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RESEARCH ARTICLE

Effects of the functional *Gpc-B1* allele on soft durum wheat grain, milling, flour, dough, and breadmaking quality

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Abstract

Background and objectives: Utilization of durum wheat (*Triticum turgidum* subsp. *durum*) can be enhanced by increasing grain and flour protein content. One strategy to increase protein content is by introducing the functional *Gpc-B1* allele from wild emmer (*Triticum turgidum* subsp. *dicoccoides*).

Findings: Introduction of the functional *Gpc-B1* allele into soft kernel durum increased grain and flour protein by 17 g/kg, increased dough strength as evidenced by SDS sedimentation volume and Mixograph dough mixing parameters, and increased straight-dough pan bread volume. When grown under arid conditions, high protein (151 g/kg) samples had decreased loaf volumes indicative of inelastic doughs. The functional *Gpc-B1* allele was associated with decreased test weight, a small increase in SKCS hardness, and a modest increase in flour ash; otherwise, milling performance was not affected.

Conclusions: Introgression of the *Gpc-B1* functional allele from dicoccoides into durum wheat can improve dough strength and breadmaking quality. The effect tends to be consistent over environments but overall, *Gpc-B1* made only a modest improvement in durum wheat breadmaking quality. Further studies with concomitant selection at other loci are needed to see the effects of *Gpc-B1* among elite germplasm.

Significance and novelty: Durum wheat production and consumption will increase as bread quality improves. The functional *Gpc-B1* allele contributed to improved breadmaking quality. The present report is the first to examine the effect of this allele on breadmaking in durum wheat.

KEYWORDS

bread baking quality, dough strength, durum wheat, gluten, grain protein content (*Gpc*), soft kernel

1 | INTRODUCTION

Protein content (concentration) is an essential quality-determining factor in wheat (*Triticum* sp.) grain and flour utilization. Protein content is highly influenced by weather, soil nutrients, and agronomic management. Nevertheless, protein content can be increased through phenotypic selection among wheat breeding lines and germplasm. However, few major protein-controlling loci have been identified. In this regard, Avivi (1978) reported that wild emmer (*T. turgidum* subsp. *dicoccoides*) (hereafter dicoccoides) had exceptionally high protein, higher than domesticated durum (*T. turgidum* subsp. *durum*) and emmer (*T. turgidum* subsp. *dicoccum*). This discovery highlights the value and opportunities that reside in wild genetic resources.

