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High-molecular-weight glutenin subunit variation in a spring wheat collection.

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The composition of high-molecular-weight glutenin subunits (HMW-GS) and allele frequencies in 26 Pakistani cultivars and 47 CIMMYT wheat accessions were identified. Sixteen different *Glu-1* alleles were found, three at the *Glu-A1* locus, nine at the *Glu-B1* locus, and four at the *Glu-D1* locus (Figs. 1 and 2). Those loci in the CIMMYT accessions, but not in the local cultivars, included four alleles (8, 13+19, 14+15, and 20) at *Glu-B1* and two (5+11 and 2+11) at *Glu-D1*. No Pakistani cultivars had alleles that were absent in the CIMMYT accessions (Figs. 1 and 2). These sixteen alleles at *Glu-A1*, *Glu-B1*, and *Glu-D1* loci resulted in 28 allelic HMW-GS combinations (Table 1). Of these 28 combinations in both groups, five were present only in the Pakistani cultivars (Table 1, p. 95), whereas 12 combinations were present only in CIMMYT accessions (Table 1). Ten different alleles were identified in all the Pakistani cultivars; three corresponding to the *Glu-A1* locus, five to *Glu-B1*, and two to *Glu-D1* (Fig. 1). All of the commonly found allelic variants at the *Glu-A1* locus (null, 1, and 2*) were found in the germplasm. The frequency of HMW-GS (Table 2, p. 107) and the percent partial frequency (Fig. 2) of the 2* allele were 12 and 46.15%, respectively, and were high among all the alleles at the *Glu-A1*locus. At the *Glu-B1* locus, five different HMW-GS combinations (17+18, 13+16, 7+9, 7+8, and 7) appeared in the Pakistani cultivars. Among these, subunits 7+9 and 17+18 were more frequent with a frequency and partial frequency of 9 and 34.62% (Fig. 1). Subunit 7 occurred

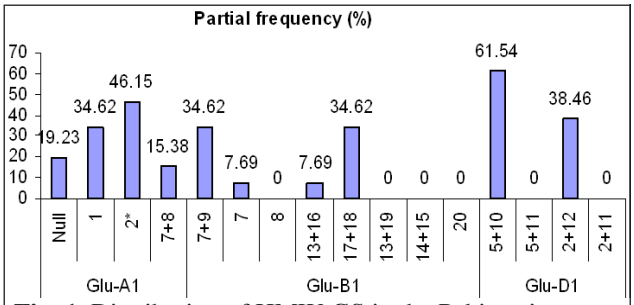

Fig. 1. Distribution of HMW-GS in the Pakistani genotypes for the *Glu-A1*, *Glu-B1*, and *Glu-D1* loci.

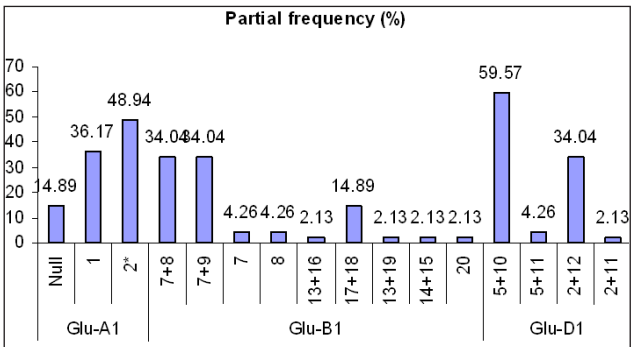

Fig. 2. Distribution of HMW-GS in the CIMMYT genotypes for the *Glu-A1*, *Glu-B1*, and *Glu-D1* loci.

Table 1. Combination of *Glu-1* alleles and quality scores in Pakistani wheat cultivars.

