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RESEARCH

Association Mapping of Agronomic Traits in Bread Wheat Under Late Drought and Non-Stressed Conditions

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Abstract
Late drought is a major constraint to wheat productivity and yield stability in semi-arid regions. This study investigated marker–trait associations (MTAs) for agronomic traits in 64 bread wheat genotypes evaluated under well-watered and late drought conditions during the 2011–2012 and 2012–2013 growing seasons in Erzurum, Türkiye. Genotypes were characterized by using 120 simple sequence repeat (SSR) markers and 34 inter-primer binding site (iPBS) primers. Association mapping was performed separately for each growing season and water regime using the corresponding phenotypic datasets and a mixed linear model incorporating population structure (K = 3) and kinship. Late drought reduced grain yield, biological yield, and 1000-kernel weight by approximately 36.0%, 24.6%, and 16.9%, respectively. At an adjusted $P \leq 0.05$ based on 1000 permutations, 82 SSR markers were involved in 219 significant MTAs across the individual year × water-regime datasets, explaining 1.4–24.7% of the phenotypic variation. In on the other hand, only six iPBS markers showed significant and environment-specific associations. Notably, *iPBS-2390* and *iPBS-2392* were associated with 1000-kernel weight under late drought in 2011–2012, with each marker explaining 9.0% of the phenotypic variation. Collectively, these results demonstrate the broader utility of SSR markers for detecting agronomically relevant associations across contrasting environments, while iPBS markers provide complementary information on environment-specific variation. The identified MTAs represent potential molecular resources for improving drought adaptation and yield stability in bread wheat.

Keywords *Triticum aestivum* L. · Drought tolerance · Association mapping · SSR · iPBS · Yield stability

Introduction

Common wheat (*Triticum aestivum* L.) is one of the world's most important cereal crops, playing a crucial role in global food security. It is estimated to provide approximately 20% of the daily caloric and protein intake in the human diet (Shiferaw et al. 2013). According to recent 2026 forecasts, global wheat production is projected to reach 806.5 million tonnes (FAO 2026). Concurrently, Türkiyethe geographical context of the present studyis expected to achieve a record production of 22.5 million tonnes, underscoring the continuous strategic importance of this staple crop at both national and global scales (FAO 2026). Despite its global importance, sustainable wheat production is increasingly threatened by climate variability, particularly the increasing frequency and intensity of drought events (Lesk et al. 2016). Drought stress substantially reduces wheat grain yield, with the magnitude of yield loss depending on its severity and

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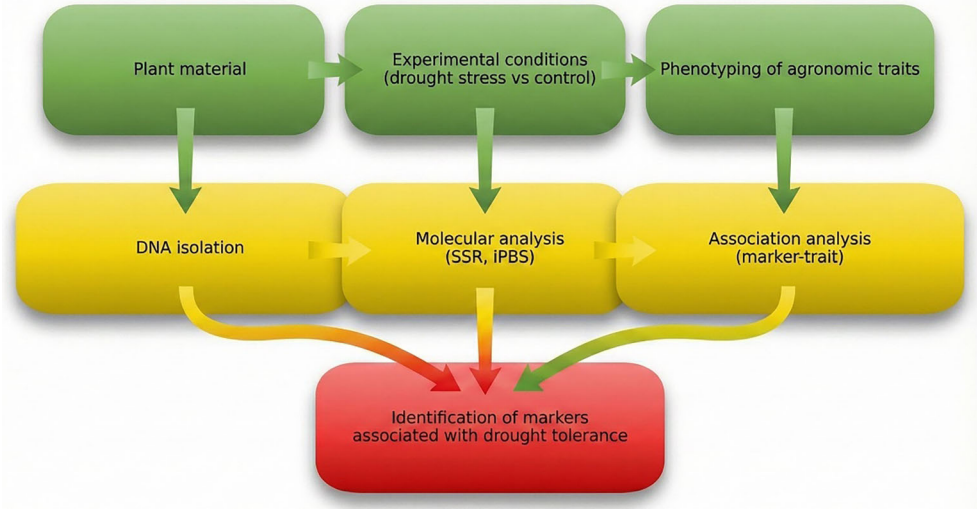
Graphic abstract



the developmental stage at which it occurs. Terminal or late-season drought is particularly detrimental because it disrupts grain filling and reduces grain weight and quality (Farooq et al. 2014). This form of stress markedly impairs photosynthetic activity, restricts nutrient translocation to developing grains, and accelerates leaf senescence, ultimately leading to pronounced reductions in thousand-kernel weight and harvest index (Latief Bashir et al. 2024). Understanding the genetic basis of adaptation to terminal drought is therefore important for developing climate-resilient wheat cultivars.

Studies on the genetic basis of drought tolerance in wheat have predominantly focused on identifying quantitative trait loci (QTLs) associated with yield and yield-related traits. Conventional QTL mapping strategies have provided substantial knowledge of the genetic architecture of drought-responsive traits (Gupta et al. 2017; Quarrie et al. 2005); however, these approaches are constrained by their reliance on biparental populations, which restrict allelic diversity and mapping resolution. The development of such populations is also labor-intensive and time-consuming (Sadeghzadeh 2013; Sinha et al. 2022).

Association mapping has emerged as an effective complementary strategy for identifying marker–trait associations across genetically diverse germplasm collections (Bocianowski and Leśniewska-Bocianowska 2025). This approach exploits historical linkage disequilibrium (LD) patterns within natural or breeding populations (Yu and Buckler 2006) and offers higher mapping resolution, enables the detection of multiple alleles, and permits the direct use of existing breeding materials (Madhusudhana 2015). It is therefore particularly useful for dissecting complex adaptive traits such as drought tolerance in wheat.

In wheat breeding, Simple Sequence Repeat (SSR) markers hold particular significance due to their high polymorphism, strong reproducibility, and uniform distribution across the genome (Röder et al. 1998). Despite the widespread use of high-density SNP platforms, the multiallelic nature of SSRs remains advantageous for detecting genetic variation in the hexaploid wheat genome, and their effectiveness in identifying loci associated with yield-related traits under drought stress has been demonstrated (Eujayl et al. 2002; Maccaferri et al. 2011). In contrast, iPBS (inter Primer Binding Site) markers, a relatively new class of molecular markers based on retrotransposon sequences, are gaining increasing importance in genetic diversity and phylogenetic analyses (Kalendar et al. 2010). Because retrotransposons constitute a substantial component of the wheat genome and may respond to environmental stress, iPBS markers can provide information complementary to SSRs on stress-responsive genomic variation (Andeden et al. 2013; Nadeem 2021). Additionally, iPBS analysis is cost-effective and does not require prior sequence information.

