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6 QTL analysis in Barley Across Environments in Egypt

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BARLEY is one of the most important cereal crops worldwide. An advanced backcross doubled haploid mapping population was grown in four locations across Egypt (Assuit, Al Wady Al Asuity, Matrouh and Nubaria). The population included 301 BC2DH lines derived from crossing between a German elite cultivar of H. vulgare ssp. vulgare 'Scarlett' with an exotic accession of H. vulgare ssp. spontaneum 'ISR42-8'. A linkage map including 371 different types of genetic markers was used to perform QTL analysis. We detected 56 putative QTLs for traits of interest. In addition, the study identified four markers with marker main and marker × environment interaction effects. The exotic alleles of those four markers could be responsible for increasing their traits across environments. Furthermore, eight markers showed pleiotropic effect across locations. Some DH lines performed better than their parents and check varieties in each environment and across four environments as well. These results might be useful in MAS for barley breeding programs in Egypt.

Keywords: Barley, Epistatic effects, Multiple environments, Pleiotropic effects, Quantitative trait loci.

INTRODUCTION

Barley (*Hordeum vulgare* L.) is an important cereal crop that comes next after wheat, maize and rice based on the production and the harvested area (FAOSTAT 2014). It is adapted to hot and dry climate, salinity, low soil fertility, however moderately cool and dry climate is suited for the crop production (Mishra & Shivakumar , 2000). The crop is cultivated in a wide range of environments including North Africa, the near and Middle East, South Asia, Russia, Eastern Asia, Europe, Australia and South America. In Egypt, almost 93% of the cultivated area of barley is mainly under rainfed condition in the North Western Coastal Zone (NWCZ) covering an area of 126,000 ha with an average productivity of 1.29t ha^{-1} (Noaman, 2010) as of 2008/2009 season.

Barley variety development in Egypt is concentrated in developing drought-tolerant and high yielding-cultivars to satisfy the environmental needs in the marginal areas (under low rainfall and prolonged salinity and heat stress conditions). Because of these efforts for highly drought-tolerant, high-yielding barley cultivars have been recently released, namely Giza 125 (Noaman *et al.* 1995a and b), Giza126 (Noaman *et al.* 1995c), Giza 2000 (Noaman *et al.* 2007a) and Giza 132 (Noaman *et al.* 2007b). Moreover, great efforts have been made to release new barley cultivars for special purposes, for example; two two-row barley cultivars for the malting and brewery industries *i.e.,* Giza 127 and Giza 128 (El-Sayed *et al.,* 1995) and three hull-less barley cultivars for human feed were released namely Giza 129, Giza 130 and Giza 131 (El-Sayed *et al*., 2003).

The differential response of a genotype across environments is defined as the genotype (G) × environment (E) interaction (GEI) (Beyene *et al.* 2011 and Kang, 2004). The GEI is a crucial objective in the breeding programs; first, it helps

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to identify the adapted genotype for each location instead of using the genotypes mean over all the studied locations or environments in the selection process (Adugna, 2007). Secondly, it examines the adaptability of subdividing the target region to mega-environments (Yan *et al.,* 2000)

Seed yields of all crops including barley depends mainly on the yield components, which are controlled by several genes, and the effects of these genes are modified by environmental factors. (Singh *et al.,* 1993 and Hayes *et al.* 1993). With the advancement in the molecular markers and mapping techniques, the locations of the genes which influence the agronomic traits related to the yield can be detected, and these locations are called quantitative trait loci (QTLs) which is vitally important for marker-assisted selection for yield improvement (Li *et al.* 2011). When these QTLs have different expressions across the tested environments, this called the QTL by environment interaction (QEI).

QTL analysis has been intensively utilized for all crops including barley. Since the first barley genetic map was constructed from RFLP marker, many genetic maps were created using various genetic markers, including the use of one type of markers *i.e.* RFLP (Kandemir *et al.* 2000) SSR (Li et al., 2006) to map quantitative trait loci (QTLs) in an advanced backcross population of barley, DArT marker (Tondelli *et al.,* 2014) to study the QTLs responsible for barley yield adaptation to the Mediterranean environments. Some studies used two type of markers *i.e.,* RFLP and SSR (Wang, *et al.* 2014) , SNP and SSR markers (Wang *et al.,* 2016) to identify QTLs and QTL × environment interactions for ten grain yield-related traits in a late-generation double haploid population (DH) derived from the Huaai 11 × Huadamai 6 cross . Cuesta-Marcos *et al*. (2008) used 215 markers: 10 RFLP, 5 STS, 5 15 RAPD, 112 AFLP and 73 SSR (15 ESTs and 58 genomic-derived markers, to discover grain yield QTL in a doubled haploid 25 population of barley that is highly productive under the inland plains of Spain. These maps were utilized to identify the QTLs for various economic traits.

Epistasis states to the phenotypic effects of interactions among alleles at multiple loci. It is defined as the deviation from additivity of the effects between alleles of different loci (Cockerham, 1954). With the expanding use of molecular markers in plant species, it has been revealed that epistatic effects play a crucial role on understanding the genetic basis of quantitative traits (Lark *et al.,* 1995; Maughan *et al.* 1996; Li *et al.,* 1997 and Yu *et al*., 1997). The objective of the current study was to identify QTLs controlling important characters such as yield and yield components of barley grown in different environments in Egypt.

MATERIALS AND METHODS

Plant material

An advanced backcross doubled haploid mapping population consisted of 301 BC2DH lines (DH) derived from crossing between a German elite cultivar of *H. vulgare* ssp. vulgare 'Scarlett' with an exotic accession of *H. vulgare* ssp. spontaneum 'ISR42-8'. The population was designated as S42 and used for QTL analysis across environments in current study. The cultivar Scarlett was used as the recurrent parent whereas ISR42-8 was utilized as the donor. More details about development of this population and proportion of donor genome are given in von Korff *et al.* (2004) and Schmalenbach *et al.* (2008). For comparison with barley local cultivars, four commercial cultivars of barley, *i.e.* Giza 123, Giza 127, Giza 129 and Giza 2000 were used in this study as check cultivars.

Experimental sites and design

These experiments were conducted in the 2013/2014 and 2014/2015 growing seasons at four different locations in Egypt (Fig. 1) namely, Assiut (AS), Wadi El-Assiuty farm (WAD) Nubaria farm (NU) Matrouh farm (MA).

The four locations names, latitudes, longitudes, soil type and irrigation system are presented in Table 1. The experiments were arranged in a randomized complete block design (RCBD) with two replications. The genotypes were randomly grown in plots; each plot consisted of one row 6 m long and 0.20 m apart .

Cultural practices

Plants were irrigated using surface irrigation system, while sprinkle irrigation system was used to irrigate plants in the other environments. Total irrigation requirements in these areas were applied as recommended for such these locations. In case of having rains, we omitted the amount of water gained by rains from the total irrigation requirements. The recommended doses of NPK fertilizers were added and normal cultural practices of growing winter cereals conducted in the usual manner followed by the farmers of this district.

Phenotypic data

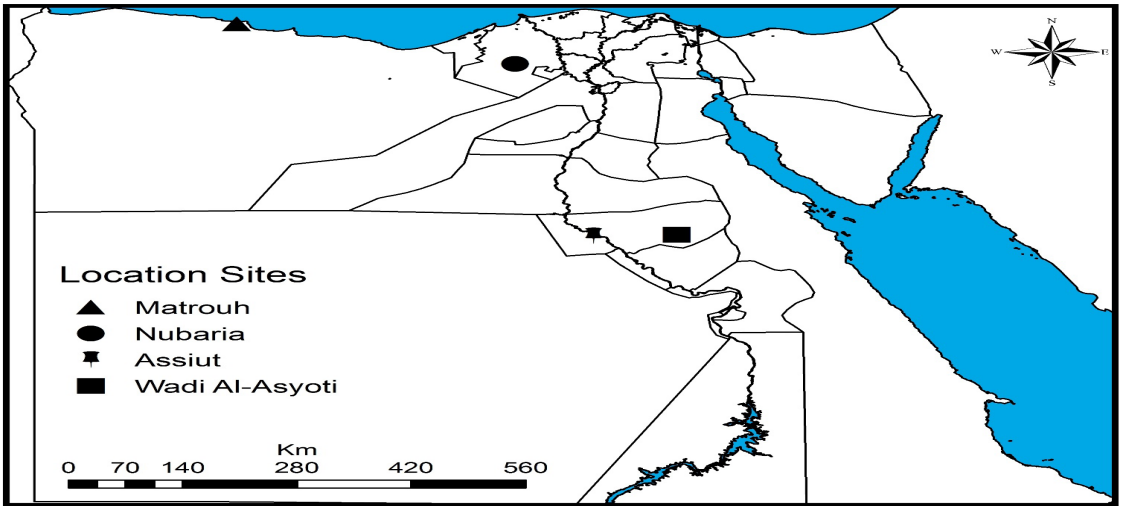

Fig. 1. Map of Egypt showing the four locations.