Glu-A1	*Glu-B1*	*Glu-D1*	Frequency	Pakistani cultivar	Quality score
1	7+8	5+10	1	Kohsar-95	10
1	13+16	5+10	1	SA-75	10
1	17+18	5+10	1	Zamindar-80	10
2*	17+18	5+10	1	Zardana-89	10
1	7+9	5+10	3	Lu-26, Punab-76, Punjab-85	9
2*	7+9	5+10	4	Karwan, Manthar, Pasina-90, Satluj-86	9
Null	17+18	5+10	2	Naeem-82, Pavon-76	8
2*	7+8,	2+12	2	Fareed-6, Shahkar-95	8
2*	17+18	2+12	4	Bulbul, Parwaz-94, Punjab-81, Punjab-96	8
2*	7	5+10	1	MH-97	8
1	13+16	2+12	1	Ufaq	8
1	7	5+10	1	Pari-73	8
1	7+9	2+12	1	Kohinoor-83	7
Null	17+18	2+12	1	SA-42	6
Null	13+16	2+12	1	Shalimar-88	6
Null	7+9	2+12	1	Blue Silver	5

Table 2. Combination of *Glu-1* alleles and quality scores in CIMMYT wheats lines and cultvars.

Glu-A1	*Glu-B1*	*Glu-D1*	Frequency	Pakistani cultivar	Quality score
1	7+8	5+10	5	Hoosam-3, KAUZ/STAR, PBW65/ROEK, SW89-5277/BOR95, Milan	10
1	17+18	5+10	2	SNI/PBW65, TE173	10
2*	17+18	5+10	3	TOBA97/BAV-92, Pastor//2*Milan/KAUZ, HUW234/LR 34	10
2*	7+8	5+10	3	PVN/YACO, F60314.76, VEE/PVN	10
1	7+9	5+10	6	NG 8201/KAUZ, RL6043/4*NAC, JUP/ZP//COC, SW91-4903/Circus, Opata//SOR, Johara-14	9
1	7+9	5+11	1	AMSEL/2*BAU	9
1	7+9	5+11	1	AMSEL/2*BAU	9
2*	7+9	5+11	1	SKAUZ	9
2*	7+9	5+10	1	Mango	9
Null	17+18	5+10	1	Crow ‘S’	8
2*	7+8	2+12	6	SHA7/VEE5, Girwill-7, Gamdow-6, Local White, BAYA ’S’, Kanchan	8
2*	17+18	2+12	1	Myna ’S’	8
2*	7	5+10	1	Attila/Pastor	8
2*	20	5+10	1	Weaver/TSC	8
2*	13+19	2+12	1	Weaver/VEEP	8
2*	7+8	2+11	1	HD29/2*Weaver	8
1	7	5+10	1	PBW343*2/Kuruku	8
Null	7+8	5+10	1	KAUZ/TSC	8
Null	7+9	5+10	0	KAUZ ’S’	7
Null	14+15	5+10	1	ESDA/SHWA	7
2*	7+9	2+12	4	SLVS/Pastor, NG8201/KAUZ/Pastor, PBW343*2/Chapio, V763.2312	7
1	8	5+10	2	KAUZ*2/MNV, Kasyon	6
Null	7+8	2+12	1	HXL8246	6
Null	7+9	2+12	2	Opata/Rayon/KAUZ, HP-1744	5

with the least frequency (2) and lease partial frequency (7.69%) (Fig. 2, p. 94). Two alleles (5+10 and 2+12) were found at the *Glu-D1* locus. Allele 5+10 had a higher frequency (16) and partial frequency (61.54%).

Sixteen HMW-GS combinations were observed in the Pakistani cultivars (Table 1, p. 95). Subunit compositions of 2*, 7+9, 5+10 and 2*, 17+18, 2+12 were the most frequent and each was observed in four of the 26 Pakistani cultivars. The second most frequent combination was 1, 7+9, 5+10 found in three of the 26 cultivars. Subunit compositions 2*, 7+8, 2+12 and N, 17+18, 5+10 were present in two cultivars. Eleven other subunit combinations had low frequencies (1) and were present in only one cultivar.