Agronomic traits related to drought adaptation, including thousand-kernel weight, spike number, and harvest index, are genetically complex and strongly influenced by environmental conditions (Sallam et al. 2019). Integrating phenotypic and molecular information is therefore important for identifying genomic regions contributing to adaptation under terminal drought. Maintenance of grain filling, delayed senescence, and efficient assimilate remobilization are particularly important for yield stability under water deficit, emphasizing the value of identifying loci associated with stable performance under stress (Lopes and Reynolds 2011; Sapega 2019; Sareen et al. 2014).

Despite the extensive use of molecular markers in wheat, comparative association mapping with SSR and retrotransposon-based iPBS markers under contrasting water regimes remains limited. Therefore, this study aimed to identify marker–trait associations for agronomic traits in bread wheat under well-watered and late drought conditions using SSR and iPBS markers. The novelty of the study lies in the complementary use of these two marker systems to compare broadly distributed SSR-based associations with potentially environment-specific retrotransposon-based associations across contrasting water regimes. The identified associations may provide useful molecular resources for improving drought adaptation and yield stability in bread wheat.

Materials and Methods

Plant Materials

The plant material for this study comprised 64 bread wheat (*Triticum aestivum* L.) genotypes, with their variety names listed in Table 1. The wheat genotypes were sourced either from the institutes where they are officially registered or from the seed stocks of the Department of Field Crops, Faculty of Agriculture, Ataturk University.

Phenotypic and Morphologic Data Measurement and Analysis

The field experiment was conducted using an 8 × 8 alpha-lattice design with two replications to evaluate the agronomic performance of 64 bread wheat genotypes in Erzurum, Türkiye (29°55′ N, 41°16′ E; 1850 m altitude), over two consecutive growing seasons (2011–2012 and 2012–2013). The experimental site has a cold temperate climate, with an average annual temperature of 5.0 °C and annual precipitation of approximately 388 mm, most of which occurs during winter. The genotypes were evaluated under two contrasting water regimes: well-watered and late-season drought conditions. The trials were established on land that had been left fallow during the previous growing season. Seeding rates were standardized to achieve a plant density of 475 viable seeds m^{-2}. Plot dimensions and sowing methods differed between the two water regimes because of the field infrastructure required to establish and manage the contrasting water treatments. Well-watered plots were machine-sown in six rows, each 6 m long and 20 cm apart, whereas late-drought plots were manually sown in two rows, each 1.5 m long and 20 cm apart. Despite these differences in plot configuration and sowing method, plant density, row spacing, fertilizer application, and other crop-management practices were maintained consistently between the two water regimes; thus, the principal experimental contrast was water availability.

Table 1 The bread wheat genotypes used in this study

Code	Genotype/Variety Name	Code	Genotype/Variety Name
G1	Aksel 2000	G33	Pehlivan
G2	Aldane	G34	Prostor
G3	Alparslan	G35	Soyer02
G4	Altay 2000	G36	Sönmez 2001
G5	Atlı 2002	G37	Sultan 95
G6	Aytın 98	G38	Süzen 97
G7	Bağcı 2002	G39	Tosunbey
G8	Bayraktar 2000	G40	Türkmen
G9	Bolal 2973	G41	Uzunyayla
G10	Bereket	G42	Yakar 99
G11	Çetinel 2000	G43	Zencirci 2002
G12	Dağdaş 94	G44	Ak-702
G13	Demir 2000	G45	Ak Buğday
G14	Doğu 88	G46	Ankara 093/44
G15	ES 26	G47	Conkesme
G16	Gerek 79	G48	Haymana 79
G17	Gün 91	G49	Hawk (Şahin)
G18	Harmankaya 99	G50	Kılçıksız Buğday
G19	İkizce 96	G51	Kırkpınar 79
G20	İzgi 2001	G52	Kırmızı Kılçık
G21	Karahan 99	G53	Kırmızı Yerli
G22	Kate A-1	G54	Koca Buğday
G23	Kıraç 66	G55	Köse 220/39
G24	Kırgız 95	G56	Özlü Buğday
G25	Kırik	G57	Polatlı Kösesi
G26	Kutluk 94	G58	Sert Buğday
G27	Lancer	G59	Sürak 1593/51
G28	Mızrak	G60	Tir
G29	Müfitbey	G61	Yayla 305
G30	Nacibey	G62	Zerin
G31	Nenehatun	G63	Bezostaja 1
G32	Palandöken 97	G64	Karasu 90

Fertilizer application consisted of 60 kg N ha^{-1} supplied as ammonium sulfate and 50 kg P ha^{-1} supplied as triple superphosphate. All phosphorus and half of the nitrogen were applied at sowing, while the remaining nitrogen was top-dressed at the onset of stem elongation (Zadoks growth stage 30–31). Biotic stresses were minimized through manual weed control and preventive fungicide applications during the booting stage (Zadoks growth stages 41–49) and one week after anthesis. Nine agronomic traits were recorded: vegetative period (days), grain-filling period (days), plant height (cm), number of spikes per m^2, number of kernels per spike, thousand-kernel weight (g), biological yield (kg ha^{-1}), grain yield (kg ha^{-1}), and harvest index (%). Descriptive statistics for all traits were calculated using SAS software

(version 9.1) and Genstat version 23.1 (VSN International, 2023).

DNA Extraction

Genomic DNA Isolation and Molecular Marker Analysis

Genomic DNA was extracted from fresh leaves of 14-day-old seedlings according to the protocol described by Haliloğlu et al. (2023), which is based on the CTAB method with minor modifications. The quality and integrity of the extracted DNA were assessed by 1% agarose gel electrophoresis. Concentrations were measured with a NanoDrop ND-1000 UV/Vis spectrophotometer (Thermo Fisher Scientific, Waltham, MA, USA), and all samples were diluted to 25 ng μL^{-1} for the subsequent PCR steps.

Genotyping of the wheat germplasm was performed using two types of molecular markers, namely Simple Sequence Repeats (SSR) and Inter-Primer Binding Site (iPBS), following the protocols we had previously established (Haliloğlu et al. 2023; Türkoğlu et al. 2023).