Joppa and Cantrell (1990) used one of these high protein dicoccoides lines (FA-15–3 ≡ Israel-A) to create a set of chromosome disomic substitution lines in the durum cultivar cv. "Langdon" (LDN). The 6B dicoccoides substitution line (LDN[DIC-6B]) had the highest grain protein of any of the substitution lines and was significantly higher than Langdon (179.5 versus 167.9 g/kg, respectively). In a follow-up study, LDN(DIC-6B) sib lines had a mean grain protein content of 174.9 g/kg versus 161.7 g/kg for Langdon. Further, this grain protein increase was associated with an increase in semolina protein content of 16.2 g/kg. The LDN(DIC-6B) lines had higher 10-g Mixograph scores and superior spaghetti quality. Steiger et al. (1996) used the LDN(DIC-6B) line of Joppa and Cantrell (1990) to develop a recombinant population with the durum cv. Vic. The LDN(DIC-6B)/Vic population had significantly higher mean protein than the control Langdon/Vic population (159.0 versus 155.6 g kg^{-1}). SDS sedimentation volumes, however, did not differ. Kovacs et al. (1998) also used the LDN(DIC-6B) line of Joppa and Cantrell (1990) to develop a recombinant population with the recurrent Canadian durum parent "DT367." In general, BC_2-derived lines were higher in protein than DT367 and had higher SDS sedimentation values, higher Mixograph total energy, and superior pasta quality. Klindworth et al. (2009) and Ohm et al. (2010) compared the quality of the LDN(DIC-6B) line of Joppa and Cantrell (1990) with similar 6B substitution lines developed using dicoccoides lines PI 481,521 and PI 478,742 (LDN521 and LDN742, respectively). Of the three, LDN(DIC-6B) and LDN742 had significantly higher grain and semolina protein content than Langdon, while only LDN742 had a better (higher) Mixograph score. Grain protein differences compared with Langdon ranged from −0.1 (ns) to 20.2 g/kg ($p < .05$). Molecular marker analysis indicated that LDN742 carried the *Grain protein content-B1* (*Gpc-B1*) alleles such as LDN(DIC-6B) whereas LDN521 did not (Langdon allele). Molecular marker analysis of parents PI 481521 and PI 478742 for *Gpc-B1* was consistent with these results. In Ohm et al. (2010), the dicoccoides chromosome 6B in LDN(DIC-6B) and LDN742 was associated with greater quantity of size-exclusion HPLC fractions comprised of high-molecular-weight polymeric protein and ω-gliadins compared with Langdon, and higher Mixograph scores. Brevis and Dubcovsky (2010) developed two pairs of BC_6 near-isogenic lines (NILs) (± *Gpc-B1*) using a LDN(DIC-6B) derivative ("RSL 65"). The durum breeding line UC1113 and the cv. Kofa were used as recurrent parents. The *Gpc-B1* NILs with the functional allele had significantly higher grain protein content compared with the NILs lacking a functional *Gpc-B1* (in 2005, 136.2 versus 132.1 g/kg and in 2006–2007, 146.5 versus 132.7 g/kg). Brevis et al. (2010) produced an additional pair of NILs in the durum cv. Kronos and included them with the UC1113 NILs, above. The presence of the functional *Gpc-B1* allele was associated with higher grain protein content and wet gluten, longer Mixograph mixing time and peak height, and improved spaghetti quality. Salmanowicz et al. (2017) used the LDN(DIC-6B) line of Joppa and Cantrell (1990) and compared it to Langdon over three environments: N deficit, water deficit, and control. The grain protein content, wet gluten, and Zeleny sedimentation volume of LDN(DIC-6B) were significantly higher than Langdon under all three environments. LDN(DIC-6B) also had greater Rheometer area under the curve, peak time, peak height, and bandwidth after 10 min, and greater R_{max}, extensibility and W_{max} on the Keiffer system compared with Langdon under all three environments. Tab bita et al. (2017) reviewed 25 studies involving *Gpc-B1* conducted over 10 years. In all eleven studies comparing grain protein content, the functional allele of *Gpc-B1* significantly increased grain protein (mean protein content over studies was 155 g/kg). Further details of individual studies are provided above. Fatiukha et al. (2020) used a durum cv. Svevo ×dicoccoides Y12-3 recombinant inbred line (RIL) population to confirm the chromosome 6B short arm (6BS) location of *Gpc-B1*. Like most commercial durum cultivars, Svevo lacked the *Gpc-B1* functional allele for higher protein.

No study to date has examined the effect of *Gpc-B1* on breadmaking in durum wheat. This is likely because first, most durum utilization is focused on pasta, and secondly, that durum has not been viewed as having gluten properties well suited for bread (Morris, 2021). This latter view is not entirely borne out by research (Ammar et al., 2000; Edwards et al., 2007; Hernández-Espinosa et al., 2019; Murray et al., 2017). A secondary factor influencing the lack of research on the effect of *Gpc-B1* on the breadmaking quality of durum wheat is the very hard kernel of durum. The hard kernel texture of durum

precludes milling durum grain into flour without an unacceptably high increase in starch damage and a marked increase in dough water absorption (Dexter et al., 1981; Murray et al., 2016). However, with the advent of soft kernel durum wheat (Morris et al., 2011), this confounding issue has been eliminated (Boehm et al., 2017a; Murray et al., 2017). Here, we examine the effects of the introgression of the functional allele of *Gpc-B1* into soft durum wheat grain, milling, flour, dough, and breadmaking quality.