TABLE 1. Latitude, longitude, soil type and rain status of the four investigated environments.

Location	Assiut Farm (AS)	Al-Wady Al-Asyoti (WAD)	Nubaria (NU)	Matrouh (MA)
Growing season	2013/2014	2013/2014	2013/2014	2014/2015
Latitude	27° 11' 1.13"	27° 12' 20.83"	30° 32' 14.73"	31° 21' 12"
Longitude	31° 9' 49.49"	32° 4' 28.51"	30° 17' 56.11"	27° 11' 14"
Type of soil	Clay	Sandy Loam	Sandy Loam	Sandy clay loam
Rains status	rare	rare		81.60 mm
Irrigation system	surface	Sprinkle	Sprinkle	Sprinkle

Heading date (HD) for each genotype was recorded as the number of days from the sowing date until 50% of tillers had emergence a half of spikes from the flag leaf sheath (Zadok *et al.,* 1974). At anthesis time, chlorophyll content (CC) of the flag leaf was measured using a self-calibrating SPAD chlorophyll meter (Model 502, Spectrum Technologies, Plainfield, IL) from 10 randomly flag leaves, then the average was scored. This measurement directly estimated the chlorophyll content of the flag leaf (Xu *et al*., 2000). At maturity time, 10 individual plants were randomly chosen in the middle for each row to measure plant height (PH; cm). At harvest, 8-12 guarded individual plants were randomly harvested to measure the yield traits: the average spikes number per plant (NSP), 100-grain weight (100-GW; g) and the average grain yield per plant (GYP; g).

Genotyping of population S42

The S42 population was genotyped with a total number of 371 genetic markers containing 106 SSRs according to von Korff *et al.* (2004), 255 DArT following (Sayed *et al.,* 2012) and ten gene-specific DNA markers referred to Wang *et al.* (2010) in order to perform QTL analysis. The linkage map of this population was drawn using MapChart ver.2.2 (Voorrips, 2002).

Statistical and QTL analysis

Analysis of variance

To detect the differences among tested genotypes, among environments and the G×E interaction, the combined analysis of variance was performed with the Statistical Analysis System SAS (SAS Institute, ver. 9.2 2008), using PROC GLM procedure. The phenotypic correlations among trait performances were computed using the correlation procedure (PROC CORR). The LS-means of the investigated traits across the DH

lines over replication were used for the calculation of the Pearson correlation coefficients (r).

Broad-sense heritability estimation

Broad-sense heritability (h^2B) was computed as $h^2B = \delta^2G / (\delta^2_G + \delta^2_{G\times E} /e + \delta^2_e/er)$, where δ^2_G, $\delta^2_{G\times E}$ and δ^2_e were the estimates of genetic, genotype × environments interaction and error variances, respectively, derived from the expected mean squares of the combined analysis of variance. Also e and r were the number of environments (locations) and replications, respectively.

Relative performance of the exotic parent $RP_{[Hsp]}$

The relative performance of the exotic parent $RP_{[Hsp]}$ was computed by this formula:

$$RP_{[Hsp]}=(([Hsp]-[Hv])/[Hv]) * 100,$$

where [Hsp] represents LS-means of the homozygous exotic genotype and [Hv] represents LS-means of the elite genotype.

QTL analysis

The QTL analysis was conducted using a multiple QTL model iteratively extended and reduced by forward selection and backward elimination, respectively using the PROC MIXED procedure in SAS software as per (Sayed *et al.,* 2012). Starting point was the following mixed hierarchical model:

$$X_{ijkl}=\mu+Mi+L_j(M_i)+E_k+L_j*E_k+M_iE_k+ \varepsilon l(ijk),$$

where the total of phenotypic value was sum of general mean μ, fixed effect Mi of the i-th marker genotype, random effect Lj(Mi) of the j-th DH line nested in the i-th marker genotype, fixed effect Ek of the k-th environment, fixed interaction effect L_j*E_k of the j-th DH line and the k-th environment, fixed interaction effect Mi*Mk of the i-th marker genotype and the k-th environment and residue $\varepsilon l_{(ijk)}$ of $X_{ijkl.}$ P values from F-tests were adjusted genome-wide across all single marker tests using the false discovery rate (FDR). The significant marker main effects as well as marker × environments interaction with PFDR ≤ 0.05 were accepted as putative QTLs for the next iteration, however, the final model was:

$$X_{ijkl}=\mu+\sum QTL+Mi+Lj(Mi)+E_k+Lj*Ek+Mi*Ek+\varepsilon l(ijk),$$

where ∑QTL represents the detected QTL from the forward/backward selection process. The contribution of a QTL to trait genotypic variance was estimated by the R^2 coefficient (percentage of the explained genotypic variance) according to von Korff *et al.* (2004).

Digenic epistatic effects

The digenic epistatic interactions between all DArT and SSR marker pairs were tested with SAS procedure MIXED (SAS ver. 9.2, SAS Institute 2008) using the following mixed hierarchical model:

$$X_{ijklm}=\mu+\sum QTL+M1_i+M2_j+M1_i*M2_j+Lk(M_{1i}*M2j) +El+Lj*Tk+ +\varepsilon_{l\,(ijkm)}$$

where $M1_i$ and $M2_j$ are the fixed effects of the i-th marker and j-th marker (M2). $M1i*M2_j$ is the fixed interaction effect of the i-th M1 genotype with j-th M2 genotype, Lk(M1i*M2j) is the random effect of the k-th BC2DH line nested in the *i-th* M1 and *j-th* M2 marker genotype interaction.

RESULTS AND DISCUSSION

Analysis of variance

Data in Table 2 shows the combined analysis of variance of the investigated traits across four environments. There were highly significant differences among environments, among the 307 genotypes (301 DH lines, their parents and four check cultivars) for all investigated traits Furthermore, the genotype × environment interaction was highly significant for all studied traits. This finding reflected the existence of sufficient variation among genotypes for investigated traits. The coefficient of variation ranged between 3.13% (heading date) and 25.68% (number of spikes per plant). Across locations, grain yield per plant and seed index showed the lowest values of heritability in broad sense, while heading date showed the highest heritability value.

Data presented in Table 3 shows the mean, minimum, maximum and standard deviation (SD) values of Scarlett, ISR 42-8, S42 population, check cultivars and over all genotypes in each location and across environments. Wide ranges of all studied traits were observed for all genotypes at each environment and across environments as well. Across environments, Scarlett was earlier than ISR 42-8 in all investigated environments, by values ranged between 4 days (Nubaria and Matrouh) and 10 days (Assiut). Furthermore, Scarlett was shorter, less in chlorophyll content, less in number of spikes per plant, heaver in 100-grain weight and produced more grains per

plant than the wild accession ISR 42-8. The S42 population exhibited transgressive segregation in all studied traits in each environment and across environments as well, reflecting the sufficient variation among DH lines for selection. On average, DH lines were significantly earlier than ISR 42-8 and later than check cultivars in all environments .