PCR Amplification Conditions

PCR amplifications for both SSR and iPBS markers were performed using a SensoQuest Labcycler (Göttingen, Germany) under optimized conditions described by (Haliloğlu et al. 2023; Türkoğlu et al. 2023). The reaction mixture was prepared in a total volume of 10 µL, containing 25 ng genomic DNA template, 1 × PCR buffer, 2 mM MgCl2, 0.25 mM dNTPs, 1 µM (20 pmol) primer, and 0.5 U *Taq* DNA polymerase. The thermal cycling profile consisted of an initial denaturation at 95 °C for 3 min, followed by 38 cycles of denaturation at 95 °C for 60 s, annealing at 50–60 °C (depending on the specific primer) for 60 s, and extension at 72 °C for 120 s, with a final elongation step at 72 °C for 10 min.

SSR and iPBS Genotyping

SSR analysis was conducted using the marker set and screening procedures detailed by Türkoğlu et al. (2023). A total of 425 SSR primers were initially screened, and 120 polymorphic primers were selected to genotype the entire set of wheat genotypes. PCR products were separated using polyacrylamide Mega-Gel dual vertical electrophoresis (Model C-DASG-400-50). The gels were stained with ethidium bromide (1 µg mL^{-1}), and banding patterns were visualized under UV light using a digital camera (Nikon Coolpix500, Nikon, Japan).

For iPBS analysis, 34 primers developed by Kalendar et al. were utilized to evaluate genetic diversity, as previously applied to wheat germplasm by Haliloğlu et al. (2023). Following PCR amplification, the products were resolved on 1.5% agarose gels at 100 V for 105 min. The gels were visualized and photographed under UV light (Nikon Coolpix500) for data scoring.

Scoring of Molecular Data

SSR and iPBS alleles profiles were converted into binary matrices (1 = band present, 0 = band absent). Only clear, reproducible bands were included in analyses. Despite the codominance of SSR markers, binary scoring was used to maintain consistency with iPBS data and to enable integrated association analysis using the MLM technique, as effectively demonstrated in previous wheat association mapping studies (Maccaferri et al. 2011).

Statistical Analyses

Estimation of Genetic Parameters

Genetic parameters were estimated to determine the magnitude of genotypic and phenotypic variability among wheat genotypes and to assess the heritability of the traits studied. The analysis of variance (ANOVA) was used to derive the mean squares required for these.

Calculation of Genetic Parameters

The environmental variance (V_E), genotypic variance (V_G), and phenotypic variance (V_P) were calculated using the Mean Squares (MS) from the ANOVA table, according to the equations described by Zaki and Radwan (2022).

$$V_E = MS_e V_G = \frac{MS_g - MS_e}{r} V_P = V_G + V_E$$

To compare the variation among different traits, the Phenotypic Coefficient of Variation (PCV) and Genotypic Coefficient of Variation (GCV) were calculated. These were expressed as a percentage of the grand mean, following the method of Burton and DeVane (1953). Similarly, PCV and GCV values were categorized as low (< 10%), moderate (10–20%), and high (> 20%) as suggested by Sivasubramaniam and Madhava Menon (1973).

$$PCV = \frac{\sqrt{V_P}}{\bar{x}} \times 100; GCV = \frac{\sqrt{V_G}}{\bar{x}} \times 100.$$

Heritability

Broad-sense heritability (Hb) was estimated as the ratio of genotypic variance to phenotypic variance, expressed as a percentage (Burton and De Vane 1953):

$$H_b = \frac{V_G}{V_P} \times 100$$

Heritability estimates were classified as low (0–30%), moderate (30–60%), or high (>60%) following Robinson et al. (2011).

Association Mapping Analysis Using iPBS and SSR Markers

Population Structure

The population structure of the wheat genotypes was evaluated based on genotypic data from both SSR and iPBS markers using the Bayesian model-based clustering method implemented in STRUCTURE v2.3.4 software (Pritchard et al. 2000). The analysis parameters were set according to the methodology successfully applied in our previous studies (Haliloğlu et al. 2023; Türkoğlu et al. 2023). The output from STRUCTURE was analyzed using Structure Harvester (Earl and VonHoldt 2012) to determine the optimal number of subpopulations based on the ad hoc Delta K statistic (Evanno et al. 2005). Consistent with the findings reported in our previous investigations (Haliloğlu et al. 2023; Türkoğlu et al. 2023), the optimal number of subpopulations was identified as $K = 3$ for both SSR and iPBS marker systems. Consequently, the population structure matrices (Q-matrices) corresponding to $K = 3$ were retrieved and used as covariates in the subsequent association mapping analysis.

Association Mapping

Marker-trait associations (MTAs) were evaluated using a Mixed Linear Model (MLM) implemented in TASSEL v5.0. To rigorously control false-positive associations arising from population stratification and cryptic relatedness, the MLM incorporated both population structure (Q-matrix) and a relative kinship matrix (K-matrix) as covariates. The Q-matrices were directly adopted from the pre-validated genetic structures of this specific wheat germplasm, as previously characterized using SSR (Türkoğlu et al. 2023) and iPBS (Haliloğlu et al. 2023) markers. The K-matrix was computed from genotypic data within the TASSEL environment. Linkage disequilibrium (LD) was quantified by calculating the squared allele-frequency correlation (R^2) between marker pairs. The statistical significance of the MTAs was validated using adjusted *P*-values derived from a 1000-permutation test (Mandoulakani et al. 2017).

Results

Table 2 presents the phenotypic summary statistics and genetic parameters of the 64 wheat genotypes under well-watered and late-drought conditions. Late-season drought markedly affected the mean performance of several agronomic traits. Grain yield decreased from 6208.40 kg ha^{-1} under well-watered conditions to 3962.90 kg ha^{-1} under late drought, corresponding to a reduction of approximately 36.0%. Biological yield declined from 17,395.50 to 13,106.30 kg ha^{-1}, while 1000-kernel weight decreased from 41.62 to 34.58 g. The grain-filling period was shortened from 38.06 to 29.14 days, and the number of kernels per spike decreased from 31.98 to 26.07. Harvest index also declined from 36.82 to 30.93%.

Phenotypic variance exceeded genotypic variances for all traits under both water regimes. Environmental variance increased under late drought for grain-filling period, number of spikes per m^2, 1000-kernel weight, and several other traits, whereas genotypic variance increased for grain-filling period, number of kernels per spike, and biological yield.