The HMW-GS quality scores for the individual cultivars ranged from 5 to 10 (Table 1). According to the quality score, Kohsar-95, SA-75, Zamindar-80, and Zardana-89 had the highest scores of 10. Seven cultivars (Lu 26, Karwan, Manthar, Pasina 90, Punjab-85, Satluj-86, and Punjab-76) had a quality score of 9. Blue Silver had the lowest score of 5.

Sixteen different alleles at the *Glu-1* locus were identified in the 47 CIMMYT accessions, three corresponding to the *Glu-A1* locus, nine to *Glu-B1*, and four to *Glu-D1* (Table 2, p. 95). At the *Glu-A1* locus, three HMW-GS (Null, 1, and 2*) were present. The frequency and partial frequency of the 2* allele were 23 and 48.94%, respectively, were among the highest of all the alleles at the *Glu-A1* locus (Fig. 2, p. 94). Subunit 1 was second most frequent with a frequency and partial frequency of 17 and 36.17%, respectively (Fig. 2). At the *Glu-B1* locus, nine different subunit combinations (17+18, 13+16, 7+9, 7+8, 7, 8, 13+19, 14+15, and 20) appeared in the CIMMYT accessions. Of these subunits, 7+8 and 7+9 were the most frequent, each with a frequency and partial frequency of 16 and 34.04%, respectively (Fig. 2). Subunits 13+16, 13+19, 14+15, and 20 occurred with the least frequency (1) and partial frequency of (2.13%) (Fig. 2). Four subunits were found at the *Glu-D1* locus (5+10, 5+11, 2+12, and 2+11). Subunits 5+10 had the highest frequency (28) and partial frequency (59.57%), and subunit combination 2+11 was the least frequent (1) and partial frequency (2.13%) (Fig. 2).

Twenty different allelic combinations of *Glu-A1*, *Glu-B1*, and *Glu-D1* were found (Table 1, p. 95). Each of the combinations, 1, 7+9, 5+10 and 2*, 7+8, 5+10, was of the highest frequency of 6 (Table 1). Combination 1, 7+8, 5+10 had the next highest frequency of 5. Fourteen different subunit combinations were the lowest in frequency at 1 and each combination was found in only one accession.

Thirteen accessions, SW89-5277/BOR95, Milan, TOBA97/BAV-92, Astor//2*Milan/KAUZ, HUW234/LR34, PVN/Yaco, SNI/PBW65, VEE/PVN, Hoosam-3, KAUZ/Star, TE173, F60314.76, and PBW65/ROEK had the maximum score of 10, indicating their use to improve bread-making quality. The second highest score (9) for HMW-GS was observed in NG-8201/KAUZ, SW91-4903/Circus, RL6043/4*NAC, OPTA//SOR JUP/ZP//COC/3, AMSEL/2*BAU, Skauz, Mango, and Johara-14. Thirteen accessions, including Crow 'S', SHA7/VEE5, Girwill-7, Gamdow-6, Local White, Baya 'S', Kamcjam, Myna 'S', Attila/Pastor, Weaver/TSC, Weaver//VEEP, HD29/2*Weaver, PBW343*2/ Kuruku, and KAUZ/TSC had a quality score of 8. Only two CIMMYT accessions, Opata/Rayon/KAUZ and HP-1744 had the lowest quality score of 5 (Table 1, p. 95).

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Phenotype-based genetic diversity in spring wheat germplasm for wheat yield improvement.

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Diverse genetic resources are necessary for adequate food production in changing environments. Germplasm is often exploited to develop improved culitvars for changing needs and challenges. Variability for economic traits in the working germplasm is very important for rewarding utilization following recombination breeding and selection. Selecting genetically diverse parents for recombination breeding in a self-pollinated species such as wheat to produce transgressive segregants has been repeatedly emphasized. Assessing the genetic diversity can also be invaluable for analyzing genetic

variability in cultivars and introgressing desirable traits from diverse germplasm into the available genetic base. A collection of 500 cultivars and breeding lines of spring bread wheat was evaluated to determine (i) the magnitude of variability in the germplasm for twelve quantitative traits, (ii) the grouping pattern of the genotypes, and (iii) identify genetically diverse and agronomically promising genotypes for exploiting in breeding programs to improve grain yield potential of wheat.

