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Response to heat stress and glutenins allelic variation effects on quality traits in durum wheat

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ORIGINAL ARTICLE

HEAT STRESS



WILEY

Response to heat stress and glutenins allelic variation effects on quality traits in durum wheat

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Abstract

In the context of climate change, high temperature is one of the main abiotic stresses hampering durum wheat production. Through the characterization of an international panel of 271 genotypes, this study investigates the effects of heat stress on quality traits and identifies which glutenins (*Glu-1*, *Glu-2* and *Glu-3* loci) alleles are the most important to obtain high gluten strength under optimal and high temperature conditions. In parallel with the wide variability observed in the panel, the genotype and environmental effects, including their interaction, showed highly significant effect on test weight, thousand kernel weight, grain protein content (GPC), sodium dodecyl sulphate sedimentation volume (SDSS) and SDSS index. Only one genotype maintained test weight and thousand kernel weight under heat-stress conditions whereas for GPC, SDSS and SDSS index, most genotypes increased values. All *Glu* loci had significant effects on grain protein content (with the exception of *Glu-B2*), SDSS and SDSS Index. None of the *Glu* loci interacted with the environment or years under study. Among the identified alleles, *Glu-A1b*, *Glu-B1an*, *Glu-B1a*, *Glu-B2a*, *Glu-A3a.x*, *Glu-A3d*, *Glu-B3a* and *Glu-B3ax* (including the LMW-2 pattern) were associated with high values for SDSS and SDSS Index. Genotypes identified in this study, with good performances under optimal and high temperature growing conditions, could be useful for breeding programs. The non-interaction of the *Glu* loci with the environment facilitates the introgression of desired alleles regardless of high growing temperatures.

KEYWORDS

gluten quality, glutenins, heat stress, SDS-sedimentation volume, wheat quality

Key points

- A durum wheat panel of 271 genotypes was characterized for grain quality traits under optimal and heat-stress conditions.
- Genotypes with positive increases in quality traits under heat-stress conditions were identified.
- All *Glu-1*, *Glu-2* and *Glu-3* locus had significant effects on quality traits, except *Glu-B2* for grain protein content.

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- None of the *Glu* loci interacted with the environment or years under study.
- *Glu-1*, *Glu-2* and *Glu-3* loci associated with positive effects on quality traits are reported.

1 | INTRODUCTION

Durum wheat (*Triticum turgidum* subsp. *durum* (Desf.) Husnot) accounts for 6% of the total wheat produced with a projected global production of 33 million tons for 2022 (CMO, 2022). Durum grain is milled into semolina which is used to make pasta as well as other products (Martínez-Moreno et al., 2020). In the context of climate change, abiotic stresses bring great challenges for the improvement in durum wheat to assure global production and meet future demands (Xiao et al., 2020). Rising global temperatures have made the past decade (2010–2019) the warmest on record (NOAA, 2020) while by 2050, the global average temperature could rise by 2–5°C (IPCC, 2014) constraining future food security (FAO, 2019; IPCC, 2018, 2019). As a consequence, cultivars must be adapted to increasing temperatures in order to mitigate their negative impact and ensure food systems resilience (Hays et al., 2022).

Heat stress has been shown to have a negative impact on yield (Mondal et al., 2015; Poudel et al., 2021). Grain protein content (GPC) is one of the most important traits for durum pasta-making quality and is especially affected by heat stress. Different studies reported increases in GPC because of heat stress (Liu et al., 2016; Zhang et al., 2019). Gluten properties (mainly gluten strength), on the other hand, are other important parameters influencing pasta-making quality (Delcour et al., 2012; Guzmán et al., 2022). Gluten is composed of gliadins and glutenins. Glutenins are further divided into high- and low-molecular-weight glutenins (HMW-Gs and LMW-Gs, respectively) and in durum wheat are encoded by the *Glu-A1*, *Glu-B1*, *Glu-B2*, *Glu-A3* and *Glu-B3* loci. In earlier studies, the LMWGs were classified as LMW-1 and LMW-2 associated with low and high gluten strength, respectively. Later, specific alleles for those loci have been associated with different levels of gluten strength. For instance, the alleles *Glu-B3t*, *Glu-B3j* and *Glu-B3r* are associated with high gluten strength while the alleles *Glu-B3s*, *Glu-B3k* and *Glu-B3aa* are linked with low gluten strength (Ruiz & Giraldo, 2021). This information is useful for durum breeders to select parents for crosses and as a selection tool when other approaches are not available.

Glutenins, as major components of GPC, are also affected by heat; cultivars affected by this stress had lower glutenin/gliadin ratios resulting in weaker and more extensible gluten (Labuschagne et al., 2016). Additionally, stability of gluten properties across different environmental conditions, and therefore ranking of genotypes for quality parameters, has been only investigated by few studies (Guzmán et al., 2016; Sissons et al., 2018); consequently, determining possible associations between heat stress and *Glu* loci variation is also of importance for breeding programs.

Comparative studies are carried out at best in broad, diverse and collections representative of the germplasm of interest. Herein, we characterized the “UNIBO Durum Panel” that includes in balanced proportions a representation of varieties and breeding lines from the Mediterranean area, Europe, North America and CIMMYT/ICARDA breeding programs (Condorelli et al., 2018; Maccaferri et al., 2016).

The objectives of this study were: 1- to analyse the effects of heat stress on quality traits on a panel representative of cultivated durum germplasm; 2- to define which *Glu* locus, alleles and their haplotype combinations are the most relevant and suitable to obtain a production characterized by high gluten strength under both optimal and heat-stress conditions. This information will be useful to develop cultivars that combine heat-stress tolerance and desirable quality, which is critical for securing reliable wheat production in the future climate.

2 | MATERIALS AND METHODS

2.1 | Plant materials, field trials and experimental design

The trials were conducted at Ciudad Obregon, Sonora, in the north-western Mexico, during two seasons, 2017–2018 and 2018–2019. The plant material used consisted of an international panel of 271 genotypes (breeding lines and commercial cultivars) assembled and maintained by University of Bologna (“UNIBO durum panel”). Table S1 contains detailed data of the genotypes studied in this investigation. The experimental design was a randomized complete block with two replicates under optimal growing conditions -sown in November- and heat stress -sown in February- (referred as the environment effect). All the trials had full irrigation (>500mm). Temperatures during crop development for both seasons are detailed in Figure 1.