The phenotypic coefficient of variation (PCV) was higher than the genotypic coefficient of variation (GCV) for all traits under both water regimes. Under late drought, the highest PCV values were recorded for number of spikes per m^2 (26.59%) and number of kernels per spike (23.50%). Compared with well-watered conditions, GCV increased under late drought for grain-filling period (1.97 to 4.10%), number of kernels per spike (14.23 to 17.66%), biological yield (0.91 to 1.38%), and grain yield (1.10 to 1.31%).

Broad-sense heritability varied considerably among traits and between water regimes. Under well-watered conditions, the highest heritability estimates were recorded for vegetative period (81.01%) and plant height (75.85%). Under late drought, these traits also showed high heritability values of 74.64% and 74.79%, respectively. Heritability increased under late drought for grain-filling period (12.28 to 37.87%), number of kernels per spike (49.07 to 56.46%), biological yield (26.50 to 42.98%), and grain yield (39.60 to 40.61%). In contrast, heritability decreased for number of spikes per m^2 (46.10 to 22.93%), 1000-kernel weight (58.67 to 29.83%), and harvest index (34.31 to 14.57%).

Only six significant iPBS marker–trait associations were detected across the four environmental effects (years × water-regime) datasets (Table 3). Association mapping was performed separately for the 2011–2012 and 2012–2013 growing seasons and separately under well-watered and late-drought conditions using the corresponding phenotypic data; two-year mean phenotypic values were not used for

Table 2 Phenotypic summary statistics and genetic parameters, including minimum (*Min.*), maximum (*Max.*), mean, coefficient of variation (*CV*), environmental variance (*Ve*), genotypic variance (*Vg*), phenotypic variance (*Vp*), phenotypic coefficient of variation (*PCV*), genotypic coefficient of variation (*GCV*), and broad-sense heritability (*H*) of 64 bread wheat genotypes evaluated under well-watered and late-drought conditions. Values represent the means of the 2011–2012 and 2012–2013 growing seasons.

Traits	Water regime	Min.	Max.	Mean	CV	Ve	Vg	Vp	PCV (%)	GCV (%)	H (%)
Vegetative period (days)	Well-watered	10.00	22.00	16.05	4.95	1.02	4.33	5.35	14.41	12.97	81.01
Grain filling period (days)		27.00	51.00	38.06	5.05	4.04	0.57	4.60	5.64	1.97	12.28
Plant height (cm)		57.20	126.40	96.44	6.89	51.22	160.84	212.06	15.10	13.15	75.85
Spikes per m^2		300.00	1415.00	738.44	13.00	13,210.84	11,299.54	24,510.38	21.20	14.40	46.10
Kernels per spike		15.40	49.80	31.98	13.91	21.50	20.72	42.22	20.32	14.23	49.07
1000-kernel weight (g)		27.68	55.55	41.62	6.89	8.67	12.31	20.98	11.00	8.43	58.67
Biological yield (kg/ha)		9125.00	33,875	17,395.50	12.88	69,436.81	25,034.91	94,471.72	1.77	0.91	26.50
Grain yield (kg/ha)		3333.33	13,628.57	6208.40	11.70	7102.62	4656.10	11,758.71	1.75	1.10	39.60
Harvest index (%)		16.89	54.40	36.82	10.45	14.96	7.82	22.78	12.96	7.59	34.31
Vegetative period (days)	Late drought	10.00	22.00	16.73	5.02	1.49	4.38	5.87	14.48	12.51	74.64
Grain filling period (days)		19.00	40.00	29.14	4.58	2.34	1.43	3.77	6.66	4.10	37.87
Plant height (cm)		50.40	118.40	93.36	6.20	44.55	132.13	176.68	14.24	12.31	74.79
Spikes per m^2		300.00	1460.00	643.71	5.10	22,582.22	6717.37	29,299.59	26.59	12.73	22.93
Kernels per spike		12.04	51.60	26.07	15.44	16.33	21.18	37.51	23.50	17.66	56.46
1000 kernel weight (g)		22.79	65.19	34.58	11.61	16.99	7.22	24.21	14.23	7.77	29.83
Biological yield (kg/ha)		5500.00	23,812.5	13,106.30	12.40	43,280.90	32,625.13	75,906.03	2.10	1.38	42.98
Grain yield (kg/ha)		1200.00	6000.00	3962.90	14.40	3925.42	2684.05	6609.46	2.05	1.31	40.61
Harvest index (%)		16.73	44.75	30.93	9.89	11.92	2.03	13.95	12.08	4.61	14.57

Table 3 Significant iPBS marker–trait associations identified for nine agronomic traits in 64 bread wheat genotypes evaluated under well-watered and late-drought conditions during the 2011–2012 and 2012–2013 growing seasons.

Traits/ Markers	2011–12				2012–13			
	Well-watered		Late drought		Well-watered		Late drought	
	P-value	R^2	*P*-value	R^2	*P*-value	R^2	*P*-value	R^2
Vegetative period								
iPBS-2390	0.05	0.092	–	–	–	–	–	–
Grain filling period								
iPBS-2376	–	–	–	–	0.023	0.131	–	–
Plant height								
iPBS-2274	–	–	–	–	–	–	0.02	0.125
Spikes per m^2								
iPBS-2381	–	–	0.02	0.110	–	–	–	–
1000-kernel weight								
iPBS-2390	–	–	0.05	0.090	–	–	–	–
iPBS-2392	–	–	0.05	0.090	–	–	–	–

P-values and the proportion of phenotypic variation explained by individual marker associations (R^2) are presented separately for each year × water-regime combination

this analysis. The detected associations were specific to individual year × water-regime combinations. Under well-watered conditions in 2011–2012, *iPBS-2390* was associated with vegetative period ($P = 0.050$, $R^2 = 0.092$). Under late drought in the same growing season, *iPBS-2381* was associated with spikes per m^2 ($P = 0.020$, $R^2 = 0.110$), while *iPBS-2390* and *iPBS-2392* were associated with 1000-kernel weight ($P = 0.050$), with each marker explaining 9.0% of the phenotypic variation. In 2012–2013, *iPBS-2376* was associated with grain-filling period under well-watered conditions ($P = 0.023$, $R^2 = 0.131$), whereas *iPBS*-2274 was associated with plant height under late drought ($P = 0.020$, $R^2 = 0.125$). No iPBS marker showed a significant association with the same trait across both growing seasons and water regimes, indicating that the detected iPBS associations were specific to individual phenotyping environments.