2 | MATERIALS AND METHODS

"Soft Svevo" (Morris et al., 2011) was crossed with Desert King-High Protein (Desert King HP, PVPP 201000585) (experimental line UC1627, pedigree UC1113-GPV(PI 638741)/6*Desert King), which carries the *Gpc-B1* functional allele derived from wild emmer (dicoccoides). In 2016, the progeny ($F_{4:6}$) RILs were grown as single rows at Yuma, AZ, and at the Washington State University Dryland Research Station near Lind, WA, and in 2017 at the Spillman Agronomy Farm near Pullman, WA. The 2017 samples were grown in replicated plots with two replications for all RILs and the two parents. These full-sib RILs were developed as follows. Beginning at the F_3, kernels were visually inspected and only nonvitreous (i.e., soft) kernels were selected to be advanced via single seed descent. The same process was repeated in the F_4, resulting in 30 soft F_6 lines, 15 of which carried the functional *Gpc-B1* allele from Desert King-High Protein and 15 that carried the nonfunctional Svevo allele at the same locus.

The presence of the functional *Gpc-B1* allele was confirmed in the F_5 generation using the codominant molecular marker *Xuhw89* developed by Distelfeld et al. (2006). Specifically, leaf tissue from F_5 plants was collected for genomic DNA and extracted using the DNeasy 96 Plant Kit (Qiagen). PCRs were carried out in 25 μl reaction volumes containing 100 ng of genomic DNA, 1x Standard Taq Buffer (New England Biolabs), 200 μM dNTPs, 0.2 μM primers, and 0.5 μl of Taq DNA Polymerase (New England Biolabs). Amplifications were performed in a Peltier Thermal Cycler PTC-200 using an annealing temperature of 57°C. PCR products with the fluorescent label were diluted 1:8 in water, and 3 μl of the dilution was added to 9 μl of HiDi Formamide and 0.5 μl of 500-Liz™ internal size standard (Applied Biosystems). The mixtures were denatured at 95°C for 10 min and separated by capillary electrophoresis using a 3130xl DNA Analyzer (Applied Biosystems). The allele size of the PCR products was determined by using the GeneMarker software v3.7 (SoftGenetics).

Test weight, Single Kernel Characterization System (SKCS) kernel hardness, grain protein, flour protein, modified Quadrumat milling, flour ash, and flour Na-dodecyl sulfate (SDS) sedimentation volume were conducted according to Kiszonas et al. (2013). Straight-dough pan bread baking was conducted according to Kiszonas et al. (2015).

Mixograph parameters provided an assessment of dough strength and a prediction of breadmaking potential. "Mixograph time to peak" is the time in minutes required to mix the flour and water dough to the optimum condition for bread baking to the point of minimum dough mobility. This time is evidenced by the "peak" of the mixing curve (Chung et al., 2001). With an optimally hydrated dough, the highest point of the midline Mixograph mixing curve is defined as the "Mixograph time to peak"; the height of the curve at this point is the "Mixograph peak height." "Mixograph work" is the integration of the area under the midline of the mixing curve from time zero to the peak. Lastly, "Mixograph curve width 2 min after peak" is self-explanatory and is related to resistance to overmixing. Mixograph parameters were determined using the Mixsmart software (Mixsmart for Windows version 1.0.404, Lincoln, NE).

Analysis of variance was conducted using a factorial model including genotype (equivalent to the presence or absence of the functional *Gpc-B1* allele), location (representing the individual environments), and the interaction term. Statistical significance of whole models and components thereof were evaluated using the *F* test at alpha =0.05. Individual recombinant inbred lines represented replicates. Trait means were calculated for each allele group and tested for significance using the least significant difference (alpha =0.05).