Days to heading of DH lines ranged between 60.5 and 111 days, this means selection for earliness can be done among these lines in each environment. Scarlett and DH lines were shorter than check cultivars and ISR 42-8 across all environments. DH lines, their parents and check cultivars showed approximately stability values of chlorophyll content across the four locations (Table 3). For number of spikes per plant, DH lines showed a wide range of spikes per plant with an average of 8.28 spike across environments. On average, DH lines had higher seed index (3.81 g) than ISR 42-8 (1.82 g) and Scarlett (3.73 g) across environments. While the local check cultivars showed the maximum mean value of seed index (4.32 g) across environments. Some of the DH lines exceeded in seed index (maximum 6.7 g) the average of check cultivars (4.32 g) and Scarlett (3.73 g), this may be indicating the ability of finding high genotypes in grains weight in each environment. The average of DH lines for grain yield/plant (GYP) was lower (5.51 g) than the best parent Scarlett (5.95 g) and check cultivars (5.56) but they have a wide range of GYP across environments. This wide range refers to the possibility for selection of superior genotypes of barley in each environment.

In addition, it can be observed that, the genotypes were earlier at Assiut and Wadi El-Assiuty environments than in Nubaria and Matrouh, this may be due to the effect of high temperature in Upper Egypt than in Delta and North of Egypt. While the plants were taller in Assiut and Wadi El-Assiuty than in Nubaria and Matrouh. Assiut was the best environment for plant growth and productivity of the current materials, since it produced the higher grain yield per plant and high seed index. This result may be due to the clay soil conditions that rich in nutrients and availability of irrigation, while the other environments, the soil is sand and rely on sprinkle irrigation system. Our results are consistent with Zhu *et al* (1999) who found significant variation among DH lines within each environment and there were both positive and negative transgressive segregates. Furthermore, Xue *et al* (2008) studied chlorophyll content in barley and found significant transgressive segregation among DH lines.

Correlation among traits

Mutual correlation coefficients among studied traits across the four environments are presented in Table 4. There was negative and significant correlation between days to 50% heading and each of plant height (r= − 0.391**), chlorophyll content (r= − 0.172**), seed index (r= − 0.448**), while it was positive and highly significant with each of number of spikes per plant (r=0.384**) and grain yield per plant (r=0.225**) across all environments. Plant height

TABLE 2 . Mean squares, coefficient of determination, coefficient of variation and heritability in broad sense of six studied traits for 307 genotypes across four environments.

Source	d.f.	Mean squares					
		HD	PH	CC	NSP	SI	GYP
Environment (E)	3	33834**	204960**	3238.52**	6193.3**	335.02**	4046.15**
E(Rep)	4	55.35	92.45	41.05	70.91	3.21	31.60
Genotype (G)	306	149.27**	565.29**	101.37**	65.70**	1.68**	12.33**
G*E	918	41.76**	248.89**	35.72**	20.18**	0.67**	14.07**
Error	1224	9.01	25.38	13.77	5.04	0.03	0.94
R^2		0.94	0.97	0.81	0.90	0.99	0.96
C.V. %		3.13	7.37	7.64	25.68	4.27	17.64
h^2_B		0.720	0.575	0.666	0.626	0.069	0.064

* and **; significant at p-values of 0.05 and 0.01, respectively.

TABLE 3 . Summary statistics of Scarlett, ISR 42-8, DH lines and check cultivars for the studied traitsin each environment and across the four environments.

Geno	Trait	Assiut				Wadi El-Assiuty				Nubaria				Matrouh				Across environments			
		Mean	SD	Min.	Max.	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.
ISR 42-8	HD	100.5	0.71	100	101	95.5	0.71	95	96	105	0	105	105	103.5	0.37	103	104	101.13	4.19	95	105
	PH	107	4.24	104	110	94.5	14.85	84	105	77	5.66	73	81	55	1.41	54	56	83.38	22.57	54	110
	CC	53.55	3.12	51.34	55.75	51.89	3.38	49.5	54.28	46.7	1.7	45.5	47.9	49.5	1.8	48.23	50.77	50.41	2.98	45.5	55.75
	NSP	8.22	0.31	8	8.43	5.08	0.35	4.83	5.32	7.5	0.71	7	8	8.03	0.76	7.5	8.57	7.21	1.45	4.83	8.57
	SI	2.47	0.12	2.39	2.55	1.46	0.39	1.19	1.74	1.46	0.33	1.3	1.63	1.87	0.12	1.79	1.96	1.82	0.48	1.19	2.55
	GY	3.33	0.62	2.89	3.77	2.83	0.17	3.43	3.67	2.88	0.07	2.83	2.92	2.69	0.06	2.64	2.73	2.93	0.28	2.64	3.77
Scarlett	HD	90.5	0.71	90	91	89.5	0.71	89	90	101	0	101	101	99.5	0.37	99	100	95.13	5.96	89	101
	PH	82	4.24	79	85	69	5.66	65	73	75.5	7.78	70	81	40	2.83	38	42	66.63	18.53	38	85
	CC	49.64	11.17	41.74	57.54	46.25	10.11	39.1	53.4	46.85	2.19	45.3	48.4	49.66	2.32	48.02	51.3	48.10	1.81	39.1	57.54
	NSP	4.27	0.14	4.17	4.36	5.92	0.36	5.67	6.18	7.5	0.71	7	8	8.03	0.76	7.5	8.57	6.43	1.70	4.17	8.57
	SI	5.01	0.08	4.95	5.06	4.49	0.21	4.34	4.64	2.8	0.09	2.73	2.86	2.61	0.08	2.55	2.67	3.73	1.20	2.55	5.06
	GY	5.86	0.26	5.68	6.04	4.52	0.29	4.31	4.72	7.75	0.15	7.64	7.85	5.67	0.77	5.12	6.22	5.95	1.34	4.31	7.85
DH lines	HD	92.11	0.35	75	108	87.5	0.25	80	100	103.5	0.19	77	111	100.64	0.17	60.5	108.5	95.94	7.42	60.5	111
	PH	90.02	0.66	60	145	68.52	0.46	42	115	68.92	0.46	40	105	45.3	0.55	45	98	68.19	18.20	40	145
	CC	51.54	0.28	31.04	72.29	47.75	0.24	26.77	67.1	46.14	0.19	33.3	65.3	48.91	0.21	35.3	69.22	48.59	2.27	26.77	72.29
	NSP	6.04	0.07	2.27	11.16	5.93	0.06	1	10.3	10.37	0.23	3	20	10.77	0.25	3.21	20.0	8.28	2.65	1	20
	SI	4.67	0.02	2.16	6.7	4.18	0.02	1.64	6.29	3.3	0.03	1.2	6.4	3.08	0.03	1.12	5.98	3.81	0.75	1.12	6.7
	GY	6.35	0.1	1.85	13.94	3.61	0.03	1.31	7.16	8.83	0.15	3.06	16.22	3.26	0.12	1.27	12.63	5.51	2.61	1.27	16.22
Checks	HD	76.5	3.16	72	81	72.5	3.16	69	77	94.5	2.45	91	97	97.26	2.1	93	99	85.19	12.50	69	99
	PH	117.88	7.28	105	127	77.25	10.01	63	93	78.38	5.58	69	83	59.88	7.92	51	72	83.35	24.53	51	127
	CC	55.23	5.88	44.08	62.69	51.06	5.49	42.9	59.7	43.49	5.71	34.6	51.8	46.1	6.06	36.68	54.91	48.97	5.22	34.6	62.69
	NSP	6.34	1.98	5	9.87	8.34	1.98	6.52	11.85	4.25	1.16	2	6	4.55	1.25	2.14	6.43	5.87	1.89	2	11.85
	SI	4.66	1.4	2.66	6.4	4.34	0.59	3.6	5.23	4.27	0.58	3.46	5.24	3.99	0.54	3.23	4.89	4.32	0.28	2.66	6.4
	GY	7.66	3.69	3.26	13.03	5.14	0.89	3.9	6.45	4.04	0.38	3.12	4.25	5.39	2.67	1.64	8.43	5.56	1.52	1.64	13.03
Overall	HD	89,90	8.7	72	108	86,25	6.38	69	100	101	4.64	77	111	100.22	4.19	60.5	108.5	94.34	7.40	60.5	111
	PH	99.18	16.35	60	145	77.32	11.36	42	115	74.95	11.38	40	105	50.05	13.43	38	98	75.37	20.10	38	145
	CC	52.49	6.98	31.04	72.29	49.24	5.92	26.77	67.1	45.80	4.76	33.3	65.3	48.54	5.05	35.3	69.22	49.02	2.75	26.77	72.29
	NSP	6.22	1.68	2.27	11.16	5.93	1.49	1	11.85	7.41	5.65	2	20	7.85	6.05	2.14	20	6.95	0.81	1	20
	SI	4.42	0.58	2.16	6.7	4.14	0.57	1.64	6.29	3.31	0.82	1.2	6.4	3.09	0.76	1.12	5.98	3.74	0.64	1.12	6.7
	GY	5.59	2.45	1.85	13.94	3.68	0.86	1.19	7.16	5.52	3.8	1.3	16.22	4.05	2.86	1.27	12.63	4.71	0.99	1.19	16.22
LSD 5%	HD	2.24				9.71				5.13				6.33				2.94			
	PH	10.79				13.62				7.45				5.95				4.94			
	CC	8.67				7.84				6.01				6.36				3.63			
	NSP	0.69				0.74				0.98				1.41				2.20			
	SI	0.27				0.05				0.42				0.39				0.16			
	GY	0.56				0.34				1.62				0.99				0.95			