Our analysis of variance (ANOVA) revealed that the genotypes included in the study had significant variation for most of the traits. In 2008–09, spike density and chlorophyll content had no workable diversity in the germplasm. Chlorophyll content was the only trait that showed no significant variation among the genotypes in 2009–10. Spike density was significant in 2009–10. The means of all traits decreased from 2008–09 to 2009–10. The range for grain yield was 10.5–71.0 g/plant in 2008–09 and 10.3–66.8 g/plant in 2009–10. The number of kernels/plant ranged from 253 to 1,812 in 2008–09 and 246 to 1,764 in 2009–10. The minimum and maximum kernel size for the year 2008–09 was 25.6 and 68.6 g/1,000 kernels, respectively. The range in kernel size in 2009–10 was 24.7–66.4 g/1,000 kernels. The number of spikes/plant was 6.3–55.2 in 2008–09 and 6.1–53.7 in 2009–10. The range for the number of spikelets/spike was 16.7–27.2, maximum number of fertile florets/spikelet was 3–508, spike dry weight was 2.3–5.9 g, plant height was 62.1–129.4 cm, spike length was 8.1–16.8 cm, awn length was 0.0–13.6 cm, spike density was 1.5–2.2 spikelets/cm, and chlorophyll content was 36.9–65.8 in 2008–09. In 2009–10, the number of spikelets/spike was 16.2–26.5, maximum fertile florets/spikelet was 2.9–5.6, spike dry weight was 1.8–5.6 g, plant height was 60.9–126.8 cm, spike length was 7.8–16.0 cm, awn length was 0.0–13.2 cm, spike density was 1.4-4.7 spikelets/cm, and chlorophyll content was 35.5–63.2.

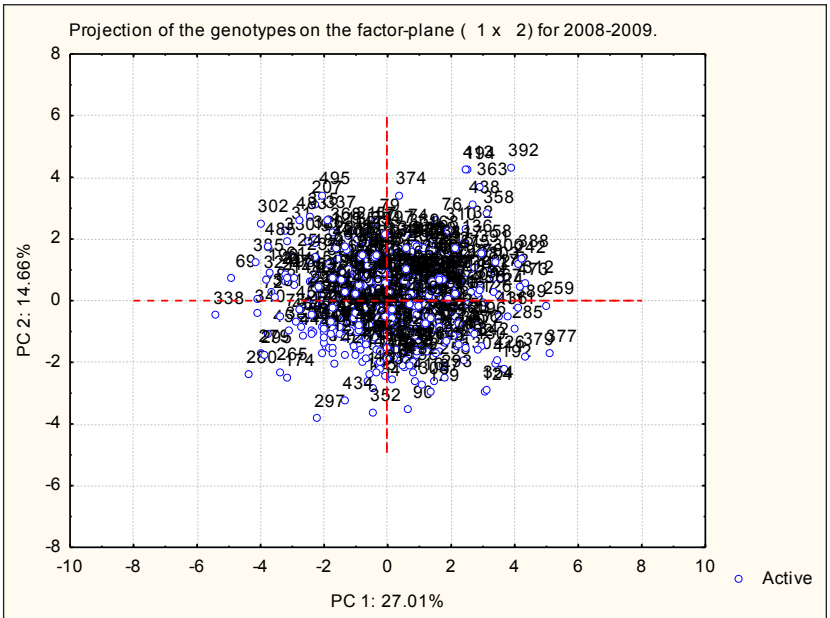

Fig. 3. Two-dimensional ordination of 500 wheat genotypes on prinicpal components PC1 and PC2 in 2008–09.

Of the 12 principal components (PCs), the first four had eigen values (latent root) > 1 (significant) in 2008–09 and 2009–10. The other eight PCs explained a nonsignificant amount of variation and were not worth interpreting. For 2008–09 and 2009–10, the first four PCs showed 62.03% and 64.47% variation, respectively, in the germplasm. The first PC accounted for 27.01% of the variance, the second for 14.66%, the third for 11.77%, and the fourth for 8.59% in 2008–09 (Fig. 3). The first PC showed 27.76% of the total variance, the second for 16.28%, the third for 11.86%, and the fourth for 8.57% in 2009–10 (Fig. 4).