2.2 | Quality traits assessed

Test weight (TW, kg/hL) and thousand kernel weight (TKW, g) (also referred to as grain morphological traits) were obtained through the digital image system SeedCount SC5000 (Next Instruments, Australia). Near-infrared spectroscopy (NIR Systems 6500, Foss Denmark) was used to determine grain protein content (GPC, %) following AACC method 39–10.01, which was calibrated using approved AACC method 46–11.02 (AACC, 2010). Grain samples were milled to whole meal using a Udy type mill. Sodium dodecyl

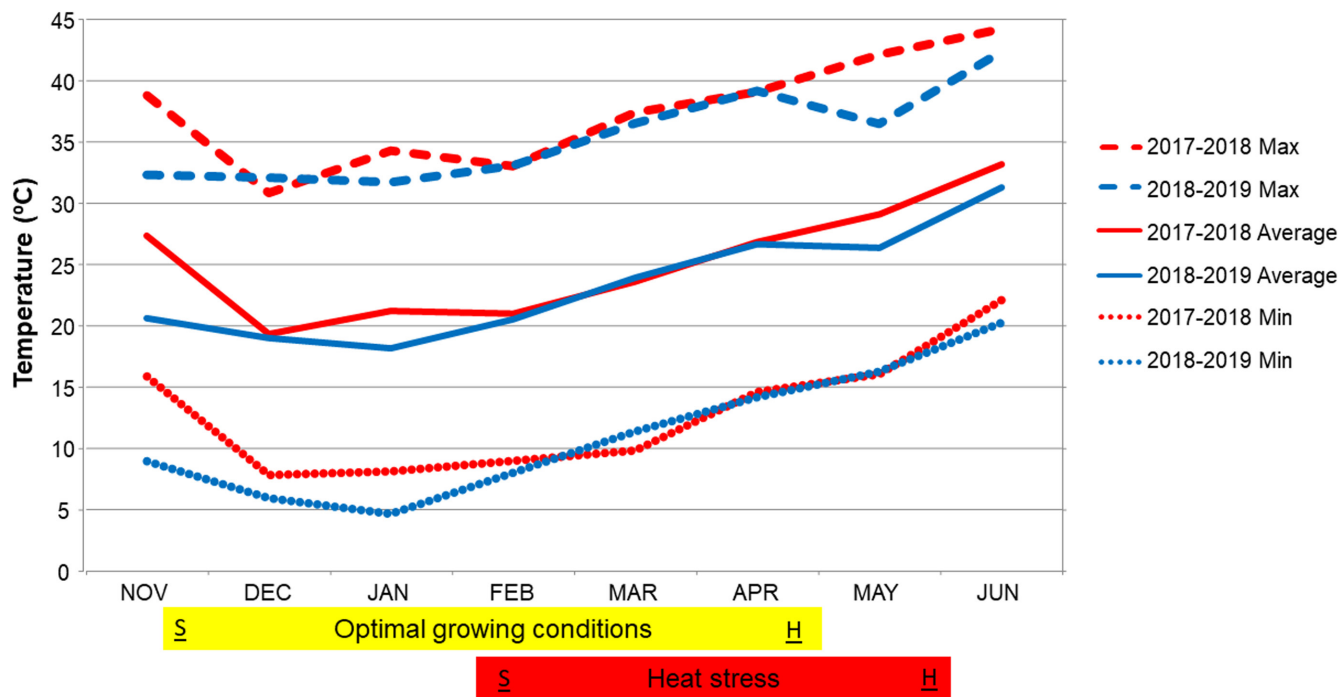


FIGURE 1 Temperature data at Ciudad Obregon, Sonora, Mexico for the 2017–2018 and 2018–2019 field seasons. Underline S and H refers to sowing and harvest time, respectively.

sulphate sedimentation volume from flour samples (SDSS, mL) was carried out according to Peña et al. (1990) using 0.5 g of whole-meal flour. SDSS index was obtained by dividing SDSS by GPC.

2.3 | Glutenins composition

Glutenins subunits composition was determined by sodium dodecyl sulphate polyacrylamide gel electrophoresis (SDS-PAGE) (Maryami et al., 2020). Glutenins were classified using the nomenclature of Branlard et al. (2003) and Jackson et al. (1996); the LMW-1 and LMW-2 classification was also considered (Payne et al., 1984).

2.4 | Statistical analyses

The statistical analyses were performed with SAS® OnDemand for Academics (SAS Institute, Cary, NC, USA). ANOVA analyses were performed with PROC GLM and LSmeans function was used to calculate the least square (LS) means and to determine significant differences between the values using the Fisher's protected LSD at the $\alpha=0.05$ significance level. To assess stability and adaptability, we calculated the Eberhart and Russell parameters available in the GEA-R software (Pacheco et al., 2015). For adaptability, if the "Regression coefficient" parameter (b_i) is close to 1, we have adaptable genotypes while values close to 0 for the "Mean square deviation" parameter (S^2_{di}) indicate stable genotypes across environments.

3 | RESULTS

3.1 | Genotype, environment, year and interaction effects

According to the ANOVA analysis, all factors, including double and triple interactions, had a highly significant effect on all analysed traits (Table S2). The genotype effect explained more than half of the variation found (more than 50% for TW, TKW, and GPC and nearly 80% for SDSS and SDSS Index), followed by the environmental effect (Figure 2).

Under normal planting (control and optimum) conditions, the panel showed wide variability in the order of two to four-fold variations for TKW, SDSS and SDSS Index (Figure 3). GPC and TW had smaller fold-changes of 1.5 and 1.15, respectively. Similar fold variations were found under heat stress. The heat stress had a clear influence, where values were reduced for TW, TKW and increased for protein content. When the 2 years were compared, similar trends were observed among seasons and environment effects.

One of the primary objectives of this study was to identify potential candidates adapted to heat stress to be used in a breeding program; to achieve this goal, we compared the performance of each genotype under optimal growing conditions and heat-stress conditions by estimating the percentage of variation among them. Figure 4 shows percentage of variations and the number of genotypes that decreased or increased performance for both years, as well as the number of genotypes that decreased and increased performance 1 year or the other due to heat stress. The results for TW