For comparison among environment's meansLSD 5% HD=0.34, PH=0.56, CC=0.42, NSP=0.25, SI=0.02 and GYP=0.11

was associated positively and significantly with each of chlorophyll content (r=0.153**), seed index (r=0.552**) and grain yield per plant (r=0.259**), while it was negative with number of spike per plant (r= − 0.346**). There was positive correlation between chlorophyll content and seed index (r=0.152**), while negative correlations were found between CC and each of NSP and GYP across all locations. Highly positive correlation (r=0.321**) between number of spikes per plant and grain yield per plant was detected across environments. Also positive correlation was found between grain yield and seed index (r=0.064*) across environments. von Korff *et al.* (2006) found negative correlation between yield and plant height, and positive correlation with number of spikes and days until heading .

Identification of QTL in the S42 population

Altogether, 56 putative QTLs as marker main effect and marker × environments interaction were detected for six studied traits across four environments namely; Assiut, Wadi El-Assiuty, Nubaria and Matrouh (Table 4 and Fig. 2). Among these loci, 25 (44.6 %) QTLs showed marker main effect, 27 (48.2%) QTLs showed marker × environment interaction effects and 4 (7.1%) QTLs showed both effects. 29 regions (51.7%) exhibited desirable effects of the presence of the exotic alleles on the performance of the DH lines for the traits under investigation. All detected QTLs were covered the whole genome. Numerous studies on the same population revealed that detected QTL showed desirable effects resulted from the presence of exotic alleles of the homozygous Hsp genotype in population S42 ranged between 26 to 34.1% (Pillen *et al*., 2003 ; 2004 and Sayed, 2011).

TABLE 4 . Correlation coefficients (r) of the studied traitsacross environments.

	PH	CC	NSP	SI	GYP
HD	-0.391**	-0.172**	0.384**	-0.448**	0.225**
PH		0.153**	-0.346**	0.552**	0.259**
CC			-0.071*	0.152**	-0.012
NSP				-0.39**	0.321**
SI					0.064*

* and **; significant at p-values of 0.05 and 0.01, respectively.

Days to 50% heading (HD)

Time of flowering is a major trait of a crop adaptation to the environment, particularly when the growing season is prone to periods of drought and high temperatures. Developing early maturing varieties has been an effective strategy to mitigate yield losses of the crop exposed to an environmental stress and the end of the season (Kumar & Abbo, 2001). Twelve putative QTLs for HD were mapped on chromosomes 1H, 2H, 3H, 6H and 7H (Table 4 and Fig. 2). Eight loci exhibited significant marker main effects, while four regions showed QTL × environment interaction effects. According to the relative performance of the exotic allele ($Rp_{[aa]}$), the alleles of nine QTLs were exhibited a desirable performance of reducing HD by 10 %. These QTLs showed negative additive effects. The strongest QTL was QHD.S42-3Hf showed main effect and explained 30.15% of the genetic variance. Furthermore, the QTL QHD.S42-1Hc exhibited increase in HD due to presence of the exotic allele that increased HD by 3.12%, this QTL showed marker × environments. von Korff *et al.* (2006) identified ten QTLs for days until heading and covered the whole genome except chromosome 5H, at five locations the exotic allele (Hsp) was associated with a reduced heading time of 7.9%. The marker locus EBmac415 on 2H where the exotic allele decreased time to heading and coincided with the major flowering QTL on chromosome arm 2HS detected by Pillen *et al.* (2003), Li *et al*. (2004) and von Korff *et al*. (2006).

Plant height (PH)

Plant height is an important morphological trait, where shortening height of a plant can improve lodging resistance and may indirectly increase grain yield (Alam *et al.,* 2007). Fifteen QTLs were detected for PH covered the whole genome except chromosome 7H (Table 4 and Fig. 2). Among these loci, seven QTLs showed significant marker main effects, six QTLs exhibited MEI effects and two loci showed both effects. Four chromosomal regions were responsible for shortening height of the plant by values ranged between -4.15 and 10% due to the presence of the exotic alleles. The strongest QTL was QPH.S42-2Hb and explained 14.85% of the genetic variance. The other QTLs were