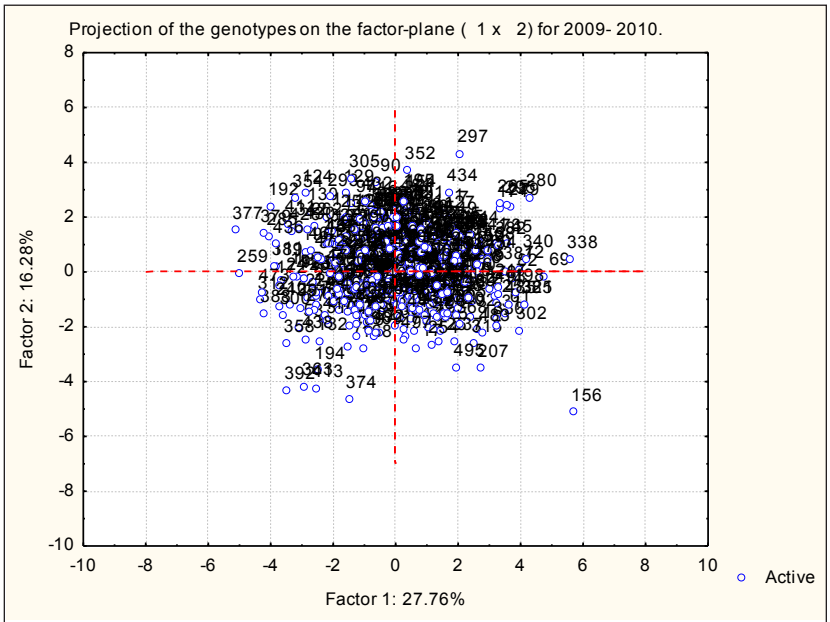

Fig. 4. Two-dimensional ordinations of 500 wheat genotypes on PC1 and PC2 in 2009–10.

The importance of a trait coefficient for each significant principal component was determined. The first PC was highly related to grain yield, number of kernels/plant, spike dry weight, and

spike length for both years, implying that PC1 is a weighted average of these four traits. The number of spikes/plant, 1,000-kerne. weight, and the number of kernels/plant was of significant importance in PC2 in 2008–09. The important traits in PC2 in 2009–10 were the number of spikes/plant, 1,000-kernel weight, number of kernels/plant, and spike density. The third PC was related to the number of spikelets/spike and PC4 to 1,000-kernel weight and the maximum number of fertile florets/spikelet in 2008–09. The significant trait in PC3 was the number of spikelets/spike and in PC4 were 1,000-kernel weight and spike length in 2009–10. The projection of traits on PC1 and PC2 revealed that the number of kernels/plant, the number of spikes/plant, and the number of spikelets/spike were positively related to grain yield in both years. Spike density was opposite grain yield and other yield contribution traits on PC1 in both years and, therefore, it had a negative correlation with all other traits. Becaise the variation in chlorophyll content wasa not significant among the genotypes, it was not projected significantly on the first two PCs by the principal component analysis. The projection pattern of the traits on first two PCs for both years indicated that the key yield-contributing traits were the number of kernels/plant, spike dry weight, and spike length. The projection of genotypes on the first two PCs was useed to identify diverse groups of parents for better transgressive segregation. The projection of genotypes on PC1 and PC2 showed a population structure in both years (Figs. 3 and 4). For 2008–09, the following hetrotic groups were identified: 192, 363, 392, 414, and 488 (Kambara-1, KAUZ//TFAU/VEE#5, V-97100, and Jauhar-78) were opposite to 174, 297, 265, and 280 (Local White, Condor 'S'/ANA75//Condor 'S'/MUS 'S', and Abadgar-93) (Fig. 3). Genotype 338 (Qafzah-21) was in contrast to 259 (Goshawk 'S'). Genotype 374 (Hibara-3) had the maximum diversity from 352 (Bolsena 'S'). Genotypes 69, 385, and 485 (Oasis AGA/3*YR, IZAZ-1, and Abadgar-93) were opposite to 124, 192, 334, and 377 (Webelli/Kambi, Kambara-1, Crow 'S'/BOW#1, and Qafzah-18) (Fig. 3). In 2009–10, the most diverse parents were 280 (BLS/KLT 'S') vs. 392 (KVZ/3/TOB/CFTN//BB/4/BLO 'S'/5/VEE#5/6/BOW 'S'/3/YDING 'S'//BB/CHA), 352 (Bolsena 'S') vs. 374 (Hubara-3), and 302 (Parula) vs. 307 (BUC 'S'/BJY 'S'/3CNDR 'S'/ANA//CNDR 'S'/MUS 'S') (Fig. 2, p. 94).