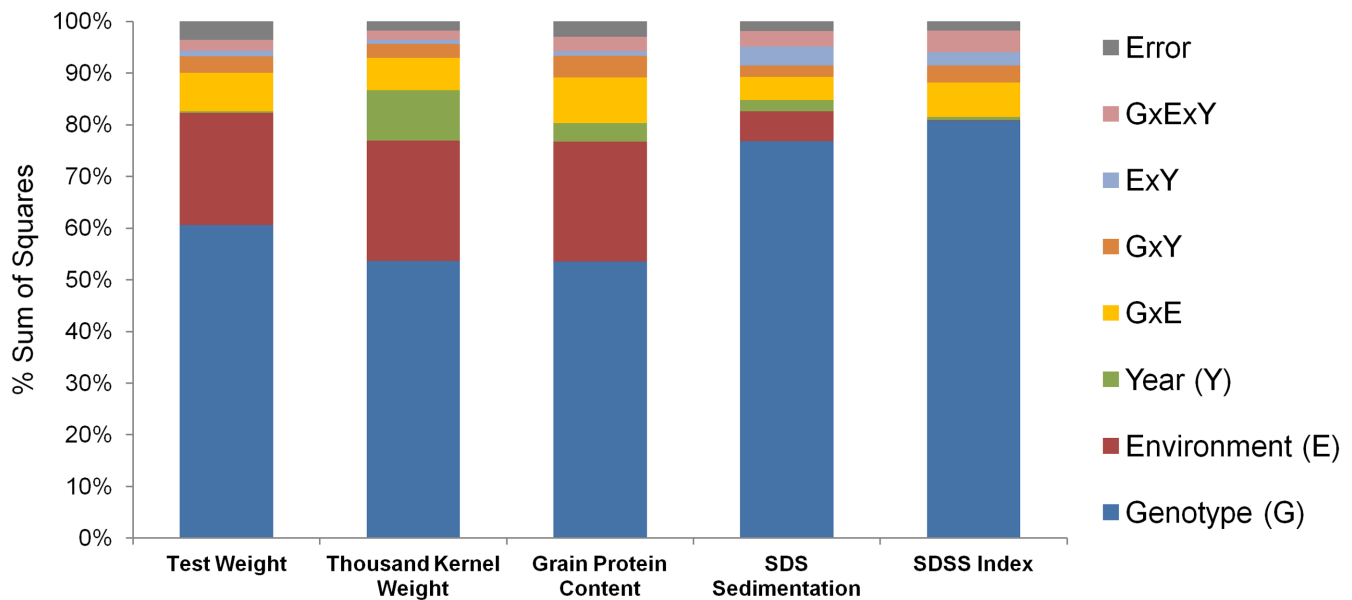


FIGURE 2 Percentage of the total sum of squares from the ANOVA analysis for each independent factor and their interactions, for the quality traits analysed in a durum wheat panel sown in Ciudad Obregon, México, during the 2017–2018 and 2018–2019 seasons. All individual factors and their interactions were significant ($p < .001$).

and TKW clearly showed that most genotypes reduced values as a result of heat stress, whereas for GPC and SDSS, most genotypes increased values. For SDSS Index, there was a tendency for values to decrease and increase depending on the year.

Table S3 shows individual values and percentages of variation for each genotype, trait and season. For grain morphology-related traits, Lira B 45, Telset 5, Helidur and Normanno were the only genotypes of the panel that did not show a decrease in TW values for both seasons. From these genotypes, Lira B 45 was the only one that keep the same TKW under heat conditions. Other genotypes able to keep the same TKW value across both seasons under heat were Ixos, Ofanto, Platani, and Levante. In total, 52 genotypes exhibited greater GPC, SDSS and SDSS Index during both seasons, when grown under heat stress compared with optimal growing conditions. Correlation analyses confirmed the tendencies where negative associations between grain morphological and quality traits both under optimal and heat-stress conditions were observed (Table S4). In general, looking at the overall end-use quality results, the genotypes could be divided into two sub-groups: those with large increases in processing and end-use quality traits but also large decreases in TW and TKW, and those with positive increases in GPC, SDSS and SDSS Index but small decreases in TW and TKW. Genotypes Ombit 1, Waskana and Kamilaroi were the best within the second sub-group.

To describe the genotypes evaluated in greater depth, two further analyses were performed to complement previous characterization. The first involved an ANOVA followed by an LSD fisher's test on the combination of years and treatments as individual environments (E): E1: 2017–2018_Optimal conditions, E2: 2017–2018_Heat stress; E3: 2018–2019_Optimal conditions and E4: 2018–2019_Heat stress. The second was carried out to characterize the genotypes' adaptation and stability using the Eberhart and Russell parameters.

ANOVA analyses showed that for all traits the double interactions Environment x Genotype were significant (data not shown); based on this, Tables S5–S9 show LSD Fisher's tests for each trait while Table S10 shows Eberhart and Russell's coefficients for adaptability and stability. The combination of these analyses with the previous ones allows a more accurate assessment of each genotype's performance. For instance, for TW and TKW, Lira B 45 did not show significant differences for the same years between treatments but showed significant differences between some treatments for different years. In this regard, it showed good adaptability and stability for TW and medium for TKW compared to the other genotypes. For those genotypes with positive increases in technological quality and small decreases in TW and TKW (Ombit 1, Waskana and Kamilaroi) similar trends were observed: null or low significant differences for TW and some differences for TKW and quality traits among the four environments; these genotypes, also showed intermediate adaptability and stability compared to the other genotypes.

3.2 | Glutenins composition and its relationship with heat stress

Limited information is available on the interaction between different glutenins and heat stress and the effects on quality traits. For this reason, the contribution of the different glutenin loci and their interactions with heat stress on quality traits was investigated in the panel. The number and frequency of each allele at each *Glu* locus and LMW patterns used for the analysis are shown in Table S11 (full description in Table S1).

According to the Catalogue of Gene Symbols for Wheat and supplements (<https://wheat.pw.usda.gov/GG3/wgc>), the subunits