3 | RESULTS AND DISCUSSION

The durum variety Desert King-High Protein (DKHP) is a popular "desert durum" adapted to the Southwest United States and carries the functional allele of *Gpc-B1* (hereafter referred to as *Gpc-B1*-plus). DKHP was crossed with Soft Svevo, a soft kernel durum variety, to evaluate the effects of *Gpc-B1* on grain quality, the protein content of grain and flour, milling, flour, dough, and breadmaking quality of soft durum. Soft Svevo carries the nonfunctional allele of *Gpc-B1* (hereafter referred to as *Gpc-B1*-minus). After the initial cross was made, only soft-textured kernels were selected, that is, those that carried the puroindoline-containing *Hardness* translocation from the D genome (Boehm et al., 2017; Ibba et al., 2019). For example, the average SKCS hardness value for all genotypes planted in the study was 22.0. All lines were F_4-derived full sibs and can be considered soft-textured RILs. For quality and statistical analyses, the progeny was divided into two allele groups: *Gpc-B1*-plus and *Gpc-B1*-minus.

TABLE 1 Analysis of variance of grain and milling quality of soft durum wheat sibling lines with or without introgression of *Gpc-B1* grown at three locations

Source	Test weight	SKCS hardness	Wheat protein	Flour yield	Break flour yield	Milling score	Flour ash
Whole model R^2	0.84	0.30	0.79	0.30	0.35	0.21	0.30
Whole model *F* value	140.8***	14.9***	133.6***	11.0***	14.3***	9.1***	14.8***
Gpc-B1 F value	328.5***	15.4***	92.1***	0.17	0.54	12.3***	15.1***
Location *F* value	146.9***	28.7***	308.6***	23.2***	33.2***	8.2**	29.2***
Gpc-B1 * location *F* value	10.5***	0.02	2.5	4.7*	5.4**	4.7*	0.0

*0.05–0.01.; **0.01–0.001.; ***<0.001.

TABLE 2 Analysis of variance of flour, dough, and baking quality of soft durum wheat sibling lines with or without introgression of *Gpc-B1* grown at three locations

Source	Flour protein	Flour SDS sedimentation	Mixograph time to peak	Mixograph peak height	Mixograph work	Mixograph curve width 2 min after peak	Loaf volume
Whole model R^2	0.84	0.61	0.43	0.47	0.40	0.32	0.40
Whole model *F* value	139.6***	39.3***	19.9***	23.2***	17.2***	11.2***	12.8***
Gpc-B1 F value	122.7***	26.9***	7.9**	18.0***	6.1*	24.1***	6.3*
Location *F* value	267.6***	83.9***	41.7***	35.5***	37.4***	11.2***	28.1***
Gpc-B1 * location *F* value	4.5*	1.8	1.5	10.2***	0.5	2.6	0.46

*0.05–0.01.; **0.01–0.001.; ***<0.001.

TABLE 3 Mean separation of grain and milling quality soft durum wheat sibling lines with or without introgression of *Gpc-B1*, and location of production

Variable	Test weight ($kg.hL^{-1}$)	SKCS hardness	Wheat protein ($g.kg^{-1}$)	Flour yield ($g.kg^{-1}$)	Break flour yield ($g.kg^{-1}$)	Milling score	Flour ash ($g.kg^{-1}$)
Gpc-B1 plus	76.5	24.3	160	644	426	67.3	5.5
Gpc-B1 minus	79.3	20.1	145	647	427	70.3	5.1
LSD	0.3	2.1	3	NS	NS	1.7	0.2
Lind	77.5	24.8	165	643	426	67.6	5.5
Spillman	77.4	19.1	138	635	407	70.3	5.0
Yuma	80.5	NA	NA	671	463	NA	NA
LSD	0.4	2.1	3	10	14	1.7	0.2

Note: SKCS hardness, wheat protein, milling score, and flour ash from only 2017.

Abbreviations: NA, not available; NS, not significant.