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Association mapping identifies drought-tolerance QTL on wheat chromosome 2A.

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Most of the association mapping studies so far have been reported under favorable conditions. In the previous studies, a number of QTL for agronomic traits (spike length, spikelets/spike, grains/spike, plant height, spikelet density, and 1,000-kernel weight) were identified on different chromosomes. For complex traits, such as drought tolerance and yield, the knowledge of the interaction between the marker/QTL and the environment are necessary to efficiently utilize marker-assisted selection in plant breeding. Comparing the performance of the same genotype across environments, the best-suited environment for the expression of a particular QTL, can be identified, but hundreds of markers are required for sufficient mapping resolution covering the whole genome of wheat. Therefore, targeting an individual linkage group is a quite reasonable strategy. This study identified the population structure among a collection of 108 germplasm lines, the extent of LD decay on chromosome 2A, and the association of SSR markers with drought-tolerance traits on chromosome 2A.

Association mapping analysis was performed on a panel of 108 diverse wheat accessions to dissect the genetic background of drought-adaptive traits. These genotypes were characterized with 25 SSR loci on chromosome 2A. Sixteen agronomic traits were evaluated under well-irrigated and drought-stress conditions. The population structure and kinship were inferred on the basis of 30 unlinked SSR loci covering all 21 wheat chromosomes, which enhanced the mapping strength by eliminating spurious associations.

The admixture, model-based analysis with the STRUCTURE software was used to investigate the genetic relationship among the population. An optimal number of subpopulations was identified when K was set to three, because the likelihood peaked at K = 3 in the range of 2–20 subpopulations. The number of genotypes assigned to each inferred subpopulation was 33, 37, and 36. The FST values between all subpopulations were significant ($P < 0.001$), confirming a real difference among these subpopulations and supporting the prevalence of genetic structure.

A mixed, linear model approach was used to determine marker–trait associations (MTAs) for the 16 phenotypic traits and 28 SSR loci on chromosome 2A. Subpopulations were used as covariates for association mapping analysis. A total of 10 MTAs were identified for five morphological traits under drought-stress conditions at a probability level of 0.001 with the range of 3.63 to 29.16% of the phenotypic variation (Table 3). Under well-irrigated conditions, only four MTAs were found, and the r^2 range was 3.55 to 10.04 (Table 4). The highest number of associations was observed for awn length under drought stress. Other traits that showed significant associations under drought include days-to-heading, glaucausness, shoot length, and the stress susceptibility index. Under well-irrigated conditions, significant marker trait associations were found for 1,000-kernel weight, shoot length, and coleoptile length. Nineteen SSR markers showed significant association with morphological traits, 11 (*Xcfa2121*, *Xwmc382*, *Xwmc407*, *Xgwm122*, *Xwmc445*, *Xwmc552*, *Xbarc212*, *Xgwm445*, *Xwmc445*, *Xbarc5*, and *Xgwm558*) were associated only with one trait and, therefore, can be considered as trait-specific MTAs. Markers *Xcfa2099*, *Xcfa2043*, *Xcfa2263*, and *Xgwm95* were associated with two traits, and markers *Xcfa2086*, *Xbarc124*, *Xgwm312*, and *Xgwm265* were associated with three traits.