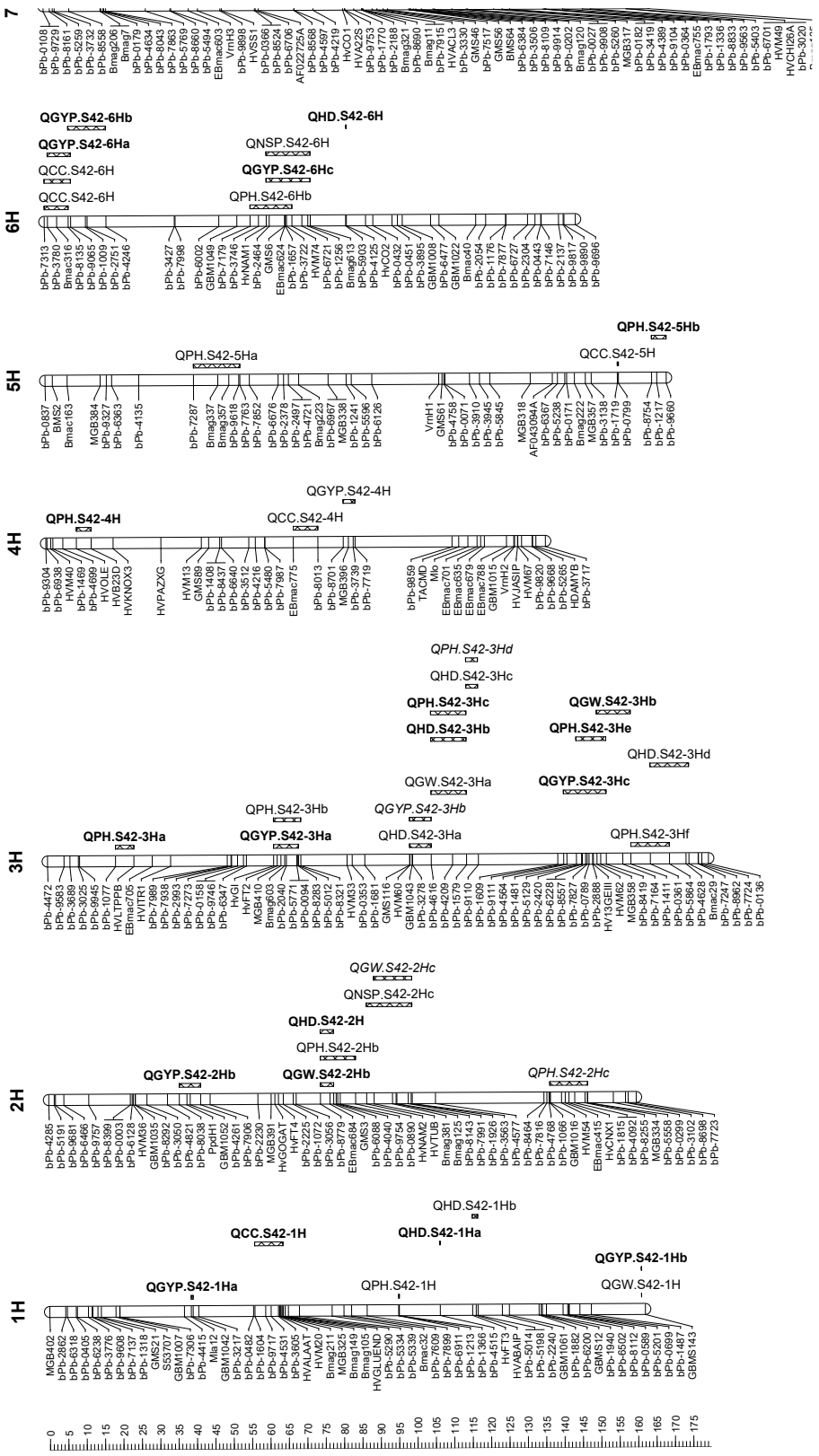

Fig. 2. Mapping of 56 putative additive QTL detected days to 50% heading (HD), plant height (PH), chlorophyll content (CC), number of spikes per plant (NSP), grain weight (GW) and grain yield per plant (GYP) across four environments in Egypt. Non-bold QTL were specified as marker main effect, bold QTL specified as marker × environment interaction effect and Italic-non bold QTL were assigned for QTL that showed both effects

responsible of increasing plant height by values ranged from 4.6 to 19.87% due to the presence of the exotic alleles. The strongest QTL was QPH.S42-3Hd posed 45.78% of the genetic variance. This locus showed marker main and marker × environment interaction effects. This finding is agreement with that obtained by Forster *et al.* (2004a) who detected QTL for plant height on 7H between 89 and 120 cM. We detected two marker (bpb_4092 on 2H and bpb_9110 on 3H) that showed marker main and marker × environment interaction effects. The exotic alleles of these loci were responsible for increasing plant height. This reflects the stability of these markers across environments. previous studies detected QTL associated to PH on chromosome 7H, where Baum *et al.* (2003) identified QTL with major effects on 2H, 3H and 7H. In addition, Chloupek *et al.* (2006) and Gyenis *et al.* (2007) reported QTLs for PH on chromosomes 7H. The detected QTL for PH in the current study are different from those reported by Sayed (2011) and Wang *et al.* (2010) in the same population. ISR 42-8 was taller than Scarlett under both treatments (Table 2), however the Hsp alleles led to shortening plant height in the DH lines. These results are consistent with the findings of Saal *et al.* (2010) and von Korff *et al.* (2010).

Chlorophyll content (CC)

Altogether four QTLs were associated significantly with CC, three showed marker main effects and located on chromosomes 4H, 5H and 6H, on the other hand, a single locus showed MEI effect and mapped on 1H (Table 4 and Fig. 2). Relative performances of the exotic genotype ranged between -4.07% and 10.55%. The most desirable QTL was QCC. S42-5H and exhibited desirable performance of exotic alleles and revealed an increasing of CC by 9.83% and accounted 7.78% of the genetic variance. Xue *et al.* (2008) who detected four putative QTLs for chlorophyll content on chromosomes 2H, 3H and 6H obtained similar result. Since, individual QTL explained the variation from 6.3% to 20.2% of the total phenotypic variation. In addition, Guo *et al.* (2008) identified 5 QTLs on chromosomes 2 H and 4H associated with chlorophyll content in flag leaves at post-flowering stage under well-watered and drought conditions using a RIL population with 194 lines. Eshghi *et al*. (2013) who mapped five QTLs for chlorophyll content, with the H, obtained similar results. , with the H. spontaneum alleles contributing to increased chlorophyll content at two of the five loci. The QTL with largest effect was located at 43-45 cM of chromosome 1H (linked to Bmag0105) and exotic alleles from wild barley increased this character by 33.8%. The remaining four QTLs for chlorophyll content were detected on chromosomes 2H, 5H and 6H.

Number of spikes per plant (NSP)

Spikes number per plant is one of the most important grain yield-related traits in cereals. Six QTLs were detected for NPS and located on chromosomes 2H, 6H and 7H (Table 4 and Fig. 2). Four QTLs presented significant marker main effects ,moreover two showed MEI effects. The relative performances of the exotic genotype ranged between -10.71% and 11.54%. Among these, four QTLs showed desirable performance of the exotic genotype alleles and revealed an increasing of NSP. The strongest QTL was QNSP.S42-2Hb and explained 8.56% of the genetic variance. This result indicates that the introgressions from wild barley may increase number of spikes/ plant in S42 population. Saal *et al.* (2010) have identified three QTLs as marker main effects associated with NSP and localized on chromosomes 1H (HVABAIP), 6H (GMS6) and 7H (BMAG7). In wheat, Ibrahim *et al.* (2010) detected five QTL associated to NSP, one of them increased NSP by 10.8% and 16.3% under well-watered and drought stress, respectively.

100 - Grain weight (100-GW)

Grain weight or seed index, is known as a representative quantitative trait. It is determined by synthesis and accumulation of starch in grain endosperm (You *et al.,* 2006 and Mei *et al.,* 2005). Results revealed that ISR 42-8 yielded less and had lower 100-grain weight than Scarlett under well-watered and drought conditions. Locations close to the six chromosomal regions (QTL) on 1H, 2H and 3H were probably influencing 100-grain

weight (Table 4 and Fig. 2). Two QTLs exhibited significant marker main effects, three loci exhibited significant MEI effects and one QTL showed both effects. Four QTLs revealed a desirable increase in 100-GW, and the exotic alleles explained maximum 7.11% of the genetic variance with favorably increased 100-GW by 6.57%. We identified one marker (Bmag125 on 2H) that showed marker main and MEI effects. The exotic alleles of this locus was responsible for increasing this trait. Nine QTLs were responsible for 1000-GW and mapped on all chromosomes except 1H (von Korff *et al.,* 2006).

Grain yield/plant (GYP)

Recently with the development of molecular approaches, QTL analysis was used to detect yield and its-related traits. QTLs associated with yield have been derived from wild species (Swamy & Sarla , 2008). In our study, thirteen QTLs were detected for GYP and mapped in all choromosomes except 5H (Table 4 and Fig. 2). One QTL revealed significant marker main effect and showed undesirable effect by reducing GYP by -8.63%. Eleven QTLs revealed MEI effects and the relative performance of the exotic genotype ranged from -12.6 to 5.94% and accounted maximum 10.01% of the genetic variance. Only on QTL showed both effect with desirable increase in GYP due to the presence of the exotic alleles. This results are in harmony with those obtained by (Pillen *et al.,* 2003 ; 2004; von Korff *et al.* 2006 ; 2010; Wang *et al.,* 2010 and Sayed, 2011). We detected one marker (bpb_3278 on 3H) which revealed marker main and MEI effects. Therefore, this locus might be responsible for increasing this trait. We found that large and small segments of the wild parent ISR 42-8 were transmitted to the S42 population; therefore, we concluded that the wild parent ISR 42-8 might be responsible for diminishing GYP in S42 population.. However, the desirable identified QTL referred to possibility existance of Hsp regions may contribute to yield improvement, especially under drought conditions.