Overall, the analysis of variance modeled the variation in the study moderately well (Tables 1 and 2), with test weight, and wheat and flour protein contents having R^2 values of 0.79–0.84. Other traits were modeled less well, although all models had significant whole model *F*-values. *Gpc-B1* allele status was significant for test weight, SKCS hardness, wheat protein, milling score, flour ash, flour protein, SDS sedimentation volume, the four Mixograph parameters, and bread loaf volume. Only flour yield and break flour yield were not significantly

TABLE 4 Mean separation of flour, dough, and baking quality soft durum wheat sibling lines with or without introgression of *Gpc-B1*, and location of production

Variable	Flour protein (g/kg)	Flour SDS sedimentation ($mL.g^{-1}$)	Mixograph time to peak (min)	Mixograph peak height (units)	Mixograph work ($units^2$)	Mixograph curve width 2 min after peak (units)	Loaf volume (cm^3)
Gpc-B1 plus	143	13.9	2.3	51.1	88.6	10.3	817.6
Gpc-B1 minus	126	11.5	2.0	48.3	99.5	8.0	772.4
LSD	3	0.8	0.2	1.0	7.5	0.9	34.1
Lind	151	13.9	1.7	52.0	75.3	7.8	695.0
Spillman	128	9.9	2.6	48.0	111.8	9.6	838.5
Yuma	112	NA	2.4	47.7	99.1	10.1	816.8
LSD	3	0.9	0.2	1.3	9.5	1.1	45.6

Note: Flour SDS sedimentation from only 2017.

Abbreviation: NA, not available.

influenced by *Gpc-B1* allele. Nevertheless, location was almost always a more influential source of variation compared with *Gpc-B1* allele. The only exceptions were test weight, milling score, and Mixograph curve width 2 min after peak. There were interactions between *Gpc-B1* allele and location for several parameters, though their *F*-values, and thus relative contribution to overall variation, were greatly eclipsed by the main effects. The results indicate that *Gpc-B1* exerts a significant effect on most grain, flour, dough, and breadmaking traits, but less so for milling performance. Overall, environmental influences, though usually greater than that of the *Gpc-B1* allele, were consistent across the study (small interactions). As such, the *Gpc-B1*-plus allele has significant and predictable effects. The actual effects on quality are detailed following.

Tables 3 and 4 present the mean values for each sets of RILs with and without the functional *Gpc-B1* allele, and for the three growing environments. The *Gpc-B1*-plus lines had lower test weight and harder textured kernels. Joppa et al. (1991) reported a significant reduction in test weight associated with the dicoccoides chromosome 6B, whereas Klindworth et al. (2009) and Ohm et al. (2010) found no effect. The recombinant dicoccoides 6B in Brevis et al. (2010) was associated with reduced test weight.

Wheat (grain) protein content was significantly higher in the *Gpc-B1*-plus lines, 160 versus 145 g/kg, respectively. These values are equivalent to the average of eleven studies summarized by Tab bita et al. (2017), which showed a 15.5 g/kg average increase in protein content due to the functional *Gpc-B1* allele.

Flour yield and break flour yield did not differ significantly according to *Gpc-B1* allele status, despite the difference in test weight. Although not the same as soft wheat milling in the present study, Joppa et al. (1991) reported a reduction in semolina and total milling extraction due to the dicoccoides chromosome 6B. Klindworth et al. (2009), however, found no effect of 6B on semolina extraction or ash content. Ohm et al. (2010) similarly found no effect of 6B on semolina yield, but semolina ash was higher in the *Gpc-B1*-plus lines. Brevis et al. (2010) also reported increased semolina ash for *Gpc*-B1-plus recombinants. In the present study, flour ash content was significantly higher in the *Gpc-B1*-plus lines (Table 3). Milling score, a composite score that includes flour ash, was significantly lower for the *Gpc-B1*-plus lines, likely due to the higher flour ash.

Flour protein content paralleled grain protein closely (Tables 3 and 4), with greater mean flour protein levels for the *Gpc-B1*-plus lines (143 versus 126 g/kg). The difference (17 g/kg) was identical to the difference in average grain protein between the two sets of RILs.

