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Marker-trait associations of yield related traits in bread wheat (*Triticum aestivum* L.) under a semi-arid climate

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Abstract: Identifying QTLs (quantitative trait loci) that control yield related traits under a stressed environment is very useful for marker-assisted selection (MAS). Marker-trait associations (MTA) for several agro-morphological traits were performed with 130 Tunisian and exotic spring bread wheat (*Triticum aestivum* L.) accessions under a semi-arid climate in El Kef, Tunisia. Grain yield and other important traits were evaluated. A population structural analysis identified two sub populations. In total, 29 MTAs were detected at $-\log P \geq 3$ using an MLM (mixed linear model), and only 5 MTAs with $-\log P \geq 4$. The locus on chromosome 4A was detected to control the heading date accounting for up to 22% of the trait variance. Two other loci located on chromosomes 3B and 7B were found to be stable during the two cropping seasons and have a pleiotropic effect on the heading date, yield, internodes length and grain per spike. These two regions are candidates for further genetic analysis.

Keywords: association mapping; candidate genes; yield

Bread wheat (*Triticum aestivum* L.) is one of the most important food crops along with rice and maize in the world. It is grown widely under irrigated environments and the rainfed climate of semi-arid regions. The wheat yield is limited due to several environmental stresses that affect the growth of the plants at various stages. The grain yield is a complex trait contributed by multiple yield components, and governed by several genes that interact with each other and with the environment (Quarrie *et al*. 2005). In wheat, a large number of morphological and physiological traits are linked to a drought tolerance (del Pozo *et al*. 2012), which exhibit strong environmental interactions. Increasing the tolerance to drought stress has become a major goal for wheat breeding programmes particularly in light of the prolonged drought periods as a result of climate change (Wehner *et al*. 2015).

Association mapping uses linkage disequilibrium (LD) to link the phenotypes and genotypic data of a diverse set of lines to identify the molecular markers associated with the traits of interest. In bread wheat, association studies have been used to map and characterise QTLs (quantitative trait loci) for a wide range of traits, including the heading date (Zanke *et al*. 2014a), the plant height (Zanke *et al*. 2014b), the internodes length, the peduncle length and spike length (Cui *et al*. 2011) and the grain yield (Tadesse *et al*. 2015). These studies reported different numbers of significant marker trait associations (MTA) that have generally explained a significant proportion of the phenotypic variance.

The purpose of this study was to identify the correlation between the investigated traits using a principal component analysis (PCA) and to investigate the marker-trait associations of single nucleotide polymorphism (SNP) markers with important yield related traits using 130 bread wheat accessions under a semi-arid climate in Tunisia. This study was important in selecting the accessions carrying genomic

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regions controlling important traits for improving the local bread wheat germplasm.

MATERIAL AND METHODS

Germplasm and phenotyping. A total of 130 bread wheat accessions (*T. aestivum*), including 17 Tunisian landraces and exotic accessions (from South America, USA, Canada and the Middle East), derived from the U.S. National Plant Germplasm System (NPGS) (Table S1 in the Electronic Supplementary Material (ESM)). During two cropping seasons 2016/2017 and 2017/2018, a field trial was conducted in El Kef, Tunisia characterised by a semi-arid climate with an annual rainfall average of 380 mm. Each accession was planted in two replications, in two rows, 65 seeds in each row, 2.5 m long, with a row spacing of 30 cm. All traits were measured from five plants except for the yield. The considered traits in this study were: the grain yield (Yld, weight of the grain harvested from the whole two rows), the plant height (H, measured from the soil surface to the tip of the spike excluding awns), the days to the heading (HD, the number of days from sowing to the time when 50% of the ear had emerged), the peduncle length (PL, measured from the base of the spike to the flag leaf node), the internodes length (INL, measured from the flag leaf node to the next node), the awn length (AwL, the length of the awn in the central spikelet), the spike length (SL, from the base of the spike to the tip of the terminal spikelet excluding the awns), the flag leaf length (FLL) and the grain per spike (GpS, the number of grains per spike).