Pleiotropic effects

The collocation of QTL for different traits implies the likely presence of pleiotropic or closed linkage between the QTL control the traits (Tuberosa *et al.,* 2002b). the present study revealed eight chromosomal regions covered the whole genome except 5H. The marker locus GMS3(81 cM) on 2H was controlling days to 50% heading and plant height and led to decrease both traits across environments. This locus may be useful for marker-assistant selection (MAS) in barley improvement for earliness and height shortening. The marker locus GBMS143 (162 cM) on 1H was associated to 100-grain weight and grain yield per plant, but increased grain weight and decreased yield. The marker locus EBmac775 (137 cM) on 7H was underlying the enhancement of number of spikes per plant and reducing days to 50% heading, this locus may be used in MAS for improving NSP and HD in multi-environments trials. Another two marker loci bPb_9681 (5.27 cM)) and bPb_8292 (27.06 cM) on 2H were controlling NSP beside PH and 100-GW, respectively. The locus bPb_9110 (118.72 cM) was underlying PH and HD, while the marker locus bPb_4209 (111.69 cM) on 3H was controlling PH, HD and 100-GW. The marker locus Bmac316 (6 cM) on 6H was responsible of PH and GYP. Several genomic segments were found to include overlapped QTLs for different traits (Diab *et al.,* 2004). Some QTLs showed pleiotropic effect, *e.g.* locus HVABAIP on chromosome 1H was associated with both 1000-GW and GY (Saal *et al.,* 2010).

Detection of epistasis

Altogether 25 pairs of epistatic QTLs as additive × additive effects were detected for six studied traits in the S42 population across four environments in Egypt. Among them, five pairs exhibited QTL × QTL interaction, thirteen pairs exposed QTL by marker interaction and seven shown marker × marker interaction (Table 5). About 11 markers (44%) of main-effect QTL detected for studied traits were involved in epistatic effects. This indicates that several loci involved in epistatic interactions may not have significant effects for these traits and may affect the trait expression by epistatic interactions with other loci. Likewise, Ma *et al.* (2007) stated that 37% of the main-effect QTLs were involved in the epistatic interactions in maize grain yield and its components. Zhang *et al.* (2008) found 25% of main-effect QTLs for wheat plant height were involved in epistatic effects.

Days to 50% heading (HD)

Our results exposed seven pairs of epistatic QTLs were associated with days to 50% heading and located on all chromosomes. Among these

loci, five pairs of epistatic effects reduced the days to 50% heading. Since, the BC2DH lines carrying the Hsp/Hsp genotype at these loci were on maximum -1.89 day earlier than lines with the allelic combination Hv/Hv. The most desirable pair of epistatic QTLs for reducing heading date was (GMS3* bPb_3020) and located on chromosomes 2H (81 cM) and 7H (159.21 cM). The strongest epistatic pair (HVABAIP*bPb_9110) was mapped on 1H (118 cM) and 3H (118.72 cM) and accounted for 40.67% of genetic variation (Table 5). Several studies on barley reported epistatic QTL for days to heading (Xu and Jia 2007; Sannemann 2013).

Plant height (PH)

Epistasis is an important genetic characteristic of quantitative traits such as plant height (PH). Epistatic interaction analysis revealed six interaction effects for PH (Table 5). All pairs were responsible of increasing plant height of the DH lines across environments. The combination of Hsp/Hsp led to increase plant height by values ranged from 1.73 to 25.21 cm. The strongest pair (GMS3* bPb_9110) was mapped on 2H (81 cM) and 3H (118.72 cM) and posed of 55.79 % of the genetic variance. Similar results were obtained by von Korff *et al.* (2010) have detected four epistatic interactions between exotic alleles Hsp/Hsp transmitted from wild barley (*H. vulgare* ssp. spontaneum C. Koch) which improved plant height significantly as compared to the combination Hv/Hv. Sannemann (2013) found two significant epistatic interactions for plant height.

Chlorophyll content (CC)

Results revealed only one pair of epistatic QTL (bPb_9746* bPb_1579) associated significantly with chlorophyll content and mapped on the same chromosome 3H (54.8 and 115.5 cM). This locus accounted 4.88% of the genetic variance and the DH lines that carrying the Hsp/Hsp combination were higher in chlorophyll content by 0.62 SPAD than lines carrying Hv/Hv genotype. Zhang *et al.* (2009) detected nine pairs of QTLs with epistatic effects and/or epistasis × environment effects for chlorophyll content in wheat.

Number of spikes per plant

Epistatic analysis revealed four pairs of epistatic QTLs were associated significantly with number of spikes per plant and located on 2H, 4H and 5H. At these loci, the BC2DH lines carrying the Hsp/Hsp genotype were on maximum − 1.11 spike lower than lines with the allelic combination Hv/Hv.

100-grain weight (100-GW)

The epistasis analysis exposed five pairs of epistatic QTLs which were associated with SI and covered the whole genome except chromosome 4H (Table 5). The BC2DH lines carrying the Hsp/Hsp genotype at four loci were heavier weight by maximum 1.12 g than lines with the allelic combination Hv/Hv. The most desirable pair that showed positive effect was (bPb_9681*bPb_4389) and mapped on 2H (5.27 cM) and 7H (125.4 cM) and accounted 11.46% of the genetic variance. Sannemann (2013) found two significant epistatic effects for 1000-GW.

Grain yield/plant (GYP)

Two pairs of epistatic QTLs were associated significantly with GYP, and mapped on chromosomes 3H, 4H and 5H (Tables 5 and 6). Both pairs had positive effects of epistatsis on GYP, hence the BC2DH lines having the Hsp/Hsp genotype were higher GYP with value up to 1.47 g than lines with the allelic combination Hv/Hv. The strongest pair was (bPb_3278*bPb_5265) and posed of 18.75% of the genetic variance. In contrast, von Korff *et al.* (2010) identified 12 interaction effects the allelic combination exotic by exotic caused a strong reduction in grain yield.

CONCLUSION

Some DH lines performed better than their parents and check varieties in each environment and across four environments as well. We concluded that some of DH lines were earlier than check cultivars. These DH lines can be selected directly for earliness. For GYP, some of the DH lines were yielded more than check cultivars and might be selected directly for high grain yield. Furthermore,the exotic alleles of these loci might be responsible for increasing their traits across environments. In addition, we detected eight markers loci possessed pleiotropic effect across locations. Our findings may be beneficial for barley breeding programs via MAS.

TABLE 5. Summary of the detected QTL for six studied traits as main (M) and marker by environment interaction (M*E) across four environments.