SDS sedimentation volume has long been used as a predictor of dough strength in durum wheat (Dick & Quick, 1983). Here, the *Gpc-B1*-plus RILs had greater SDS sedimentation volume compared with *Gpc-B1*-minus RILs (Table 4). However, SDS sedimentation volume is responsive to flour protein (Carter et al., 1999) and the 17 g/kg greater average protein among the *Gpc-B1*-plus RILs likely was the primary reason for the higher SDS sedimentation volume. Steiger et al. (1996) found no significant difference between sets of progeny comparing LDN(DIC-6B)/Vic and control Langdon/Vic. Kovacs et al. (1998) stated that the average sedimentation volume of BC_2 recombinant lines with *Gpc-B1*-plus was greater than the recurrent durum parent.

Dough mixing strength was generally greater in the *Gpc-B1*-plus RILs compared with the *Gpc-B1*-minus lines as evidenced by an increased Mixograph time to peak, Mixograph peak height, and Mixograph curve width 2 min after peak (Table 4). This difference in mixing strength was particularly prominent in the curve width 2 min after peak. There was a 2.3 unit greater Mixograph curve width 2 min after peak indicating greater resistance to overmixing in the *Gpc-B1*-plus RILs. Despite the improved strength and resistance to overmixing of the *Gpc-B1*-plus lines, the Mixograph work, or area under the Mixograph curve, was lower for the *Gpc-B1*-plus lines. This decrease in work could indicate that the dough was less elastic and could not stretch sufficiently because of the extra protein. Joppa et al. (1991) found that the dicoccoides 6B chromosome increased Mixograph score, whereas Klindworth et al. (2009) and Ohm et al. (2010) found that two different dicoccoides 6B chromosomes (both with functional *Gpc-B1*) had significant (increased) and nonsignificant effects on Mixograph score, respectively. Kovacs et al. (1998) indicated that the average Mixograph total energy of BC_2 recombinant lines with *Gpc-B1*-plus was greater than the recurrent durum parent. Brevis et al. (2010) reported an increase of 0.3 min (12%) in Mixograph peak mixing time and a similar 13% increase in peak height due to *Gpc-B1*-plus.