Phenotypic data analysis. The analysis of variance (ANOVA) for all the studied traits was performed using GEA-R (genotype × environment analysis with R for Windows) (Pacheco *et al*. 2016). The traits correlation, principle component analysis, common component coefficients, eigenvalues and the proportion of the total variance for each trait were calculated. A hierarchical clustering on the principal components (HCPC) was performed for identifying the groups in the dataset. All of the above analyses were performed using the R packages: FactoMiner, and FactoExtra (Lê *et al*. 2008) for the cluster analysis of the different accessions.

Genotyping and population structure. All the accessions were already genotyped with 1744 SNP markers selected from the iSelect 90K array containing 90 000 wheat SNP markers (Cavanagh *et al*. 2013; Wang *et al*. 2014). The genotypic data of the 130 selected accessions are publicly available at https://triticeae-toolbox.org/wheat. The positions of the SNP markers along the chromosomes in terms of the genetic distance (cM) were based on the consensus genetic map (Wang *et al.* 2014). The markers were removed if they were either monomorphic or exhibited allele frequencies of less than 5% (minor alleles).

To determine the population structure of the studied accessions, the genotyping data was processed with the STRUCTURE software (Ver. 2.3.4, 2012), which implemented a model-based Bayesian cluster analysis (Pritchard *et al*. 2000). A putative number of subpopulations ranging from k = 1 to 10 was assessed using 10 000 burn-in iterations followed by 50 000 recorded Markov-Chain iterations. To estimate the sampling variance of the inferred population structure, 10 independent runs were carried out for each k. The likely number of sub-populations present was estimated following Evanno *et al*. (2005), in which the number of sub-groups (ΔK) is maximised.

Association mapping. All the traits evaluated for the 130 accessions and the corresponding 1744 SNP data were used for association mapping using TASSEL software (Ver. 5.0, Bradbury *et al.* 2007). For the best linear unbiased estimates, a mixed linear model (MLM) procedure considering the estimated population structure (Q), and the kinship matrix (K) was used. At a threshold of –log10 $P \geq 3.0$, a significant marker trait association is declared.

RESULTS AND DISCUSSION

This study was conducted in the El Kef region, Tunisia which is characterised by low and irregular rainfall distribution during the cropping season especially at the grain filling stage which will affect the grain yield (Table 1). During the heading and grain filling stage, the total rainfall increased from 19.8 mm within eight days in 2017 to 65.9 mm in 22 days in 2018. Because of this irregular rainfall distribution, we have considered each year as a separate environment.

The basic statistical parameters in each year (the mean values and standard deviations, the minimum and maximum values) for the 130 bread wheat lines are summarised in Table 2. Some traits showed an increase in their mean values between the two cropping seasons. The means of the grain yield increased from 169 to 209 g/m^2. The plant height increased from 77 cm to 86 cm. However, there was a delay in the heading date from 135 days in 2017 to 138 days in 2018. Other traits showed a stable mean value across the two years like the flag leaf length and the awn length.

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Table 1. Weather conditions during the two cropping seasons

Years	Average	Total	Nov	Dec	Jan	Feb	Mar	Apr	May
			vegetative stage					heading stage	grain filling stage
Average temperature (°C)									
2017/2018	11.9		11	7.9	9.7	8.1	12.2	15.9	18.6
2016/2017	12.5		13.4	10.5	6.3	9.4	11.9	15.7	20.8
Precipitation (mm)									
2017/2018		290.8	82.5	36.8	32.5	31.7	41.4	36.3	29.6
2016/2017		181.3	44.2	53.1	35	24.9	4.31	17.5	2.3
Days with precipitation (days)									
2017/2018		75	8	11	4	16	15	10	11
2016/2017		50	7	12	13	5	5	7	1
Humidity (%)									
2017/2018	63.8		70.8	77.8	69.7	74.6	66	61.8	61
2016/2017	65.7		68.9	81.8	76.7	73.4	63.5	53.1	42.6

The analysis of variance for the grain yield related traits of each genotype in each year based on the genotype/environment (year) interaction effects is presented in Table 3. The genotype effect was much stronger than the environment effect for all the traits ranging from 41.9% for the spike length to 94% for the awn length. The phenotypic variation, explained by the genotypes, indicates that the accessions were diverse and a major part of the variation in the majority of the traits resulted from the genetic effect.