[1]Trait	[2]QTL	[3]Marker	[4]Chr	[5]Pos	[6]Flanking	[7]F	[8]Pr.	[9]FDR	[10]R^2	[11]Effect	[12]*Hv*	[13]*Hsp*	[14]$R[_{Hsp}]$	[15]Add.
Days to 50% heading	QHD.S42-1Ha	bPb_4515	1H	106.22	106.21	11.22	0.0000	0.0000	3.9	M*E	95.37	98.07	2.83	1.35
	QHD.S42-1Hb	HVABAIP	1H	116	115 - 116.45	29.25	0.0000	0.0000	12.06	M	95.29	98.26	3.12	1.49
	QHD.S42-2H	GMS3	2H	81	77.41 - 81	8.44	0.0000	0.0000	3.03	M*E	96.1	95.69	-0.43	-0.21
	QHD.S42-3Ha	GMS116	3H	100	100 - 105.88	7.87	0.0050	0.0260	0.4	M	95.62	97.33	1.78	0.85
	QHD.S42-3Hb	bPb_4209	3H	111.69	105.88 - 115.50	29.77	0.0000	0.0000	9.62	M*E	96.89	91.42	-5.64	-2.73
	QHD.S42-3Hc	bPb_9110	3H	118.72	115.50 - 118.72	136.75	0.0000	0.0000	30.15	M	97.16	91.38	-5.95	-2.89
	QHD.S42-3Hd	bPb_5864	3H	170.68	165.54 - 176	19.54	0.0000	0.0000	8.32	M	96.47	93.76	-2.81	-1.35
	QHD.S42-6H	bPb_4125	6H	84.81	84.81	4.55	0.0040	0.0320	1.65	M*E	96	95.92	-0.10	-0.04
	QHD.S42-7Ha	Bmag206	7H	16	16 - 17.47587	23.01	0.0000	0.0000	5.93	M	96.1	91.75	-4.52	-2.17
	QHD.S42-7Hb	EBmac755	7H	137	136.56 - 141.80	10.24	0.0020	0.0100	4.3	M	96.28	94.02	-2.35	-1.13
	QHD.S42-7Hc	HVM49	7H	159.19	159.05 - 165	9.02	0.0030	0.0170	7.62	M	96.22	93.84	-2.47	-1.19
	QHD.S42-7Hd	bPb_3020	7H	159.2	159.05 - 165	9.4	0.0020	0.0150	5.4	M	96.18	92.95	-3.36	-1.61
Plant height	QPH.S42-1H	bPb_1366	1H	95.08	94.90 - 95.08	15.6	0.0000	0.0010	6.19	M	68.71	64.03	-6.82	-2.34
	QPH.S42-2Ha	bPb_9681	2H	5.27	3.54 - 7.59	9.58	0.0000	0.0000	4.11	M*E	68.86	64.41	-6.48	-2.23
	QPH.S42-2Hb	GMS3	2H	81	77.41 - 86.99	47.98	0.0000	0.0000	14.85	M	70.04	63.04	-10	-3.5
	QPH.S42-2Hc	bPb_4092	2H	146.63	139.75 - 150.10	10.49	0.0010	0.0060	5.12	M, M*E	67.84	75.3	10.99	3.73
	QPH.S42-3Ha	bPb_1077	3H	19.95	19.95 - 25	12.88	0.0000	0.0000	3.93	M*E	67.86	74.81	10.24	3.48
	QPH.S42-3Hb	bPb_2040	3H	66.54	63 - 70.35	29.55	0.0000	0.0000	12.98	M	67.55	77.46	14.66	4.95
	QPH.S42-3Hc	bPb_4209	3H	111.69	105.88 - 115.50	20.65	0.0000	0.0000	9.07	M*E	66.36	77.32	16.51	5.48
	QPH.S42-3Hd	bPb_9110	3H	118.72	115.50 - 118.72	195.67	0.0000	0.0000	45.78	M, M*E	65.53	78.55	19.87	6.51
	QPH.S42-3He	HV13GEIII	3H	150	145.40 - 153.54	17.09	0.0000	0.0000	10.29	M*E	66.33	77.85	17.38	5.76
	QPH.S42-3Hf	bPb_0361	3H	165.54	160.18 - 170.68	43.77	0.0000	0.0000	20.18	M	66.19	75.39	13.9	4.6
	QPH.S42-4H	HVOLE	4H	21	21 – 25	6.79	0.0000	0.0010	4.76	M*E	67.85	70.97	4.6	1.56
	QPH.S42-5Ha	Bmag337	5H	65	58.37 - 70.99	42.71	0.0000	0.0000	17.7	M	66.81	74.88	12.07	4.03
	QPH.S42-5Hb	bPb_8754	5H	182.99	182.99 - 186.98	10.41	0.0000	0.0000	4.31	M*E	68.2	65.37	-4.15	-1.41
	QPH.S42-6Ha	Bmac316	6H	6	2.59 - 9.75	17.57	0.0000	0.0000	12.82	M	67.46	74.04	9.76	3.29
	QPH.S42-6Hb	HvNAM1	6H	63	58.55 - 70	20.19	0.0000	0.0000	8.31	M	67.12	72.36	7.8	2.62

1) Studied trait, 2)Description of quantitative trait locus, 3) Linked DNA marker revealing strongest F-value, 4) Chromosome, 5) DNA markers positions in cM, 6) Flanking positions in cM, 7) F-value of the given marker locus, 8) Probability at $P < 0.05$, 9) False discovery rate, 10) Genetic variance, 11) Main effects (M) and marker × treatment (M×T) interaction, 12) Trait value of homozygous cultivated genotype *[Hv]*, 13) Trait value of homozygous exotic genotypes *[Hsp]*. 14) Relative performance of the homozygous exotic allele, $RP_{[Hsp]}$ and 15). The additive effect is half the difference between the phenotypic means of the homozygous elite and exotic marker genotypes.

TABLE 5 (Cont.)

[1]Trait	[2]QTL	[3]Marker	[4]Chr	[5]Pos	[6]Flanking	[7]F	[8]Pr.	[9]FDR	[10]R^2	[11]Effect	[12]*Hv*	[13]*Hsp*	[14]RI_{Hspl}	[15]Add.
Chlorophyll content	QCC.S42-1H	bPb_4531	1H	60.21	55.76 - 63.5	9.78	0.0000	0.0000	3.21	M*E	48.48	49.29	1.68	0.41
	QCC.S42-4H	EBmac775	4H	80	80 - 86.68	13.02	0.0000	0.1160	3.12	M	48.89	46.9	-4.07	-1
	QCC.S42-5H	bPb_1719	5H	173.7	173.709 - 174.04	10.12	0.0020	0.1160	7.78	M	48.12	52.85	9.83	2.36
	QCC.S42-6H	bPb_7313	6H	2.5991	2.59- 9.10	6.96	0.0100	0.2510	3.43	M	48.23	53.32	10.55	2.54
Number of spike Per plant	QNSP.S42-2Ha	bPb_9681	2H	5.27	3.54 - 7.59	12.31	0.0000	0.0000	5.76	M*E	6.51	7.14	9.58	0.31
	QNSP.S42-2Hb	bPb_8292	2H	27.06	25.73 - 30.23	28.97	0.0000	0.0000	8.56	M	6.44	7.18	11.54	0.37
	QNSP.S42-2Hc	Bmag381	2H	97	90 - 102.37	38	0.0000	0.0000	12.28	M	6.74	6.02	-10.71	-0.36
	QNSP.S42-6H	HVM74	6H	70	63 – 75	8.52	0.0040	0.0400	4.22	M	6.65	6.27	-5.64	-0.19
	QNSP.S42-7Ha	GMS56	7H	100	93 – 107	11.47	0.0010	0.0150	4.61	M	6.5	6.99	7.51	0.24
	QNSP.S42-7Hb	EBmac755	7H	137	136.56 - 141.80	7.24	0.0000	0.0020	2.11	M*E	6.54	6.86	4.85	0.16
100-grain weight	QGW.S42-1H	GBMS143	1H	162	162	6.64	0.0110	0.0970	2.57	M	3.83	4.05	5.84	0.11
	QGW.S42-2Ha	bPb_8292	2H	27.07	25.73 - 30.23	10.54	0.0000	0.0000	4.26	M*E	3.83	3.72	-2.77	-0.05
	QGW.S42-2Hb	EBmac684	2H	80	77.41 - 81	6.86	0.0000	0.0020	2.88	M*E	3.83	3.73	-2.68	-0.05
	QGW.S42-2Hc	Bmag125	2H	98	92 - 102.37	14.37	0.0000	0.0110	7.11	M, M*E	3.76	4.01	6.45	0.12
	QGW.S42-3Ha	bPb_4209	3H	111.68	105.88- 115.50	12.15	0.0010	0.0160	5.89	M	3.78	4.03	6.57	0.12
	QGW.S42-3Hb	bPb_7164	3H	157.98	151 - 160.18	14.32	0.0000	0.0000	4.43	M*E	3.79	4.03	6.37	0.12
Grain yield per plant	QGYP.S42-1Ha	Mla12	1H	38.5	38.5 - 39	6.81	0.0000	0.0010	0.89	M*E	5.05	4.41	-12.6	-0.32
	QGYP.S42-1Hb	GBMS143	1H	162	162	6.82	0.0000	0.0010	4.92	M*E	4.98	4.83	-2.99	-0.07
	QGYP.S42-2Ha	bPb_0003	2H	25.73	25.73 - 30.23	13.76	0.0000	0.0000	10.01	M*E	4.91	5.2	5.94	0.15
	QGYP.S42-2Hb	bPb_8038	2H	38.97	38.97 - 44.78	5.1	0.0020	0.0050	2.36	M*E	5.09	4.85	-4.69	-0.12
	QGYP.S42-3Ha	HvGI	3H	63	63 - 69.77	23.53	0.0000	0.0000	7.76	M*E	4.97	4.86	-2.27	-0.06
	QGYP.S42-3Hb	bPb_3278	3H	100.75	100 - 105.88	7.63	0.0060	0.0820	7.05	M, M*E	4.87	5.19	6.45	0.16
	QGYP.S42-3Hc	bPb_8557	3H	147.95	141.93 - 153.54	27.99	0.0000	0.0000	8.93	M*E	4.94	4.99	0.87	0.02
	QGYP.S42-4H	bPb_7719	4H	96.77	93.63 - 96.77	11.89	0.0010	0.0380	9.66	M	5.05	4.62	-8.63	-0.22
	QGYP.S42-6Ha	Bmac316	6H	6	3.54 - 9.75	13.05	0.0000	0.0000	8.09	M*E	4.96	4.89	-1.43	-0.04
	QGYP.S42-6Hb	bPb_2751	6H	14.35	9.10 - 19.41	4.51	0.0040	0.0090	3.07	M*E	4.98	4.76	-4.59	-0.11
	QGYP.S42-6Hc	EBmac624	6H	68.1	63 - 75	19.29	0.0000	0.0000	6.33	M*E	5.01	4.77	-4.83	-0.12
	QGYP.S42-7Ha	Bmag7	7H	16	16 - 17.47	8.73	0.0000	0.0000	5.28	M*E	5	4.79	-4.17	-0.1
	QGYP.S42-7Hb	HVACL3	7H	90	84.95 - 93	11.68	0.0000	0.0000	2.68	M*E	4.93	5.14	4.27	0.11