SSR-based association mapping revealed many significant marker–trait associations across the four environmental effect (years × water-regime) combinations (Table 4). To maintain the temporal and environmental resolution of the phenotypic datasets, association analyses were performed independently for the 2011–2012 and 2012–2013 growing seasons under well-watered and late-drought conditions. Accordingly, the marker–trait associations reported here should be interpreted within their respective year × water-regime combinations rather than based on two-year averaged phenotypic performance. Across the evaluated datasets, 82 SSR markers were significantly associated with at least one of the nine agronomic traits, resulting in a total of 219 significant marker–trait associations. Twenty-four SSR markers were associated with vegetative period, 14 with grain-filling period, 14 with plant height, 26 with spikes per m^2, 21 with kernels per spike, 13 with 1000-kernel weight, 18 with biological yield, 21 with grain yield, and 21 with harvest index. Several SSR markers were associated with more than one trait and/or were detected in more than one year × water-regime combination, whereas many associations were restricted to a specific environment. This pattern indicates considerable environmental dependence of the detected marker–trait relationships and therefore warrants caution when inferring their stability across growing seasons. The proportion of phenotypic variation explained by individual significant SSR associations varied considerably among traits and environments. The largest R^2 value was observed for WMS58 associated with spikes per m^2 under well-watered conditions in 2011–2012 ($R^2 = 0.247$, $P = 0.0003$), indicating that this marker accounted for 24.7% of the phenotypic variation in this specific environment. Other relatively strong associations included *BARC105* with harvest index under well-watered conditions in 2012–2013 ($R^2 = 0.201$, $P = 0.003$), *BARC128* with harvest index under well-watered conditions in 2012–2013 ($R^2 = 0.183$, $P = 0.005$), *BARC122* with harvest index under well-watered conditions in 2012–2013 ($R^2 = 0.180$, $P = 0.006$), *GWM337* with 1000-kernel weight under well-watered conditions in 2011–2012 ($R^2 = 0.176$, $P = 0.001$), and *BARC101* with kernels per spike under late-drought conditions in 2012–2013 ($R^2 = 0.171$, $P = 0.006$). Collectively, these results demonstrate that the magnitude of marker effects varied substantially among traits, years, and water regimes. Importantly, the year-specific marker–trait association results were not directly compared with genetic parameters calculated from two-year averaged phenotypic data. Genetic variance, phenotypic variance, coefficients of variation, and broad-sense heritability were therefore evaluated separately within the corresponding year × water-regime datasets in the revised analysis, thereby ensuring consistency between the phenotypic and molecular analyses.

Table 4 Significant SSR marker–trait associations identified for nine agronomic traits in 64 bread wheat genotypes evaluated under well-watered and late-drought conditions during the 2011–2012 and 2012–2013 growing seasons.

Traits/Markers	2011–12				2012–13			
	Well-watered		Late drought		Well-watered		Late drought	
	P-value	R^2	*P*-value	R^2	*P*-value	R^2	*P*-value	R^2
Vegetative period								
BARC59	–	–	–	–	0.03	0.072	0.03	0.063
BARC78	–	–	–	–	0.03	0.072	0.03	0.063
BARC128	–	–	–	–	0.02	0.120	–	–
BARC141	–	–	–	–	0.01	0.137	–	–
BARC197	0.04	0.094	–	–	–	–	–	–
CFA2040	–	–	–	–	0.03	0.072	0.03	0.063
CFA2187	–	–	–	–	0.03	0.072	0.03	0.063
CFA2043	–	–	–	–	0.03	0.072	0.03	0.063
CFA2155	–	–	0.05	0.083	–	–	–	–
CFA2163	–	–	0.04	0.093	–	–	–	–
CFD190	–	–	–	–	–	–	0.008	0.105
CFD287	0.02	0.078	0.01	0.089	–	–	–	–
GWM391	–	–	0.01	0.120	–	–	–	–
GWM443	–	–	0.01	0.120	–	–	–	–
WMC99	–	–	–	–	–	–	0.05	0.087
WMC420	–	–	–	–	–	–	0.03	0.063
WMC524	–	–	–	–	–	–	0.01	0.087
WMS46	0.04	0.096	0.05	0.083	–	–	–	–
WMS72	–	–	–	–	–	–	0.0399	0.06336
WMS118	–	–	0.04	0.061	0.02	0.074	–	–
WMS148	–	–	–	–	0.02	0.073	–	–
WMS189	–	–	–	–	–	–	0.01	0.096
WMS190	–	–	0.04	0.056	–	–	0.01	0.084
WMS493	0.02	0.073	0.04	0.059	–	–	–	–

Table 4 (Continued)

Traits/Markers	2011–12				2012–13			
	Well-watered		Late drought		Well-watered		Late drought	
	P-value	R^2	*P*-value	R^2	*P*-value	R^2	*P*-value	R^2
Grain filling period								
BARC105	0.02	0.112	–	–	–	–	0.04	0.099
BARC133	0.02	0.113	–	–	–	–	0.05	0.056
BARC204	0.02	0.113	–	–	–	–	–	–
BARC216	0.05	0.092	–	–	–	–	–	–
BARC240	0.05	0.092	–	–	–	–	–	–
CFA152	0.02	0.112	–	–	–	–	–	–
CFD190	–	–	0.03	0.080	–	–	–	–
WMC500	–	–	–	–	–	–	0.03	0.070
WMC765	–	–	–	–	–	–	0.05	0.058
WMS10	0.01	0.144	–	–	–	–	–	–
WMS46	–	–	–	–	–	–	0.02	0.125
WMS52	0.02	0.075	–	–	–	–	–	–
WMS493	0.04	0.062	–	–	–	–	–	–
WMS566	0.03	0.101	0.04	0.105	–	–	–	–
Plant height								
BARC1	–	–	0.03	0.109	–	–	–	–
BARC48	0.05	0.057	–	–	–	–	–	–
BARC130	–	–	0.03	0.072	–	–	–	–
BARC142	–	–	–	–	0.01	0.094	0.01	0.102
BARC197	–	–	–	–	0.05	0.098	–	–
BARC204	–	–	0.03	0.108	–	–	–	–
BARC216	–	–	–	–	0.009	0.112	0.05	0.095
CFD287	0.002	0.151	–	–	–	–	–	–
WMC406	0.02	0.080	–	–	–	–	0.03	0.070
WMC524	0.01	0.087	–	–	–	–	–	–
WMS118	0.01	0.090	–	–	–	–	–	–
WMS148	–	–	0.01	0.099	–	–	–	–
WMS189	–	–	–	–	–	–	0.03	0.074
WMS190	0.04	0.062	–	–	–	–	–	–