The phenotypic correlations of the studied traits across the two cropping seasons are presented in Table 4. The combined data over two years showed that the heading date was negatively correlated with almost all the other traits. A positive correlation has been found between the grain yield and the plant architecture traits including plant height, internode length and peduncle length. These data measure the strength of the relationship between the genetic values of both traits with the yield and the existence of the pleiotropic effects. The results of the correlation analysis suggest that the early heading is associated with an increase in the plant height and yield.

The PCA screen plot showed that 63.4% of the phenotypic variation was governed by the first three components. The first two components PCA1 and PCA2 explained 33.9% and 17% of the total variation (Figure 1a). The days to the heading has the major contribution to the first component, however the plant height and peduncle length contribute the most to the second components. Almost all the traits showed an important contribution to the two components except for the awn length trait. Two groups or clusters were identified using the first three principal components (PCA) with eigenvalues >1 that explained 63.8% of the variance. All accessions were plotted on the two axes of PCA1 and PCA2 (Figure 1b). The first group includes a short individual, a short peduncle with an early heading

Table 2. Basic statistics for each bread wheat trait during the two cropping seasons

Traits	Years	Min.	Max.	Mean	SD
Heading date (days)	2017	128	150	135.04	6.13
	2018	128	162	138.45	9.24
Plant height (cm)	2017	64	110	86.96	8.30
	2018	50.66	100	77.41	9.61
Peduncle length (cm)	2017	13.2	45	25.55	5.97
	2018	6.33	31	17.24	5.20
Internodes length (cm)	2017	8.9	118	18.98	7.10
	2018	7	22	14.51	3.28
Spike length (cm)	2017	6	15.5	11.20	1.87
	2018	5.83	14	9.268	1.82
Awn length (cm)	2017	0	10	4.90	3.15
	2018	0	8.66	4.20	2.71
Flag leaf length (cm)	2017	11	24	18.14	2.40
	2018	11.2	25	18.39	2.86
Grain per spike	2017	13	28	20.41	2.22
	2018	8	32	21.06	6.29
Yield (g)	2017	77.9	300	169.58	46.93
	2018	101	333.04	209.93	51.47

SD – standard deviation

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Table 3. The analysis of variance (ANOVA) of the studied traits in the bread wheat

Source of variation	Df	Total variability explained (%)								Means square (MS)							
		DH	PH	PL	INL	SL	AwL	FLL	GpS	Yld	DH	PH	PL	INL	SL	AwL	FLL	GpS	Yld
Genotype	129	87.1	58.1	48.2	52.0	41.9	94.0	85.9	52.1	72.7	223.9*	238.0*	93.5*	54.1*	7.2*	33.2	22.8*	45.1*	7901.9*
G × E	129	8.4	19.3	15.5	28.5	35.3	4.5	14.0	47.5	12.0	21.6	78.9	30.1	29.6	6.1	1.6	3.7	41.2	1310.1
Residuals	260	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1	3.5	1.4	19.9	0.2	0.1	0.5	1.2	271.5
CV (%)		4	10	28	42	18	69	13	11	25									

HD – the days to heading; H – the plant height; PL – the peduncle length; INL – the internodes length; SL – the spike length; AwL – the awn length; FLL – the flag leaf length; GpS – the grain per spike; Yld – the grain yield; G – the genotype; E – the environment (season); Df – the degree of freedom; *significance level at 0.01

date. However, the second group contains individuals with a long height and a late heading date.

Population structure and association mapping. The number of subgroups *k* was estimated with different *k* values. As indicated in Figure 2, the *k* value for 2 was optimal. This indicated that the accessions could be divided into two subgroups. One group comprised 23 accessions, the second subgroup 26 accessions, and the remaining accessions are considered as an admixture (Table S1 in ESM).