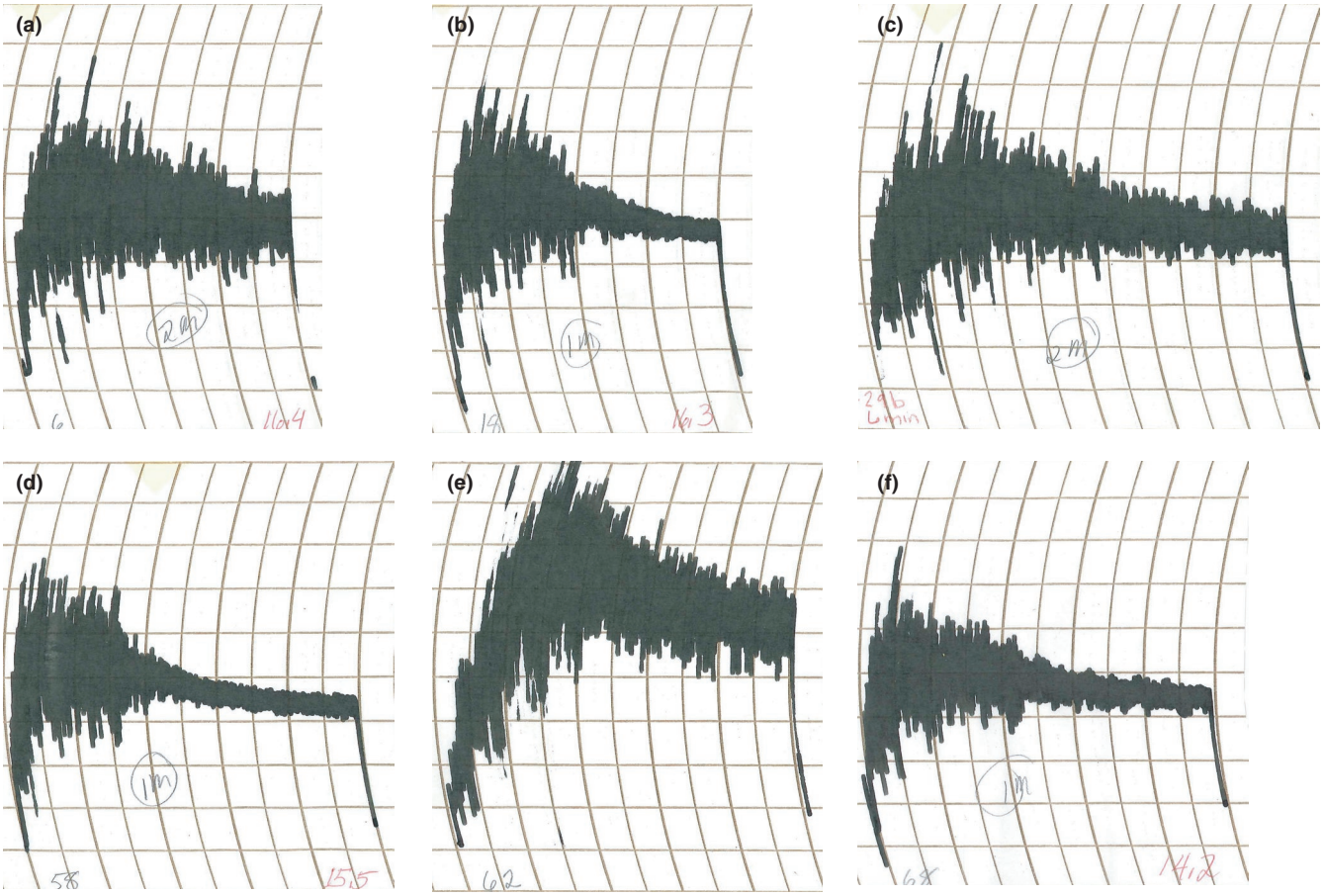

FIGURE 1 Mixograms of soft kernel durum full-sib recombinant inbred lines (RILs) and their parents (a) a *Gpc-B1*-plus RIL with 167 g/kg flour protein and the largest (870 cm^3) loaf volume for that allele class; (b) a *Gpc-B1*-plus RIL with 163 g/kg flour protein and the smallest (600 cm^3) loaf volume for that allele class; (c) a *Gpc-B1*-minus RIL with 144 g/kg flour protein and the largest (875 cm^3) loaf volume for that allele class; (d) a *Gpc-B1*-minus RIL with 155 g/kg flour protein and the smallest (505 cm^3) loaf volume for that allele class; (e) Desert King-High Protein (*Gpc-B1*-plus) with 186 g/kg flour protein and a 785 cm^3 loaf volume; and (f) Soft Svevo (*Gpc-B1*-minus) with 142 g/kg flour protein and a 575 cm^3 loaf volume

Representative Mixograms are presented in Figure 1. From a visual inspection of the Mixograph curves, especially from the higher protein location of Lind, there was considerable variation among the fifteen RILs comprising each *Gpc-B1* allele class. Indeed, this within-allele variation was greater than the effect of *Gpc-B1* allele alone. Nevertheless, *Gpc-B1* did contribute in a positive way to dough strength regardless. RILs with *Gpc-B1*-plus typically had those Mixograph parameters (see above; Table 4) that contribute to better breadmaking ability.

On this last point, bread loaf volume was significantly greater, on average by 45.2 cm^3, for the *Gpc-B1*-plus RILs, 817.6 versus 772.4 cm^3. This is the first report of the effect of *Gpc-B1* on breadmaking quality in durum wheat or soft durum wheat. More generally, breadmaking studies in durum wheat are limited (Boehm et al., 2017b; Kiszonas et al., 2021; Morris, 2021; Morris et al., 2015; Murray et al., 2017). Clearly, by referring to the Mixograms (Figure 1) and the corresponding bread loaf volumes (see figure caption), there is considerable contribution of the parent, with DKHP providing superior breadmaking alleles (probably high and low molecular weight glutenins) in addition to the effect of the functional *Gpc-B1* allele. "Desert King" possesses *Glu-B1* Bx6+By8, *Glu-A3* subunit 6, and *Glu-B2* subunit 12, whereas "Svevo" possesses *Glu-B1* Bx7+By8, *Glu-A3* subunits 6 + 11, and is null at *Glu-B2* (Magallanes-López et al., 2017). Both lines possess allele a at *Glu-B3* (Magallanes-López et al., 2017). Irrespective of kernel texture (very hard or soft kernel), there are dramatic differences among durum lines and progeny for bread baking quality, *viz.* loaf volume. In this regard, the average improvement (45.2 cm^3) in bread loaf volume was considerably less than the range within allele class which was 270 and 370 cm^3, *Gpc-B1*-plus, and *Gpc-B1*-minus, respectively (see Figure 1 caption).