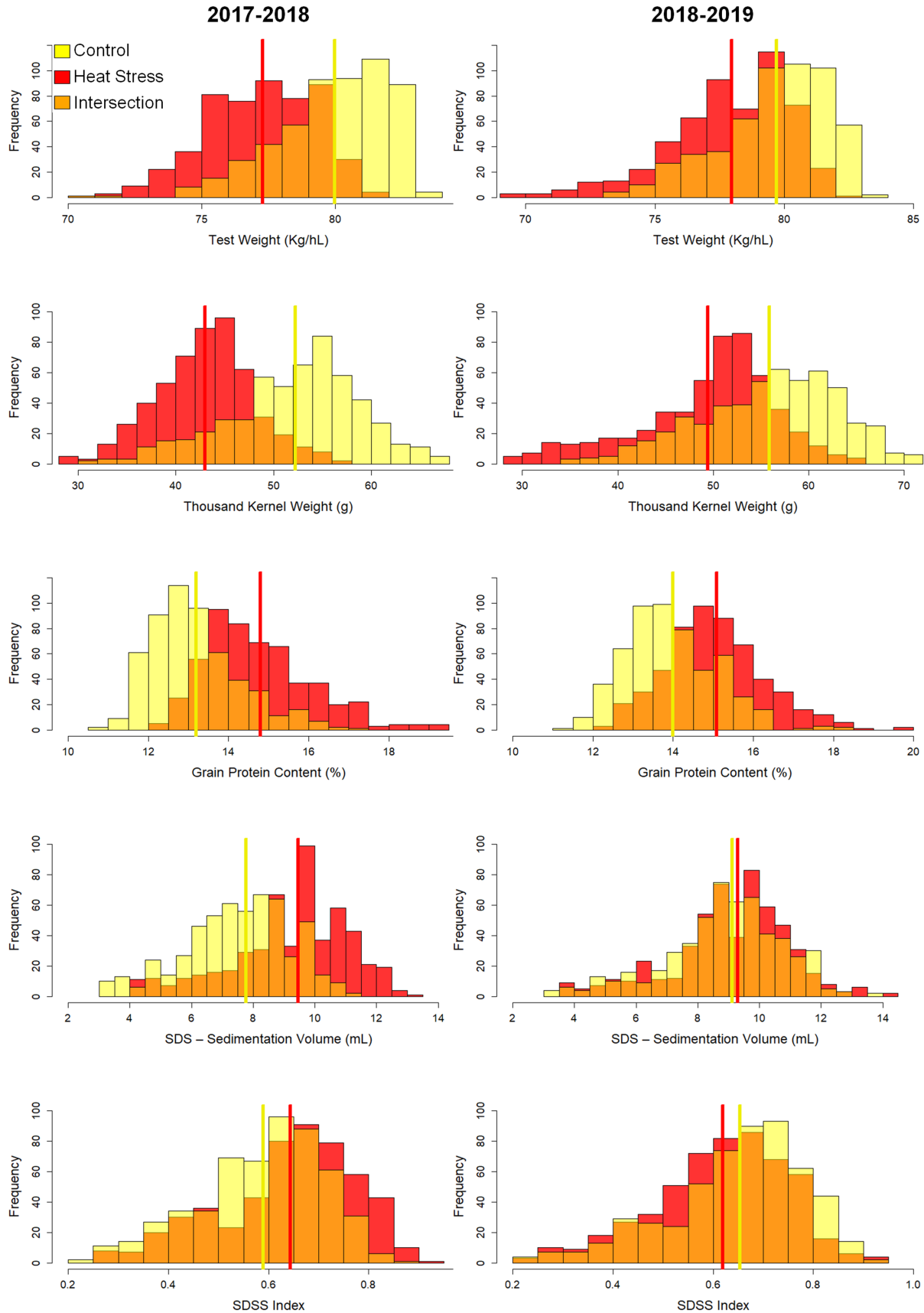


FIGURE 3 Histograms of the quality traits analysed within a durum wheat panel grown in Ciudad Obregon, México, during the 2017–2018 (left side) and 2018–2019 (right side) seasons under optimal and heat-stress conditions. Intersection refers to the overlapping between histograms. Thin lines indicate the average value for each treatment.

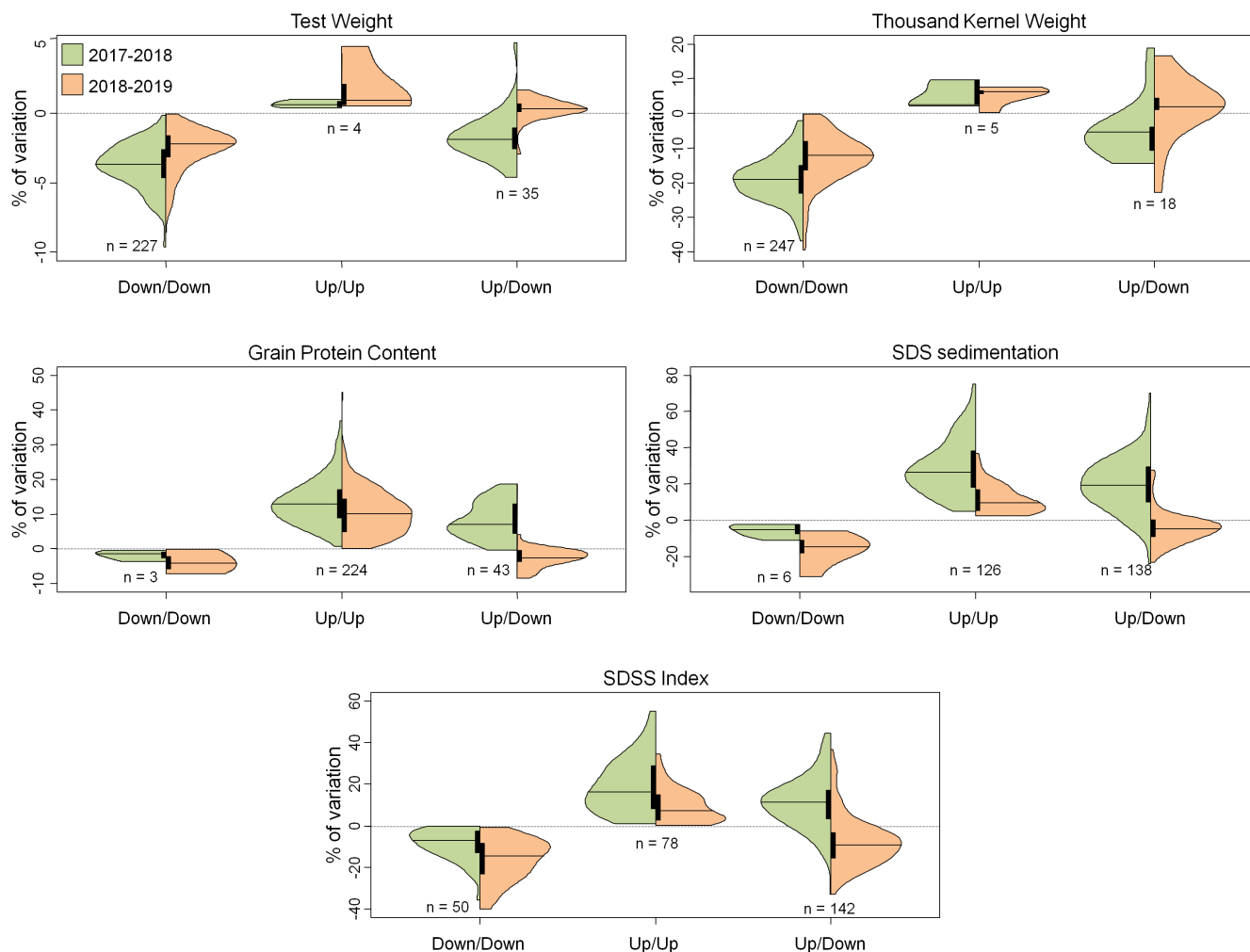


FIGURE 4 Percentage of variation and number of genotypes with reduced (Down/Down), increased (Up/Up), and reduced and increased (Up/Down) values of the analysed quality traits under heat-stress conditions during the 2017–2018 and 2018–2019 seasons.

combinations 5+10 for *Glu-A3* and 14+18, 2+4+13+19 and 2+4+15+18+19 for *Glu-B3* (described previously by Nazco et al., 2014) were not annotated, and we tentatively propose the nomenclature of *Glu-A3bd*, *Glu-B3ay*, *Glu-B3az* and *Glu-B3ba* for them. In addition to this, at the *Glu-A3* and *Glu-B3* loci, different novel combinations of subunits not reported previously were identified. Following the previous order, we proposed to name them as follows: *Glu-A3be* (5+10+11+20), *Glu-A3bf* (5+10+20), *Glu-B3bb* (13+14+18), *Glu-B3bc* (2+4+15+16+17), *Glu-B3bd* (2+4+15+16+19), *Glu-B3be* (2+4+8+9+13+16+19), *Glu-B3bf* (2+8+9+13+16+19) and *Glu-B3bg* (3+8+9+13+16). Figure S1 shows some of the identified alleles in this study by SDS-PAGE.