Table 4 (Continued)

Traits/Markers	2011–12				2012–13			
	Well-watered		Late drought		Well-watered		Late drought	
	P-value	R^2	*P*-value	R^2	*P*-value	R^2	*P*-value	R^2
Spikes per m^2								
BARC54	–	–	0.05	0.065	–	–	–	–
BARC59	0.05	0.064	–	–	–	–	–	–
BARC64	0.02	0.084	0.01	0.11	–	–	–	–
BARC73	–	–	0.05	0.065	–	–	–	–
BARC78	0.05	0.064	–	–	–	–	–	–
BARC130	–	–	–	–	0.03	0.077	–	–
BARC140	–	–	–	–	0.02	0.081	–	–
BARC141	0.03	0.118	–	–	–	–	–	–
BARC165	–	–	–	–	0.04	0.070	–	–
CFA2040	0.05	0.064	–	–	–	–	–	–
CFA2049	0.05	0.066	–	–	–	–	–	–
CFA2187	0.05	0.064	–	–	–	–	–	–
CFA2043	0.05	0.064	–	–	–	–	–	–
GWM391	0.05	0.103	–	–	–	–	–	–
GWM413	0.04	0.111	–	–	–	–	–	–
GWM443	0.05	0.103	–	–	–	–	–	–
WMC336	–	–	0.04	0.071	–	–	0.050	0.065
WMC420	0.05	0.064	–	–	–	–	–	–
WMC435	–	–	–	–	0.02	0.092	–	–
WMC687	–	–	0.05	0.065	–	–	–	–
WMS5	–	–	–	–	0.05	0.063	–	–
WMS44	–	–	–	–	0.02	0.135	0.01	0.141
WMS58	0.0003	0.247	–	–	–	–	–	–
WMS63	0.01	0.09	–	–	–	–	–	–
WMS72	0.05	0.064	–	–	–	–	–	–
WMS155	0.012	0.110	0.03	0.076	0.02	0.089	–	–

Table 4 (Continued)

Traits/Markers	2011–12				2012–13			
	Well-watered		Late drought		Well-watered		Late drought	
	P-value	R^2	*P*-value	R^2	*P*-value	R^2	*P*-value	R^2
Kernels per spike								
BARC64	–	–	0.05	0.063	–	–	–	–
BARC94	–	–	–	–	–	–	0.03	0.107
BARC101	–	–	–	–	–	–	0.006	0.171
BARC105	–	–	–	–	–	–	0.03	0.106
BARC113	–	–	–	–	–	–	0.03	0.106
BARC122	–	–	–	–	–	–	0.03	0.108
BARC128	–	–	–	–	–	–	0.03	0.107
BARC142	–	–	0.01	0.097	–	–	–	–
BARC152	–	–	–	–	0.02341	0.08688	–	–
BARC216	–	–	0.003	0.124	–	–	–	–
CFA2099	–	–	–	–	0.04	0.105	–	–
CFA2155	–	–	–	–	0.05	0.099	–	–
CFA2163	–	–	–	–	0.03	0.112	–	–
GWM497	–	–	–	–	–	–	0.005	0.129
GWM533	–	–	0.03	0.079	–	–	–	–
WMC42	0.01	0.107	–	–	–	–	–	–
WMC500	0.01	0.107	–	–	0.05	0.060	0.02	0.077
WMC807	0.02	0.130	–	–	–	–	–	–
WMS5	–	–	–	–	–	–	0.05	0.060
WMS155	–	–	0.01	0.106	–	–	–	–
WMS566	–	–	–	–	0.01	0.157	–	–

Table 4 (Continued)

Traits/Markers	2011–12				2012–13			
	Well-watered		Late drought		Well-watered		Late drought	
	P-value	R^2	*P*-value	R^2	*P*-value	R^2	*P*-value	R^2
1000-kernel weight								
BARC88	–	–	0.05	0.054	–	–	–	–
CFA2049	–	–	–	–	0.05	0.062	–	–
CFD49	–	–	–	–	–	–	0.04	0.068
CFD287	–	–	–	–	0.03	0.079	0.05	0.062
GWM319	0.04	0.067	–	–	–	–	–	–
GWM337	0.001	0.176	–	–	–	–	–	–
GWM368	–	–	0.02	0.123	–	–	–	–
GWM382	–	–	0.04	0.104	–	–	–	–
WMC356	–	–	–	–	0.01	0.099	0.01	0.094
WMC413	–	–	–	–	0.009	0.120	0.015	0.101
WMC807	0.01	0.146	–	–	–	–	–	–
WMS58	–	–	–	–	0.05	0.061	0.05	0.063
WMS148	–	–	–	–	–	–	0.04	0.067
Biological yield								
BARC37	–	–	–	–	0.03	0.071	–	–
BARC59	–	–	0.03	0.075	0.02	0.082	–	–
BARC78	–	–	0.03	0.075	0.02	0.082	0.05	0.061
BARC133	–	–	0.03	0.075	–	–	–	–
BARC141	–	–	–	–	0.03	0.105	–	–
CFA2040	–	–	0.03	0.075	–	–	0.05	0.061
CFA2187	–	–	0.03	0.075	0.02	0.082	0.05	0.06
CFA2043	–	–	0.03	0.075	0.02	0.082	0.05	0.06
CFA2099	–	–	–	–	0.05	0.086	–	–
CFD287	–	–	–	–	–	–	0.02	0.082
GWM413	0.009	0.161	–	–	–	–	–	–
WMC166	–	–	–	–	0.04	0.096	–	–
WMC317	–	–	–	–	0.02	0.110	–	–
WMC420	–	–	0.03	0.075	–	–	0.05	0.061
WMC524	0.03	0.076	–	–	0.02	0.075	0.02	0.090
WMS72	–	–	0.03	0.075	0.02052	0.08279	0.05	0.061
WMS118	–	–	–	–	–	–	0.01	0.098
WMS155	–	–	0.02	0.090	–	–	–	–

Table 4 (Continued)