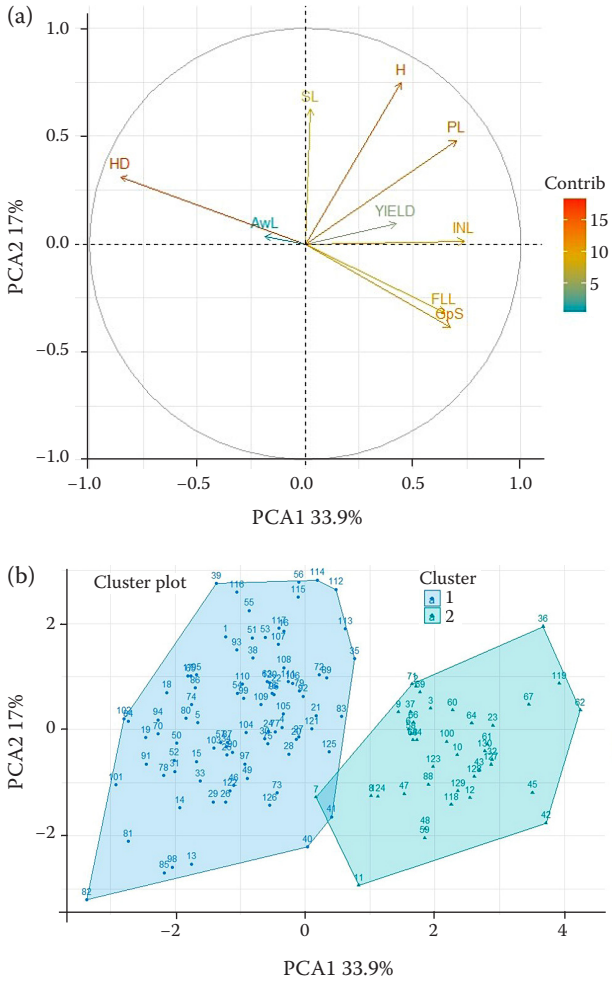

Figure 1. The principal component analysis (PCA) and cluster analysis: (a) the first two components, PCA1 and PCA2, explained 33.9% and 17% of the total variation, the days to heading (DH) and internodes length (INL) have the major contribution to the first component, the plant height (H) and peduncle length (PL) contribute the most to the second component, almost all the traits showed a major contribution to the two major components except for the grain per spike (GpS) and the awn length (AL) traits; (b) two groups or clusters were identified using the first two PCAs

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Table 4. Pearson's coefficients of correlation between the studied traits in the bread wheat

Traits	HD	H	PL	INL	SL	AwL	FLL	GpS
H	–0.15							
PL	–0.47**	0.60**						
INL	–0.58**	0.30**	0.43**					
SL	0.16	0.24**	0.19*	–0.02				
AwL	0.10	–0.06	–0.10	–0.21*	0.12			
FLL	–0.57**	0.05	0.26**	0.35**	–0.01	–0.00		
GpS	–0.66**	–0.00	0.26**	0.38**	–0.00	–0.02	0.43**	
Yld	–0.30**	0.22*	0.17*	0.23**	0.00	–0.04	0.17	0.16

HD – the heading date; HD – the days to heading; H – the plant height; PL – the peduncle length; INL – the internodes length; SL – the spike length; AwL – the awn length; FLL – the flag leaf length; GpS – the grain per spike; Yld – the grain yield; *, **significant at $P < 0.05, 0.01$

In 2016–2017, 34 significant MTAs (Table S2 in ESM) were detected for all the phenotypic traits, 10 for the AwL, two for the FLL, one for the GpS, one for the PL, 10 for the HD, three for the INL, five for the SL and two for the Yld. The percentage of the phenotypic variation ranged from 12% to 65%. The maximum percentage of the phenotypic variation was found in IWA1296 located on chromosome 7D and associated with the awn length. In 2017-2018, 52 MTAs (Table S3 in ESM) were detected for all the traits except for the peduncle length. Twenty-four significant associations with the grain yield were detected in all the chromosomes.