Ohm et al. (2010) indicated that the increased protein content associated with the *Gpc-B1* dicoccoides 6B chromosome was related to increases in HPLC fractions described as high- and low-molecular-weight polymeric proteins, and α-, β-, γ-, and ω-gliadins, both in the SDS soluble and insoluble fractions. This general broad-spectrum increase in proteins representing a large number of genes is likely due to the transcriptional regulation of the underlying *TtNAM-B1* (*Triticum turgidum No Apical Meristem*) gene (Uauy et al., 2006). Although not measured here, Brevis et al. (2010) observed increased wet gluten but not gluten index with *Gpc-B1*-plus plants. Salmanowicz et al. (2017) also observed an increase in wet gluten across three contrasting environments with the functional *Gpc-B1* allele.

Briefly, the environments used here, although markedly different, all produced consistent responses from *Gpc-B1* (Tables 3 and 4), although the environmental effects were usually larger than that of *Gpc-B1* allele alone. Lind is a dry location (<30 cm of annual precipitation) and produced greater wheat and flour protein levels. Spillman is a higher precipitation environment (>51 cm annual precipitation), and Yuma, AZ, was an irrigated location. These differences were evident in the flour protein content, which decreased with increasing water availability. Test weight was greatest at Yuma, which corresponded to the greatest flour yield and break flour yield from that location compared with the nonirrigated locations. The notably high flour protein level at Lind (151 g/kg) likely led to doughs that were too stiff and not extensible enough. This lack of extensibility is apparent in the low Mixograph time to peak, Mixograph work, Mixograph curve width 2 min after peak, and loaf volume. These characteristics are all signs of "bucky" dough, or dough that is too elastic and not extensible enough to allow for sufficient oven spring, and thus, the bread has a smaller loaf with a tight crumb.

Despite the fact that the *Gpc-B1*-plus lines had overall better dough mixing characteristics, they still would not be considered adequate when compared to a typical US hard red spring wheat variety used for making bread (Morris, 2021; Murray et al., 2017). Under the exact same testing protocols, the loaf volume of the hard red spring wheat variety Expresso was 1,050 cm^3 at 13.4% flour protein (Murray et al., 2017). Loaf volume was on average 45.2 cm^3 greater in the *Gpc-B1*-plus lines as compared to the *Gpc-B1*-minus lines. However, recent work (Kiszonas et al., 2021) indicates that introgression of *Glu-D1* Dx2+Dy12 high-molecular-weight glutenins can markedly improve breadmaking performance. It will be of considerable interest to combine the *Gpc-B1*-plus allele with *Glu-D1* Dx2+Dy12, in the presence of soft kernel texture (*Pina-D1a/Pinb-D1a*). We are also evaluating the effects of *Glu-B1al* ($Bx7^{OE}$) on dough rheology and breadmaking performance.

4 | CONCLUSIONS

Overall, there were some advantages to the introgression of the functional dicoccoides *Gpc-B1* allele into soft durum. Grain and flour protein contents were increased, dough mixing strength was increased, and bread loaf volumes increased. However, test weight decreased and flour ash increased. This introgression was not sufficient to elevate dough and breadmaking quality to a level commensurate with high-quality bread wheats, but it did make a consistent and positive contribution.

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