Traits/Markers	2011–12				2012–13			
	Well-watered		Late drought		Well-watered		Late drought	
	P-value	R^2	*P*-value	R^2	*P*-value	R^2	*P*-value	R^2
Grain yield								
BARC59	–	–	–	–	0.009	0.111	–	–
BARC78	–	–	–	–	0.009	0.111	–	–
BARC80	–	–	–	–	–	–	0.05	0.05
BARC88	–	–	–	–	–	–	0.05	0.05
BARC89	–	–	–	–	0.01	0.090	–	–
BARC133	–	–	0.02	0.086	–	–	–	–
BARC140	–	–	0.05	0.065	–	–	–	–
BARC141	–	–	–	–	0.02	0.117	–	–
CFA2040	–	–	–	–	0.009	0.111	–	–
CFA2187	–	–	–	–	0.009	0.112	–	–
CFA2043	–	–	–	–	0.009	0.111	–	–
CFD190	–	–	–	–	–	–	0.04	0.058
GWM350	–	–	0.005	0.142	–	–	–	–
GWM493	0.01	0.106	–	–	–	–	–	–
WMC320	0.01	0.096	–	–	–	–	–	–
WMC420	–	–	–	–	0.009	0.111	–	–
WMC500	0.04	0.066	–	–	–	–	0.01	0.088
WMC524	–	–	–	–	–	–	0.04	0.058
WMS72	–	–	–	–	0.009	0.111	–	–
WMS155	–	–	0.003	0.154	–	–	–	–
WMS189	–	–	0.004	0.014	–	–	–	–

Table 4 (Continued)

Traits/Markers	2011–12				2012–13			
	Well-watered		Late drought		Well-watered		Late drought	
	P-value	R^2	*P*-value	R^2	*P*-value	R^2	*P*-value	R^2
Harvest index								
BARC48	0.02	0.085	0.03	0.076	0.05	0.061	–	–
BARC54	0.05	0.059	–	–	–	–	–	–
BARC89	–	–	–	–	0.05	0.061	–	–
BARC94	–	–	–	–	0.02	0.133	–	–
BARC101	0.008	0.160	–	–	0.02	0.133	–	–
BARC105	–	–	–	–	0.003	0.201	–	–
BARC113	0.04	0.101	–	–	0.01	0.144	–	–
BARC122	–	–	–	–	0.006	0.180	–	–
BARC128	0.04	0.103	–	–	0.005	0.183	–	–
CFA2099	0.04	0.104	–	–	0.03	0.112	–	–
GWM493	–	–	0.01	0.108	–	–	–	–
GWM533	–	–	0.05	0.062	–	–	–	–
WMC500	–	–	0.005	0.141	–	–	–	–
WMC687	0.05	0.059	–	–	–	–	–	–
WMC173	–	–	0.05	0.101	–	–	–	–
WMS44	–	–	–	–	0.03	0.111	–	–
WMS46	–	–	–	–	–	–	0.05	0.099
WMS52	–	–	–	–	0.01	0.100	–	–
WMS189	–	–	0.002	0.161	–	–	–	–
WMS190	–	–	–	–	0.047	0.06	–	–
WMS493	–	–	–	–	0.007	0.12	–	–

P-values and the proportion of phenotypic variation explained by individual marker associations (R^2) are presented separately for each year × water-regime combination

Discussion

Late-season drought substantially affected the agronomic performance of the evaluated bread wheat genotypes. Grain yield decreased from 6208.40 kg ha^{-1} under well-watered conditions to 3962.90 kg ha^{-1} under late drought, corresponding to a reduction of approximately 36%. Biological yield, thousand-kernel weight, grain-filling period, and harvest index were also reduced under water deficit, demonstrating the sensitivity of reproductive development and yield formation to terminal drought. Such reductions are consistent with the adverse physiological effects of water limitation during reproductive stages, where shortened grain filling, accelerated senescence, and impaired assimilate translocation substantially decrease final grain production (Lopes and Reynolds 2011). Furthermore, terminal drought disrupts the source-sink balance, severely limiting the remobilization of water-soluble carbohydrates from the stem to the developing grain, which is a primary driver of the observed reductions in thousand-kernel weight (Senapati et al. 2019).

The genetic parameters revealed that the relative contributions of genetic and environmental variation differed considerably between water regimes and among traits. Genotypic coefficient of variation (GCV) and broad-sense heritability were higher under late drought than under well-watered conditions for grain-filling period, kernels per spike, biological yield, and grain yield. For example, heritability increased from 12.28 to 37.87% for grain-filling period, from 49.07 to 56.46% for kernels per spike, and from 26.50 to 42.98% for biological yield. In contrast, heritability decreased from 46.10 to 22.93% for spikes per m^2, from 58.67 to 29.83% for 1000-kernel weight, and from 34.31 to 14.57% for harvest index. These contrasting responses demonstrate that drought stress did not uniformly strengthen genetic control; rather, it altered the balance between genetic and environmental contributions in a trait-dependent manner. Similar variability in the genetic control of yield-related traits across contrasting moisture regimes reflects the complex genotype × environment ($G \times E$) interactions underlying drought adaptation in wheat (Sallam et al. 2019). Modern multi-environment trial (MET) analyses confirm that such dynamic shifts in heritability necessitate the use of simultaneous selection indices to identify genotypes that combine high mean performance with phenotypic stability across shifting water regimes (Olivoto and Nardino 2021). From a breeding perspective, traits maintaining substantial genetic variation and relatively high heritability under water deficit provide greater opportunities for direct selection in target stress environments, whereas traits exhibiting low heritability necessitate evaluation across MET to obtain reliable estimates of breeding value.

Following the quantitative genetic analysis, marker–trait association (MTA) mapping revealed marked differences between the iPBS and SSR marker systems. Because association mapping was performed separately for the 2011–2012 and 2012–2013 growing seasons under contrasting water regimes, the detected associations represent specific year × water-regime combinations. Accordingly, these MTAs should be interpreted within their respective phenotyping datasets rather than as robust effects based on two-year mean performances.

