature on the molecular weight of glutenin polymers during grain maturation. Our results imply that the weather conditions around physiological maturity and in the period before harvest affect the assembly of glutenin polymers and, thus, gluten quality. To counteract this, measures to secure an early harvest could be considered. In addition to the week around physiological maturity, temperature and rain in the period around the heading were found to be important for Rmax. It is not clear how the weather during this period could influence the viscoelastic properties of harvested grain. The wheat plant flowers shortly after heading, and it is reported that flowering time is highly susceptible to fungal infection. Fungal infection by some *Fusarium* spp. is also reported to have a negative effect on gluten quality (Bellesi et al., 2019; Aamot et al., 2020; Koga et al., 2019). Therefore, it can be speculated that certain weather conditions around the heading (i.e., wet conditions with favorable temperature for fungi) facilitate a fungal infection of grain, which leads to decreased gluten quality as discussed in 4.2.

There were some differences between Bjarne and Zebra in how weather parameters explained the variation in Rmax. The differences can be linked to genotypic differences in traits such as earliness and straw stiffness between the varieties. Bjarne is a variety prone to straw breakage after maturity, while Zebra has a strong straw that seldom lodges. Bjarne is earlier maturing than Zebra, and as the trial was harvested on the same day for each environment, Bjarne could systematically be harvested slightly later after maturity compared to Zebra. Moreover, differences in tolerance to fungal infection between the varieties might also be a factor. Our study showed that temperature and rainfall are important weather factors that influence the viscoelastic properties of gluten. However, temperature, rainfall, and their interaction did not fully explain the variation in gluten quality, suggesting several other factors responsible for the variation. It is presumed that these factors interact in a complex manner due to the overall environmental conditions in a field. Further research on a larger group of genotypes grown in multi-location trials could provide increased insight into other environmental factors affecting the viscoelastic properties of spring wheat grown in Norwegian conditions.

5. Conclusion

Our study gave a deeper insight into the variation in gluten quality in spring wheat when grown in a relatively cool and humid climate in Norway. There was a large variation in viscoelastic properties of gluten both between seasons and within seasons in the investigated spring wheat varieties. The variation was largely caused by environmental conditions and genotype, while G*E played a minor role. Temperature and rain were the important environmental factors that affected the gluten quality. Higher temperatures contributed to increased gluten strength, while large amounts of rain leading to high humidity had the opposite effect. The gluten viscoelasticity was mostly affected by weather conditions around heading and physiological maturity. The environmental factors investigated in this study could only explain a part of this variation, and other environmental and genotypic factors are presumed to affect gluten quality.

CRediT authorship contribution statement

Margit Oami Kollstrøm: Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis. **Ulrike Böcker:** Writing – review & editing, Resources, Methodology, Investigation, Funding acquisition, Data curation. **Anne Kjersti Uhlen:** Writing – review & editing, Visualization, Supervision, Project administration, Funding acquisition, Conceptualization. **Annbjørg Øverli Kristoffersen:** Writing – review & editing, Resources, Methodology, Investigation, Funding acquisition, Data curation. **Jon Arne Dieseth:** Writing – review & editing, Supervision, Resources, Methodology, Investigation. **Erik Tengstrand:** Writing – review & editing, Visualization, Formal analysis. **Shiori Koga:** Writing – review & editing, Visualization, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jcs.2024.104095.

- Viscoelastic properties of gluten varied largely between 70 environments.
- The variations were mainly explained by environment (E) and genotype (G).
- The effect of E*G interaction was significant, although small.
- Temperature and rain were the important factors causing the variation.
- Weather during 10-days before harvest was the crucial period for gluten quality.

Data availability

Data will be made available on request.

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