Table 3. Association (r^2) of the SSR markers with drought-related traits under stress conditions in wheat.

Trait	QTL	Flanking marker/s	R^2 (%)	P (Q+K)
Days-to-heading	*QDth.uaf.2A.3*	*Xcfa2099*	4.35	0.0063
	QDth.uaf.2A.2	*Xcfa2121*	8.1	0.0000
Awn length	*QAl.uaf.2A.2*	*Xwmc407*	12.16	0.0000
	QAl.uaf.2A.2	*Xcfa2099*	29.16	0.0000
	QAl.uaf.2A.2	*Xcfa2263*	5.82	0.0001
Glaucausness	*QGla.uaf.2A.2*	*Xwmc445*	8.75	0.0038
	QGla.uaf.2A.2	*Xcfa2043*	5.41	0.0005
	QGla.uaf.2A.2	*Xbarc212*	5.0	0.0084
Shoot length	*QSl.uaf.2A.2*	*Xcfa2263*	6.75	0.0003
Stress-susceptibility index	*QSsi.uaf.2A.2*	*Xgwm265*	4.93	0.0031

Table 4. Association (r^2) of the SSR markers with morphological traits under normal conditions in wheat.

Trait	QTL	Flanking marker/s	r^2 (%)	P (Q+K)
1,000-kernel weight	*Qgw.uaf.2A.3*	*Xwmc455*	10.04	0.002
Shoot length	*QSl.uaf.2A.3*	*Xbarc5*	4.17	0.007
	QSl.uaf.2A.3	*Xgwm265*	4.84	0.003
Coleoptile length	*QCl.uaf.2A.1*	*Xbarc124*	4.35	0.006

Under drought stress conditions, *Xcfa2099* and *Xcfa2121* showed a significant association with number of days to heading (Table 3). Awn length, which showed the maximum number of MTAs, was associated with primers wmc382, wmc407, cfa2043, cfa2086, cfa2099, cfa2263, barc124, gwm95, gwm312, and gwm122. Only three primers, wmc 382, wmc 407, and gwm312, showed non-overlapping associations. Marker–trait associations for glacousness were found with primers wmc445, wmc552, cfa2043, cfa2086, barc212, gwm265, and gwm445. Overlapping associations for glacausness were observed only for cfa2043, cfa2086, and gwm445. Shoot length was associated with cfa2263, barc124, gwm95, and gwm312, and the stress-susceptibility index with cfa2086 and gwm265. Under favorable conditions, only six marker–trait associations were found, and shoot length showed a maximum number of three MTAs. Markers *Xbarc5*, *Xgwm265*, and *Xgwm312* showed a significant association with shoot length under well-irrigated conditions, and gwm312 was associated with shoot length under both well-irrigated and drought environments (Table 4). Coleoptile length also showed two MTAs with *Xbarc124* and *Xgwm558*. Only one MTA was found for 1,000-kernel weight with wmc445 under favorable conditions.

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Association mapping identifies yield QTL on wheat chromosome 3A.

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Association mapping, which has been widely used in human and animal genetics where large segregating populations are not possible to develop, has been validated in plants. Association mapping has many advantages over the traditional FBL-based, QTL mapping including higher QTL resolution, higher allele coverage, and readily available mapping populations in the form of natural germplasm. Initially, the presence of a population structure within the mapping population was not statistically handled, causing spurious associations, compared to FBL mapping, but the recent statistical developments, such as Q and K estimates, substantially reduced false associations due to population structure. These matrices take into account population structure and combine it to covariate in association tests. Gene mapping studies in wheat using the assoication mapping approach are still few. Most of these studies have focused on individual chromosomes, where QTL have been previously identified by linkage analysis, or on monogenic traits. Grain yield increment is the most important challenging objective faced by plant breeders. Several yield-related QTL on chromosome 3A were identified using this RICL population. Covering the whole genome of hexaploid wheat with sufficient mapping resolution requires hundreds of SSR probes, therefore, targeting individual linkage group is a reasonable strategy. Marker–trait associations for grain yield traits on chromosome 3A of hexaploid spring wheat were determined. We analyzed population structure, linkage disequilibrium, and associations of SSR markers with 12 yield-related traits.