We then identified 54 haplotypes across the panel. Three combinations accounted for more than half of the haplotypes: *c-b-a-a-a* (26.2%), *c-d-a-a-a* (14.8%) and *c-e-a-a-a* (12.9%) for the *Glu-A1*, *Glu-B1*, *Glu-B2*, *Glu-A3* and *Glu-B3*, respectively (Table S1).

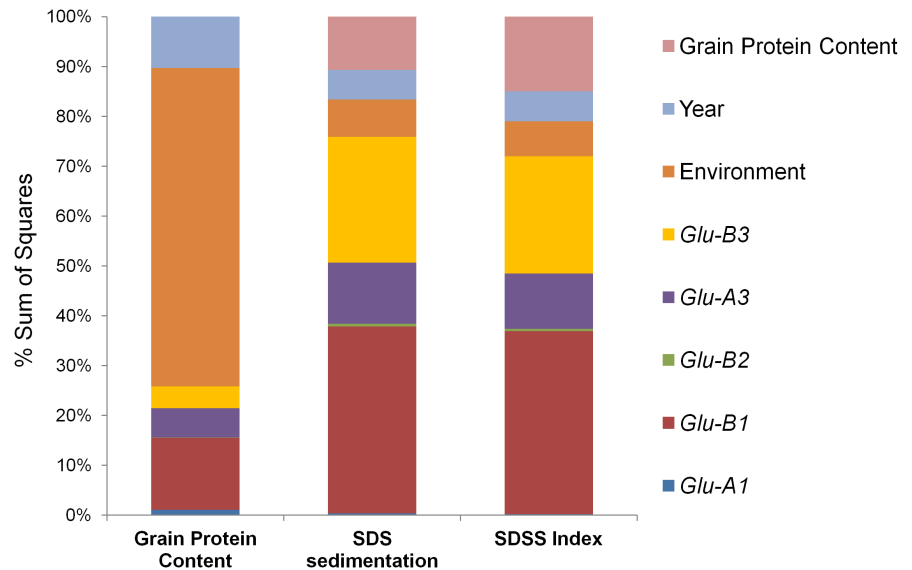
To describe the impact of each *Glu* locus and of the heat stress on the quality parameters, an ANOVA analysis including all effects was conducted (Table S12). With the exception of *Glu-B2*, all *Glu* loci had significant effects on GPC; for this trait, the environmental effect

accounted for the majority of the variation (Figure 5). For SDSS and SDSS index, all *Glu* loci had significant effect (with the exception of *Glu-A1* for SDSS index); in this case, most of the variation was explained by the *Glu-B1* and *Glu-B3* loci (Figure 5).

Individual ANOVA analyses for each *Glu* locus were performed and revealed that none of the interactions, including *Glu* loci with environmental effect, were significant (Table 1). All glutenin loci had significant effects for the three quality parameters, while the environmental effect was significant primarily for GPC. Same results were found for LMW-1/LMW-2 classification.

Figure 6 shows Ls means bar plots for each trait for each *Glu* locus and identified alleles as well as for LMW-1 and LMW-2 patterns. Data were averaged across environments and years due to no significant interactions with *Glu* loci. At the *Glu-A1* loci, *Glu-A1b* (subunit 2*) loci was associated with higher GPC, SDSS and SDSS index compared with the *Glu-A1c* (null) allele. At the *Glu-B1* locus, uncommon sub-units *Glu-B1an* (6) and *Glu-B1a* (7) had high values for GPC and highest values for SDSS and SDSS index; the common sub-unit *Glu-B1d* (6+8) also was associated with high SDSS index, followed by *Glu-B1b* (7+8). For *Glu-B2*, allele *a* (12) had the

FIGURE 5 Percentage of the total sum of squares from ANOVA analysis for each *Glu* locus and environmental effect for quality traits in a durum wheat panel sown in Ciudad Obregon, México, during the 2017–2018 and 2018–2019 seasons. SDSS Index = SDS sedimentation volume / Grain protein content.



highest SDSS and SDSS index values followed by *Glu-B2b* (null). At the *Glu-A3* loci, allele *Glu-A3i* (5 + 20) and *Glu-A3bd* (5 + 10) showed the best performance for GPC but low performance for SDSS and SDSS Index where highest values were found for *Glu-A3a.x* (6.1) and *Glu-A3d* (6 + 11). At the *Glu-B3* loci, *Glu-B3ah* (8 + 9 + 16) was associated with medium or low performance for SDSS and SDSS Index. *Glu-B3a* (2 + 4 + 15 + 19) and *Glu-B3ax* (2 + 4 + 15 + 18) showed high performance for SDSS and SDSS index. *Glu-B3f* (2 + 4 + 15 + 17), *Glu-B3bc* (2 + 4 + 15 + 16 + 17) and *Glu-B3bd* (2 + 4 + 15 + 16 + 19) alleles had acceptable and high values across the three traits. Regarding the LMW patterns, LMW-2 was associated with higher SDSS and SDSS Index.

Finally, we looked at how the three quality traits performed across the 54 haplotypes by characterizing their aptitude based on averages (Table S13). Haplotypes 18 and 23 (*Glu-A1b*, *Glu-B1d*, *Glu-B2a*, *Glu-A3a* and *Glu-B3a*, and *Glu-A1c*, *Glu-B1f*, *Glu-B2a*, *Glu-A3h* and *Glu-B3a*, respectively) showed the highest values for GPC (16.4% on average). The highest SDSS values were found in haplotype 27 (*Glu-A1c*, *Glu-B1e*, *Glu-B2a*, *Glu-A3ax* and *Glu-B3a*), and haplotype 18 (12.4 mL and 11.4 mL, respectively). Furthermore, haplotype 27 had the highest value for SDSS Index (0.87) followed by haplotype 17 (*Glu-A1c*, *Glu-B1b*, *Glu-B2a*, *Glu-A3c* and *Glu-B3g*). The low frequency of the aforementioned haplotypes should be noted since they were each represented by only one or two genotypes. Analysing the top 10 genotypes for the three quality traits we found that specifically alleles *Glu-A1c*, *Glu-A3a*, *Glu-B3a* and *Glu-B2a* were the most frequently repeated combination for highest values for SDSS and SDSS Index.