1) Studied trait, 2) Description of quantitative trait locus, 3) Linked DNA marker revealing strongest F-value, 4) Chromosome, 5) DNA markers positions in cM, 6) Flanking positions in cM, 7) F-value of the given marker locus, 8) Probability at $P < 0.05$, 9) False discovery rate, 10) Genetic variance, 11) Main effects (M) and marker × treatment (M×T) interaction, 12) Trait value of homozygous cultivated genotype [Hv], 13) Trait value of homozygous exotic genotypes [Hsp]. 14) Relative performance of the homozygous exotic allele, RP[Hsp] and 15). The additive effect is half the difference between the phenotypic means of the homozygous elite and exotic marker genotypes.

TABLE 6. Estimation of LS-means of 25 pairs of digenic interactions and epistatic effects (additive × additive) for studied traits.

Trait	Marker 1			Marker 2			F	Pr.	FDR	R^2	(1) Ls means of digenic interactions			
	M. name	Chr.	Pos.	M. name	Chr.	Pos.					*Hv/Hv*	*Hv/ Hv*	*Hv/ Hv*	*Hv/Hv*
HD	Mla12	1H	38.50	MGB338	5H	95.00	4.22*	0.012	0.027	5.19	95.63	97.47	97.64	101.63
	bPb_5290	1H	64.89	bPb_1411	3H	160.19	9.07**	0.000	0.000	12.49	96.59	97.02	93.02	95.52
	HVABAIP	1H	116.00	bPb_9110	3H	118.72	48.31**	0.000	0.000	40.67	96.64	98.50	90.52	96.44
	GBMS12	1H	134.00	EBmac624	6H	68.10	13.26**	0.000	0.000	14.96	95.30	98.64	95.29	93.63
	GMS3	2H	81.00	bPb_3020	7H	159.21	3.05*	0.040	0.069	4.34	96.34	95.81	92.27	94.45
	bPb_7987	4H	72.27	VrnH2	4H	140.20	7.62**	0.000	0.001	7.78	95.41	95.51	98.35	94.47
	bPb_6676	5H	81.39	MGB338	5H	95.00	7.64**	0.000	0.001	9.24	96.23	92.48	98.47	98.31
PH	bPb_1366	1H	95.08	bPb_9618	5H	70.75	16.17**	0.000	0.000	22.73	67.62	62.65	73.97	78.28
	bPb_2230	2H	60.45	bPb_9110	3H	118.72	58.43**	0.000	0.000	51.44	65.32	67.30	79.73	69.80
	GMS3	2H	81.00	bPb_9110	3H	118.72	78.73**	0.000	0.000	55.79	66.75	62.42	80.05	68.48
	GBM1016	2H	140.00	GBM1008	6H	100.00	3.51*	0.034	0.055	4.22	67.24	73.73	70.03	78.13
	bPb_8698	2H	161.12	HvFT2	3H	64.00	12.22**	0.000	0.000	17.66	67.17	71.33	78.66	92.38
	Bmac316	6H	6.00	bPb_9065	6H	9.75	8.26**	0.000	0.000	12.82	67.38	85.07	68.18	71.22
CC	bPb_9746	3H	54.80	bPb_1579	3H	115.50	3.61*	0.017	0.207	4.88	48.37	51.22	49.34	48.99
NSP	bPb_8292	2H	27.07	Bmag381	2H	97.00	14.65**	0.000	0.000	21.29	6.58	7.20	5.94	6.57
	bPb_8292	2H	27.07	bPb_8754	5H	182.99	10.52**	0.000	0.003	16.40	6.42	7.18	6.90	5.31
	Bmag381	2H	97.00	bPb_8701	4H	93.64	9.51**	0.000	0.003	16.60	6.76	6.36	6.78	5.76
	EBmac775	4H	80.00	HVM67	4H	141.10	4.85**	0.005	0.039	11.33	6.49	6.44	6.89	5.88
GW	GBMS143	1H	162.00	bPb_3427	6H	38.04	4.21*	0.015	0.078	4.55	3.84	4.09	3.72	3.72
	bPb_9681	2H	5.27	bPb_4389	7H	125.40	6.47**	0.002	0.033	11.46	3.84	3.61	3.84	4.96
	bPb_2225	2H	67.35	bPb_4209	3H	111.69	4.99*	0.010	0.065	11.03	3.76	3.95	4.06	4.33
	Bmag125	2H	98.00	bPb_7287	5H	58.38	5.65**	0.002	0.038	8.80	3.82	4.04	3.62	4.18
	Bmag125	2H	98.00	bPb_4634	7H	16.81	12.13**	0.000	0.004	11.55	3.72	4.14	4.15	3.95
GYP	bPb_3278	3H	100.76	bPb_5265	4H	145.10	5.14**	0.007	0.097	18.75	4.92	5.02	6.12	5.65
	bPb_6967	5H	94.96	AF043094A	5H	156.00	8.04**	0.000	0.076	15.87	5.07	4.27	4.81	6.54

*, ** indicate the significance level at 0.05 and 0.01, respectively to declare the putative epistatic QTL positions. (1) Least means of the allelic combinations of the cultivated genotype (*Hv*) and wild genotype (*Hsp*).

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تحليل المواقع الوراثية الكمية فى الشعير على مستوى البيئات فى مصر

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يعد الشعير واحدا من أهم محاصيل الحبوب في العالم. تم زراعة عشيرة مكونة من 301 سلالة أحادية التضاعف فى أربعة مواقع هى أسيوط ، الوادى الأسيوطى، النوبارية ومطروح. العشيرة ناتجة من التهجين الرجعي المتقدم بين صنف ألماني متميز "سكارليت" مع سلالة مستوردة "أي اس ار8-42" في أربعة مواقع على مستوى مصر. تم تحليل المواقع الكمية الوراثية بإستخدام خريطة إرتباط وراثية تحتوي على 371 من الواسمات الجزيئية المختلفة. تم تحديد 56 موقع وراثي للصفات محل الإهتمام. بالإضافة إلى أننا تعرفنا على أربعة واسمات للتاثيرات الرئيسية و كذا التفاعل بين الواسم و البيئة. الاليلات المستورة لهذه الواسمات الأربعة قد تكون هي المسئولة عن زيادة صفاتها على مستوى البيئات. فضلا عن أنه كان هناك 8 واسمات أظهرت تأثير متعدد على مستوى المواقع. .هذه النتائج قد تكون مفيدة في الإنتخاب بإستخدام الواسمات في برامج التربية في مصر