During the two cropping seasons, using the MLM model approach, several SNP markers significantly associated with the studied traits were identified in all chromosomes except for 1B, 1D, 2D, 5B and 7D. In total, 29 MTAs were detected at $-\log P > 3$ using MLM, and only five MTAs with $-\log P > 4$. So, in this study, a significant MTA association at $-\log P \geq 3$ was considered, as in Houston *et al.* (2014). The results of the association mapping of the grain yield related traits under the semi-arid climate are presented in Table 5. In our study, out of the 34 detected associations, 9 SNPs showed a pleiotropy associated with multiple traits. The locus at a position around 68 cM on chromosome 7B was closely associated with the GpS, the HD, the INL and the yield. The locus located on chromosome 3B at a position around 62~72 cM was linked to the Yld, the HD, the INL and the GpS. Moreover, according to the correlation coefficients of HD-GpS ($r = –0.66$, $P < 0.01$), HD-INL ($r = –0.58$, $P < 0.01$) and HD-Yld ($r = –0.3$, $P < 0.01$), these traits were highly correlated. Another important locus on chromosome 5A has a pleiotropic effect on the AwL, HD, GpS and INL. Out of the nine marker-heading date associations identified, six have a pleiotropic effect on the grain per spike. The percentage of phenotypic variation

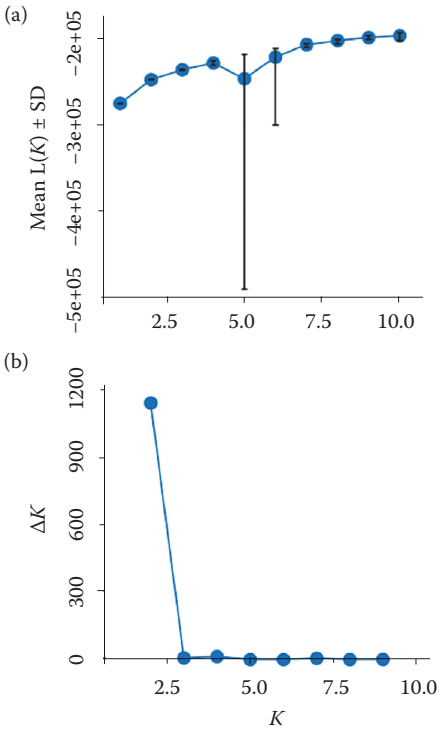

Figure 2. The population structure and the number of subgroups: (a) the means of the log likelihoods and their standard deviations computed with the STRUCTURE software over 10 runs and for a number (k) of expected clusters ranging from 1 to 10 and (b) the ΔK values as a function of k; as indicated in this figure, the k value for 2 was optimal; this indicates that accessions could be divided into 2 subgroups

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ranged from 13 to 26%. The maximum percentage of the phenotypic variation was found in IWA4581 located on chromosome 3D.

Several MTAs consistently identified in both environments were considered to be stable. Among them, six SNP markers located on chromosomes 1A, 3B, 4A, 4B, 5A, and 7B were associated with the heading date explaining a phenotypic variation ranging from 13 to 22%. One MTA located on chromosome 7B was associated with the yield (19% of the phenotypic variation; Table 3). In this study, out of the 34 associated loci, 19 have a negative effect on the studied traits. For the awn length, the two identified loci have a negative effect and decrease the awn

Table 5. The results of the marker-trait association analysis in the bread wheat using the mixed linear model with –log10 (P) ≥ 3 during the two cropping seasons