4 | DISCUSSION

With a changing climate and rising temperatures in the world's major wheat-producing areas (Toreti et al., 2019), wheat-breeding programs are critical to ensuring the development of

innovative varieties with a stable yield and end-use quality (Ferne et al., 2022). This study evaluated 271 genotypes in a diverse durum panel under heat stress environments for TW, TKW and quality traits. According to the ANOVA analyses, all the main effects and interactions, for all traits, were significant. The genotype accounted for the majority of the observed variance, demonstrating its significant influence on TW, TKW and quality traits. The effect of heat stress was also significant: it was the second source of variation for GPC and SDSS while for TW and TKW it was the Environment x Year interaction. Our findings agreed with previous research (Aberkane et al., 2021; Al-Doss et al., 2010; de Leonardis et al., 2015); however, in studies where the proportion of the sum of squares was informed, the orders of factors which explain the main source of variation, in some cases, differed. In Li et al. (2013), the environment effect explained mainly the variation in GPC and TKW, same as Aberkane et al. (2021) and Modhej et al. (2008) for TKW. For Guzmán et al. (2016) and Ozkan et al. (1998), TW was primarily defined by the environment. The different genotypes/backgrounds, environmental/management conditions (including irrigation, which may have influenced the traits), heat intensity and years effects may explain the divergences in terms of the most important sources of variation. Besides these, reduction in TW and TKW and increase in GPC due to the heat stress, were consistent across different studies (Al-Doss et al., 2010; Guzmán et al., 2016; Li et al., 2013; Sissons et al., 2018). Regarding the genotypic variation, it is important to highlight the diversity and origin of the cultivars included in the panel. Condorelli et al. (2018) previously investigated the molecular structure of the UNIBO panel through an Illumina iSelect 90K wheat SNP array (Wang et al., 2014) and discovered eight different subgroups associated with different breeding programs around the world. The significant genotypic diversity may explain why genotypic effects were larger than environmental effects in our results. Finally, the approach of delaying planting to explore the impacts of heat stress is valid and has been applied in multiple studies. However, it is important to note

TABLE 1 Effects of the *Glu* loci, environment, year and, their interactions on quality traits. For SDSS and SDSS index, GPC was included as covariate in the model.

Source of variation	df	Sum of squares		
		Grain protein content	SDS-sedimentation volume (SDSS)	SDSS index
<i>Glu</i> -A1	1	12.3**	28.4**	0.12**
Environment (E)	1	50.3***	5.2	0.02
Year (Y)	1	5.4	4.6	0.02
Grain Protein Content		-	155.0***	2.07***
<i>Glu</i> -A1×E	1	3.0	0.1	0.001
<i>Glu</i> -A1×Y	1	0.0	0.1	0.0003
E×Y	1	0.2	9.9	0.05
<i>Glu</i> -A1×E×Y	1	0.4	0.1	<0.001
<i>Glu</i> -B1	7	286.6***	856.0***	4.37***
Environment	1	99.4***	28.2**	0.12**
Year	1	11.0**	5.4	0.03
Grain Protein Content		-	113.0***	2.09***
<i>Glu</i> -B1×E	7	14.2	10.4	0.05
<i>Glu</i> -B1×Y	7	8.2	9.7	0.07
E×Y	1	3.6	27.0**	0.13**
<i>Glu</i> -B1×E×Y	7	7.2	27.0	0.14
<i>Glu</i> -B2	2	26.3***	183.1***	0.98***
Environment	1	35.8***	2.1	0.02
Year	1	3.6	2.7	0.02
Grain Protein Content	1	-	156.8***	2.07***
<i>Glu</i> -B2×E	2	0.2	4.0	0.01
<i>Glu</i> -B2×Y	2	0.1	0.2	<0.001
E×Y	1	1.1	4.4	0.03
<i>Glu</i> -B2×E×Y	2	0.1	2.5	0.01
<i>Glu</i> -A3	11	197.8***	3015.7***	15.1***
Environment	1	70.5***	1.2	0.01
Year	1	10.4**	3.0	0.02
Grain Protein Content		-	202.5***	1.54***
<i>Glu</i> -A3×E	11	24.0	22.6	0.09
<i>Glu</i> -A3×Y	11	17.1	7.6	0.03
E×Y	1	2.9	12.5*	0.06*
<i>Glu</i> -A3×E×Y	11	9.9	23.8	0.10
<i>Glu</i> -B3	18	126.0***	3497.4***	17.49***
Environment	1	63.2***	3.1	0.04*
Year	1	14.1**	7.5*	0.05*
Grain Protein Content	1	-	210.4***	1.57***
<i>Glu</i> -B3×E	18	28.1	15.8	0.04
<i>Glu</i> -B3×Y	18	17.1	13.4	0.05
E×Y	1	5.8*	7.3*	0.04*
<i>Glu</i> -B3×E×Y	18	12.3	25.2	0.10
LMW	1	15.6***	2620.3***	12.9***
Environment	1	307.4***	50.3***	0.3***
Year	1	44.8***	27.4***	0.2***

TABLE 1 (Continued)

Source of variation	df	Sum of squares		
		Grain protein content	SDS-sedimentation volume (SDSS)	SDSS index
Grain Protein Content	1	-	187.8***	1.8***
LMW×E	1	2.9	2.2	<0.001
LMW×Y	1	1.5	2.9	<0.001
E×Y	1	15.2***	47.4***	0.3***
LMW×E×Y	1	0.2	12.1*	<0.001