Only six iPBS markers exhibited significant associations with the evaluated traits, all of which were highly specific to environmental combinations. The highest proportion of phenotypic variation explained by an iPBS marker was observed for *iPBS-2376*, associated with grain-filling period under well-watered conditions in 2012–2013 ($R^2 = 0.131$, $P = 0.023$). This indicates that *iPBS-2376* may be linked to genomic regions regulating grain-filling duration in this specific environment. Several iPBS associations were distinctly detected under late drought. For instance, *iPBS-2381* explained 11.0% of the variation in spikes per m^2 under late drought in 2011–2012, while *iPBS-2274* explained 12.5% of plant-height variation under late drought in 2012–2013. Notably, iPBS-2390 and iPBS-2392 were both associated with thousand-kernel weight under late drought (2011–2012), each explaining 9.0% of the variation. Given the acute sensitivity of grain weight to terminal water limitation, these markers represent valuable candidate loci for investigating the genetic basis of kernel weight maintenance under drought stress. The relatively small number and strong environmental specificity of the iPBS associations may inherently reflect the genomic architecture targeted by this marker system. Unlike locus-specific microsatellites, iPBS markers survey polymorphisms associated with retrotransposon primer-binding sites (Kalendar et al. 2010). Retrotransposon-rich regions are known drivers of genome plasticity and can profoundly influence the regulation of adjacent genes through alterations in chromatin organization, cis-regulatory network activity, or epigenetic states under abiotic stress. Recent genomic evidence demonstrates that severe abiotic constraints, such as drought and heat, can trigger the targeted transcriptional activation of Long Terminal Repeat (LTR) retrotransposons, creating transient epigenetic states that facilitate rapid environmental adaptation (Ramakrishnan et al. 2021).. Thus, the emergence of specific iPBS MTAs exclusively under late drought suggests that these markers may capture environmentally responsive, stress-induced genomic variation (Andeden et al. 2013). This interpretation is further supported by Türkoğlu et al. (2026), who investigated marker–trait associations for physiological responses to irrigation and terminal drought in bread wheat using SSR and iPBS markers. They identified 25 iPBS markers

associated with physiological traits, with *iPBS-2376* and *iPBS-2390* showing associations with multiple physiological parameters. Notably, the recurrence of *iPBS-2376* and iPBS-2390 across the previous physiological study and the present agronomic analysis suggests that these loci may capture genomic variation relevant to multiple components of wheat response to contrasting water regimes. The broader spectrum of iPBS associations with physiological traits reported by Türkoğlu et al. (2026), compared with the relatively limited number of agronomic associations detected here, further supports the complementary value of iPBS markers for identifying environment-dependent components of drought response. Nevertheless, since association mapping alone cannot directly validate drought-induced retrotransposon activation or epigenetic reprogramming, these MTAs remain statistical relationships that warrant further functional validation.

In contrast, SSR markers demonstrated a substantially broader association profile, consistent with their established utility in dissecting multi-allelic variation in the hexaploid wheat genome (Sallam et al. 2020). A total of 82 SSR markers were involved in 219 significant MTAs across the nine agronomic traits. The most prominent SSR association was detected between WMS58 and spikes per m^2 under well-watered conditions in 2011–2012 ($R^2 = 0.247$, $P = 0.0003$). Other robust MTAs included BARC105 ($R^2 = 0.201$), BARC128 ($R^2 = 0.183$), and BARC122 ($R^2 = 0.180$) with harvest index under well-watered conditions in 2012–2013, as well as BARC101 with kernels per spike under late drought in 2012–2013 ($R^2 = 0.171$).

The contrast between the two marker systems was evident in both the frequency and magnitude of associations. The strongest SSR MTA (WMS58, $R^2 = 0.247$) explained approximately 1.9-fold more phenotypic variance than the strongest iPBS association (*iPBS-2376*, $R^2 = 0.131$). While the highly polymorphic, locus-specific nature of SSRs provides a broad detection of trait-associated allelic variation, the environmentally specific nature of iPBS markers highlights a different layer of genome-wide polymorphism. Therefore, the R^2 values should not be viewed as a direct statistical competition between marker systems, but rather as evidence that SSR and iPBS markers offer complementary genomic insights. Although high-density SNP arrays dominate contemporary mapping, the multi-allelic information provided by targeted SSR profiling remains highly effective for capturing rare allelic variants associated with yield components in diverse germplasm panels (Sallam et al. 2019).

When integrated, the quantitative genetic parameters and MTA results elucidate that the expression and detection of genetic variation in bread wheat are highly contingent upon the trait, temporal effects (year), and moisture availability. The trait-dependent fluctuations in heritability strongly align with the environmental specificity of the detected MTAs, reiterating that drought adaptation is not driven by a uniform increase in genetic control, but by complex, trait-specific genomic responses.

From a practical breeding perspective, these findings advocate for the direct selection of drought-adaptive germplasm within target stress environments. While SSR markers yielded a broader repertoire of candidate loci explaining substantial phenotypic variation, iPBS markers successfully captured highly specific loci associated with yield components under terminal drought. However, associations detected in a single environmental combination must be considered preliminary candidate loci. Validation across independent genetic backgrounds and extensive multi-environment trials will be indispensable before their deployment in marker-assisted selection (MAS) programs. Furthermore, because drought tolerance and yield are controlled by a large number of minor-effect loci, integrating these trait-specific MTAs into genomic selection (GS) models may provide a more comprehensive and robust strategy for accelerating genetic gain in modern wheat breeding programs facing fluctuating climatic conditions (Crossa et al. 2017).

Conclusions

Late-season drought substantially reduced grain yield, biological yield, and 1000-kernel weight, confirming its adverse effects on wheat productivity. The changes in genetic parameters varied among traits, indicating that drought responses were both trait- and environment-dependent. Across the four independently analyzed year × water-regime datasets, 82 unique SSR markers were associated with at least one of the nine agronomic traits. Because some markers were associated with multiple traits and/or were detected in more than one year × water-regime combination, these markers collectively produced 219 significant marker–trait associations. Thus, 82 represents the number of unique associated SSR markers, whereas 219 represents the cumulative number of significant associations detected across all traits, years, and water regimes. Under late-drought conditions, the strongest SSR association was detected between *BARC101* and the number of kernels per spike in the 2012–2013 growing season ($P = 0.006$, $R^2 = 0.171$). In contrast, only six significant iPBS marker–trait associations were identified, all of which were specific to individual year × water-regime combinations. Overall, SSR markers captured a broader range of agronomically relevant variation, whereas iPBS markers provided complementary information on environment-specific responses. Because most associations depended on the year and water regime, they should be regarded as candidate loci requiring validation in independent germplasm and multi-environment

trials before their application in marker-assisted breeding for drought adaptation and yield stability in bread wheat.

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Declarations

Ethical approval Not applicable.

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