A panel of 94 diverse hexaploid wheat accessions was used to map QTL underlying the yield-related traits on chromosome 3A. Population structure and kinships were estimated using unlinked SSR markers from all 21 chromosomes, which eliminated spurious associations and enhanced mapping strength. Analysis of variance revealed significant difference among accessions; however, the 'genotype × year' interaction was not significant for most yield-related traits.

An admixture, model-based analysis with the STRUCTURE software identified an optimal number of subpopulations when K was set at 7, because likelihood peaked at K = 7 in the range of 2–20 subpopulations. The number of genotypes assigned to each inferred subpopulation ranged from 8 to 16. The FST values between all subpopulations were significant ($P < 0.001$), confirming the real difference among these subpopulations and supporting the prevalence of genetic structure.

The unlinked markers used to detect population structure also were used to determine background LD (unlinked LD). The background LD in the genome, caused by the genetic structure, was used to set a critical value of LD for markers on chromosome 3A. The unlinked r^2 value ranged from 0.000 to 0.1303 for all unlinked loci pairs, with an average of 0.0014. The 95th percentile of the distribution of unlinked r^2 (0.015) was used as a population-specific threshold for this parameter as an evidence of LD because of linkage. The syntenic r^2 was obtained from the analysis of 23 SSRs on chromosome 3A. The value of the pairwise syntenic r^2 ranged from 0.0007 to 0.167 with an average of 0.016, significantly higher than the average of the unlinked r^2.

A decay scatterplot of the syntenic LD values of r^2 in population was made. The extent of LD on chromosome 3A was ~40 cM, with a critical value of 0.015. About 40% of the LD pairs were found with an $r^2 < 0.015$. The chromosomal region where all pairs of flanking loci were in LD, were referred to as an LD block. One LD block was observed on chromosome 3A between 37–46 cM, including markers *Xbarc45*, *Xgwm2*, *Xgwm674*, and *Xgwm30*.

We used a mixed linear model approach to determine marker–trait associations for 12 yield traits and 23 SSRs on wheat chromosome 3A. The results were similar for both years. A mixed linear model approach identified six QTL for four traits that individually accounted for 10.7–17.3% of the phenotypic variability (Table 5). Primers cfa2134 (51 cM) and gwm369 (14 cM) were significantly associated with maximum number of fertile florets/spikelet. Grain yield/plant, plant height, and spike length were significantly associated gwm155 (85 cM), wmc527 (53 cM), gwm155 (85 cM), and gwm369 (14 cM).

Table 5. Association (r^2) of SSR markers with yield traits in wheat. Map position (cM) was based on the consensus map Ta-SSR-2004; r^2 indicates the percentage of the total variation explained at the loci significant at a level of $P < 0.01$.

Trait	QTL	Flanking marker/s	r^2 (%) 2008–09	P (Q+K) 2008–09	r^2 2009–10	P (Q+K) 2009–10
Grain yield	*QGyld.uaf.3A.3*	*Xgwm155–Xwmc215*	17.3	0.0020	16.9	0.0030
	QGyld.uaf.3A.2	*Xwmc527–Xwmc269*	16.1	0.0023	15.3	0.0029
Plant height	*QPht.uaf.3A.3*	*Xgwm155–Xgwm215*	10.7	0.0093	10.7	0.0090
Spike length	*QSpl.uaf.3A.1*	*Xgwm369–Xcfd79*	16.8	0.0062	14.9	0.0013
Fertile florets/spikelet	*QMff.uaf.3A.2*	*Xgwm369–Xcfd79*	15.3	0.0070	13.6	0.0090
	QMff.uaf.3A.1	*Xcfa2134–Xwmc527*	15.4	0.0098	14.3	0.0016

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