***p<.001; **p<.01; *p<.05.

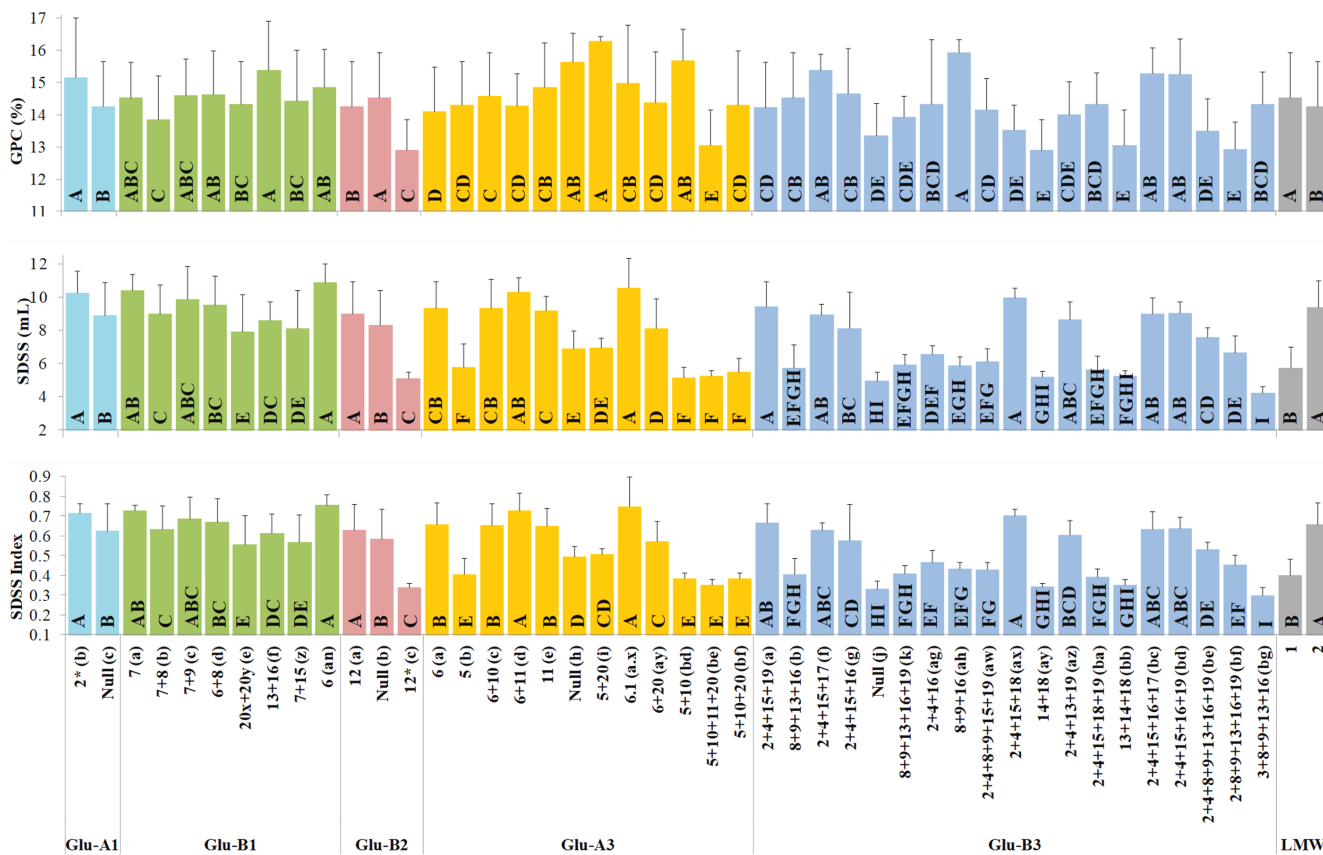


FIGURE 6 LS means values for grain protein content (GPC), flour SDS-sedimentation volume (SDSS) and SDSS Index of the genotypes carrying specific *Glu-1*, *Glu-B2* and *Glu-3* alleles; LMW classification was also included. Differences among loci are represented by capital letters based on the LSD Fisher test ($\alpha=0.05$). Black bars represent standard error.

that delaying sowing accelerates development not only due to temperature impacts, but also due to the influence of longer days, which affects not only grain filling but also the duration of the vegetative phase. This effect which can interact differently with the genotypes can also influence the traits studied here (see Fleitas et al., 2020; Sissons et al., 2018).

The study aimed to characterize heat stress-adapted candidates for breeding programs. Durum wheat varieties Telset 5, Helidur and Normanno did not show a decrease of TW values under heat stress across the two seasons, whereas varieties Ixos, Ofanto, Platani and Levante had similar TKW values under heat stress. Variety Lira B 45 was the only one that kept both TW and

TKW under stress with acceptable adaptability and stability compared to the other genotypes. The rest of the varieties reduced TW/TKW in both years or at least one of them. TW is determined by changes in grain density or shape; because it can be affected by heat at different periods during grain filling (Tashiro & Wardlaw, 1990), the phenotypes observed here were dependent on the times when stresses occurred. Well known is the negative correlation between yield and grain morphological traits with GPC which can be explained due to a concentration effect given the lower levels of starch accumulated affecting TKW, as reported in previous studies (Balla et al., 2011; Iqbal et al., 2016). In our case, it was not possible to identify genotypes with positive increases

in TW, TKW and end-use quality traits. In this context, several genotypes (52 in total) increased GPC, SDSS and SDSS Index, during both seasons under heat stress. From this group, Ombit 1, Waskana and Kamilaroi showed the smallest decreases in TW and TKW showing intermediate adaptability and stability for all the traits. It has been suggested that the accumulation of additional storage proteins would be a compensatory mechanism for the lower starch deposition by maintaining a stable grain filling rate (see Farooq et al., 2011). In line with our findings, Spiertz et al. (2006) discovered genetic variability in plant N and starch accumulation, as well as N transfer efficiency in response to heat stress. In their study, the protein content of cv. Lavett had a negative correlation with grain dry mass, whereas the cv. Attila protein content remained relatively stable throughout a wide range of grain dry mass in response to heat stress. Regarding SDSS and SDSS Index, different factors may explain positive increases. Laino et al. (2010) observed a 50% increase in gluten protein abundance under heat stress, while Dupont et al. (2006) and Phakela et al. (2021) observed increased levels of HMW proteins under high temperatures. Therefore, some specific genotypes under heat stress not only increase their protein content but also their intrinsic protein quality, at least in terms of gluten strength. In this sense, genetic variation has already been reported (Blumenthal et al., 1995), and certain genotypes exhibited improved quality despite heat stress because of greater grain protein concentration (Hernández-Espinosa et al., 2018). Nevertheless, it was not a general trend observed in the present study, particularly in the second-year trial when the heat stress was stronger, and for many genotypes a lower gluten strength was observed under such condition, despite the higher recorded protein contents. Different studies propose that the technological quality increases until it reaches the threshold of 30°C but decrease it beyond 35°C (Corbellini et al., 1997; Johansson et al., 2002, 2013; Randall & Moss, 1990; Wrigley, 2007). The generally favourable effects of late sowing on gluten strength (as measured by increases in SDSS) revealed that heat-stress levels were moderate, similar conclusions were reached by Sissons et al. (2018) in their study. In this regard, the decrease on the technological quality of specific genotypes may be explained by a greater accumulation of heat-stress proteins during grain filling, detected at temperatures above 30°C and associated with a negative impact on quality (Johansson et al., 2002, 2020; Randall & Moss, 1990). Finally, another factor to consider that impacts technological quality but has not been thoroughly investigated in our study is the variation between day and night temperatures. It has been proposed that the greater the difference, the more the quality may be negatively affected (see Farooq et al., 2011 for a review). It is possible that this effect may have differentially influenced the optimal and heat-stress conditions for the traits studied.