Traits	Markers	Chr.	Position (cM)	2016–2017	2017–2018	P value	R^2
Awn length	IWA4581	3D	12 848	+	–	3.34E–05	0.26
	IWA3313	5A	56 485	–	+	1.82E–04	0.19
Flag leaf length	IWA8053	3B	85 517	–	+	5.02E–04	0.14
	IWA8059	3D	148 409	+	–	2.93E–04	0.15
	IWA5381	4D	80 677	–	+	8.26E–05	0.18
Grain per spike	IWA4385	2A	82 768	–	–	7.57E–04	0.13
	IWA170	2B	96 987	–	–	5.83E–04	0.13
	IWA692	2B	152 590	–	–	8.02E–04	0.13
	IWA4810	3A	109 946	–	+	3.01E–05	0.20
	IWA292	3B	63 837	–	+	9.82E–04	0.13
	IWA142	4A	48 524	–	+	3.94E–04	0.15
	IWA4767	5A	35 376	–	–	4.76E–04	0.14
	IWA8122	7A	127 068	+	–	5.49E–04	0.14
	IWA2353	7B	68 835	–	+	5.16E–04	0.14
Plant height	IWA3450	6B	64 084	–	–	4.61E–04	0.14
Heading date	IWA4538	1A	101 642	+	+	6.29E–04	0.13
	IWA4385	2A	82 768	–	+	7.52E–04	0.13
	IWA692	2B	152 590	+	–	6.16E–04	0.13
	IWA1383	3B	67 455	+	+	2.79E–05	0.21
	IWA2864	4A	51 367	+	+	1.73E–05	0.22
	IWA4041	4B	77 719	+	+	2.92E–04	0.15
	IWA1486	5A	86 358	+	+	1.60E–04	0.16
	IWA52	6B	34 554	–	+	4.07E–04	0.14
	IWA2353	7B	68 835	+	+	4.40E–04	0.14
Internodes length	IWA4054	3B	62 569	+	–	8.55E–04	0.13
	IWA482	4A	51 699	–	+	6.05E–04	0.14
	IWA4767	5A	35 376	–	+	4.45E–04	0.14
	IWA8386	6A	136 805	–	+	2.13E–04	0.16
	IWA1967	6D	157 654	–	–	8.56E–04	0.13
	IWA7207	7B	89 825	+	–	7.85E–04	0.13
Peduncle length	IWA5632	3A	88 017	–	–	5.23E–04	0.13
Yield	IWA7512	3B	72 118	–	+	6.96E–04	0.15
	IWA3733	5D	67 492	–	+	9.84E–04	0.18
	IWA1543	7B	67 505	+	+	1.03E–04	0.19

+/– the presence/absence of an association

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lengths. For the GpS, only the two loci located on chromosomes 2A and 2B have a positive effect by increasing the number of grains per spike. The early heading date was governed by the alleles located on 2A, 2B, 4B, and 5A. The late heading was associated with the SNP markers located on chromosomes 1A, 3B, 4A and 6B.

In the present study, the selected SNP markers were abundant on the A (45.35%) and B (41.4%) genomes, which is due to the low level of polymorphism in the D genome (Wang *et al*. 2014). The MTAs for the studied traits were identified on all the chromosomes except for 1B, 1D, 2D, 5B and 7D. In this study, 34 markers were found to be associated with the grain yield and the related traits using the MLM approach. From these, three SNP markers were directly related to the grain yield. The two major QTLs located on chromosomes 3B and 7B have shown a pleiotropic effect on the yield related traits including the heading date, grain per spike and internode length. On chromosome 3B, the QTL for the yield was described in the genomic region proximal to RAC875_rep_c69171_92 (Qaseem *et al*. 2018). The locus on chromosome 7B linked with the marker IWA1543 is close to the yield QTL reported by Quarrie *et al*. (2005). This region is also linked to a major QTL identified for heat tolerance (Paliwal *et al*. 2012) and grains per spike (Quarrie *et al*. 2005). For the HD, a loci located closely to the marker GWM493 (Pánková *et al*. 2008) may coincide with the MTAs detected in our study. Only one QTL was identified for the plant height on chromosome 6B. Few reports described this QTL on chromosome 6B (Sadeque & Turner 2010), which may be a new QTL controlling the plant height.

In this study, we identified 32 SNP markers that are significantly associated with the yield related traits using the MLM approach. The markers identified on chromosomes 3B and 7B have a pleiotropic effect on the heading date, grain per spike, and yield and internodes length. These loci will be further validated for use in breeding programmes.

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