To investigate the role of each *Glu* locus and heat stress on quality traits, we analysed their effects in the same model. All *Glu* loci (except for *Glu-B2*) had significant effects for GPC; however, the environmental effect was clearly the largest source of variation. For

SDSS and SDSS Index, the main sources of variation were *Glu-B1* and *Glu-B3* followed by *Glu-A3*. Magallanes-López et al. (2017) found that the main source of variation for SDSS was explained by *Glu-B3* followed by *Glu-B1*; similar trends were also found by Brites and Carrillo (2001) and Martínez et al. (2004).

A possible interaction between the *Glu* loci and heat stress would imply a site-specific selection limiting breeding programs. In our case, there were no significant interactions between the *Glu* loci and environmental effect or year effects indicating that the main-individual effect of each *Glu* locus on GPC, SDSS and SDSS Index was independent of the environmental conditions. Martre et al. (2003) and Martre et al. (2006) showed using the SiriusQuality model that during grain filling, the N allocation for gliadins and glutenins remained constant and total grain N was considered to be influenced by genotype–environment interactions through source-limitation but not allocation of N between storage proteins (see also Nuttall et al., 2017 for a review); this could be one of the reasons for the lack of interaction in our analyses. This implies that the selection of the best glutenin alleles is an effective tool across different environments and that breeding programs do not need to select specific glutenins combinations for each environment. Related to this, several lines increased SDSS Index for both years and at least for 1 year under heat stress. The absence of a significant interaction between the *Glu* loci and environmental conditions indicates that these increases are not due to the superiority of certain glutenins alleles under heat stress. An increment of the HMW-GS content due to heat stress, could explain such results (Dupont et al., 2006; Laino et al., 2010; Phakela et al., 2021).

Based on the above mentioned, we identified the glutenins alleles and their combinations most favourable to obtain high gluten strength, a topic extensively discussed in the literature (see Ruiz & Giraldo, 2021 for a review). *Glu-A1c* was associated with low values on gluten strength (Aguiriano et al., 2009; Oak et al., 2004). In our study, this allele showed lower values than *Glu-A1b* (2*), however, the unbalance on frequencies (99.3% for *Glu-A3c* and 0.7% for *Glu-A1b*) does not allow for accurate conclusion on this case. According to the literature, *Glu-B1b* (7+8) and *Glu-B1d* (6+8) are associated with positive effects while *Glu-B1e* (20x+20y) with negative effects on gluten strength (Babay et al., 2015; Magallanes-López et al., 2017); this trend was also observed in our study. *Glu-B2a* represented most of the *Glu-B2* alleles in our study; in agreement with previous research (Aguiriano et al., 2009; Nazco et al., 2014), it was associated with modest but positive effects on gluten quality. Positive and negative effects have been found for *Glu-A3a* (6) and *Glu-A3c* (6+10) variants in the literature (Chacón et al., 2020; Sissons et al., 2005). In our case, they were associated with positive than negative effects as they showed one of the highest values for SDSS and SDSS Index. Regardless of having a smaller frequency in the panel (1.5%), interesting results were found for *Glu-A3ax* (6.1) which showed the highest values for SDSS and SDSS Index; Babay et al. (2015) and Magallanes-López et al. (2017) also associated this allele

with positive effects. Respecting *Glu-B3* and in accordance to the literature (Nazco et al., 2014; Vázquez et al., 1996), *Glu-B3a* (2+4+15+19) was associated with the highest values and *Glu-B3b* (8+9+13+16) with intermediate/low values for SDSS and SDSS index. Besides, two novel alleles for *Glu-A3* and six for *Glu-B3* were identified in the current study. Finally, the LMW-2 pattern was associated with higher gluten quality, as mentioned in the literature (see Giraldo et al., 2020).

At the haplotype level, positive combinations of *Glu-B1b* (7+8) or *Glu-B1d* (6+8) with *Glu-A3a* (6) or *Glu-A3c* (6+10) with *Glu-B3a* (2+4+15+19) and *Glu-B2a* (12) have been proposed (Babay et al., 2015; Magallanes-López et al., 2017; Sissons et al., 2005). In our study, haplotype 18 (*Glu-A1b*, *Glu-B1d*, *Glu-B2a*, *Glu-A3a*, *Glu-B3a*, 1 genotype) ranked second for SDSS (11.38mL) and had one of the highest SDSS Index values as well (0.69). The other positive combinations on quality indicated above showed acceptable values in our analyses as well: haplotype 1 (*Glu-A1c*, *Glu-B1b*, *Glu-B2a*, *Glu-A3a*, *Glu-B3a*), haplotype 2 (*Glu-A1c*, *Glu-B1d*, *Glu-B2a*, *Glu-A3a*, *Glu-B3a*), haplotype 4 (*Glu-A1c*, *Glu-B1d*, *Glu-B2a*, *Glu-A3c*, *Glu-B3a*), and haplotype 6 (*Glu-A1c*, *Glu-B1b*, *Glu-B2a*, *Glu-A3c*, *Glu-B3a*).

5 | CONCLUSION

Breeding for heat tolerance will become more important in the near future due to rising temperatures. In this study, we identified the most outstanding genotypes from a durum panel grown under heat stress conditions. Very few of the analysed genotypes were not negatively affected by heat stress in TW and TKW traits, whereas several genotypes grown under heat stress exhibited an equal or improved gluten strength. All these genotypes may be interesting sources of variation for breeding programs targeting areas under heat-stress conditions. None of the *Glu* loci interacted with the environmental effect or years under study, which in some way facilitates future breeding strategies. In terms of glutenin composition, the characterization of the *Glu* loci allowed the identification of alleles associated with positive effects on gluten quality. Among the most representative alleles, *Glu-A1b*, *Glu-B2a* and *Glu-B3a* had a positive performance on end-use quality traits. Alleles *Glu-B1a*, *Glu-B1an* and *Glu-A3ax*, even if were present in only few genotypes, could be promising alleles for further characterizations.

AUTHOR CONTRIBUTIONS

Facundo Tabbita: Writing – original draft; formal analysis; writing – review and editing; data curation; methodology. **Karim Ammar:** Conceptualization; resources; writing – review and editing; investigation; funding acquisition; project administration; supervision. **María Itria Ibbá:** Investigation; funding acquisition; writing – review and editing; supervision; resources; data curation. **Francisco Andrade:** Writing – review and editing; data curation. **Marco Maccaferri:** Resources; writing – review and editing; conceptualization. **Maria Corinna Sanguineti:** Conceptualization; writing – review and editing; resources. **Roberto Tuberosa:** Conceptualization; writing – review

and editing; resources. **Carlos Guzmán:** Conceptualization; investigation; funding acquisition; writing – review and editing; data curation; supervision; resources.

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DATA AVAILABILITY STATEMENT

All the data used for this study are completely available in Table S1.

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SUPPORTING INFORMATION

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