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QTL mapping of grain yield and its components under normal and drought stress conditions in barley (*Hordeum vulgare* L.)

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Abstract

A population comprising of 118 double haploids of barley derived from a cross, Nure x Tremois was evaluated for different traits for yield and its components under normal and drought stress conditions. Using a genetic map of 543 markers (DArT, SSR, SNP and AFLP), we identified 33 additive quantitative traits loci (QTLs) for phenological and morphological traits. All of these Qtls had additive and digenic effects. Five out of 67 epistatic Qtls exhibited significant Q×T interactions. The majorities of main effects were detected on chromosome 5H and affected primarily plant height (PH), number of spikes /plant (Ns/P), kernels per spike (KS), thousand kernel weight (TKW), main spike length (MSL) and harvest index (HI). We identified additive QTLs for plant height on most the chromosomes, except 4H. Five pairs of epistatic QTLs for plant height without interaction with environments were also detected. However, we did not find any additive QTLs for grain yield, but detected nine epistatic QTLs on all of the barley chromosomes. None of them had interaction with environments.

Key words: Morphological traits, agronomic traits, quantitative trait loci, drought tolerance, epistasis

Introduction

Barley (*Hordeum vulgare* L.) is one of the most important crops in Iran and because of the high import of agricultural products, plant breeders are working towards increasing the agricultural efficiency of barley through conventional and molecular approaches to improve its production by identification and introduction of stable and adaptive cultivars. Drought is the single abiotic stress causing major crop losses worldwide including Iran and continues to be a challenge to scientists (Ceccarelli et al. 2004). Response to drought stress is manifested at the whole-plant level including numerous morphological, physiological and biochemical changes (Anjum et al. 2011). Different breeding strategies to improve crop plants are known to cope with the limited water supply (Ludlow 1989). Drought tolerance is a very important but problematic trait for plant breeders. Difficulties arise from its quantitative nature. Drought tolerance undergoes a very complex genetic control involving many genes with small effects which are greatly affected by the environment (Mir et al. 2012). Because of these reasons, one of the most suitable methods for identifying genes that are involved in drought tolerance is the use of molecular markers for quantitative trait loci (QTLs). The QTLs can be used to improve the drought tolerance of the particular crop plants. The results of previous QTL mapping studies of drought tolerance-associated traits in the barley illustrate many problems in finding common regions responsible for drought adaptation (Von Korff et al. 2008). Most of the problems resulted from either different genotypes being studied under different environmental and controlled drought conditions, or various drought tolerance indicators used in phenotyping. The measures include, yield and growth analysis (Von Korff et al. 2008), CO2 assimilation rate (Lawlor and Cornic 2002), PSII

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(photosystem II) photochemical activity (Oukarroum et al. 2007), leaf water conservation (Chen et al. 2004), plasma membrane integrity (Babu et al. 2004), osmotic adjustment or relative water content (Serraj and Sinclair 2002), carbon isotope discrimination (Teulat et al. 2002) and resistance to paraquat (Altinkut et al. 2003) are some of the mechanisms, which need attention. In barley, a large number of morphological and physiological traits are related to drought tolerance (Chen et al. 2010) which exhibit strong environmental interactions (Tondelli et al. 2006). Increasing tolerance to drought stress has become a major goal for barley breeding programs particularly in light of prolonged drought periods as a result of climate change (Wehner et al. 2015).

Quantitative molecular genetics is a useful approach to study complex traits by describing the characteristics of a phenotypic continuous distribution. These interactions between QTLs and the environment have an important role in controlling quantitative traits (Würschum et al. 2011), consequently, identifying epistatic QTLs interactions and additive QTLs as well as interactions between QTLs and the environment is necessary to improve barley drought tolerance. However, few studies have reported epistatic QTLs and QxE interactions under different drought stress (Chen et al. 2011). The present study uses QTLNetwork (Yang et al. 2008) along with a double haploid population derived from a cross between barley cultivars 'Nure' and 'Tremois' to examine additive (a) and epistatic (aa) QTLs and the interaction between these QTLs and environments (ae and aae). Subsequent breeding programs can employ these QTLs for developing improved drought tolerant cultivars of barley.

Materials and methods

Plant materials and field trials

A double haploid (DH) population comprising 118 lines derived from F_1 hybrid (Nure/Tremois), following the *Hordeum bulbosum* technique as described by Chen and Hayes (1989), was used in this study. Nure (drought tolerance) is a winter barley cultivar originated from Italy, it shows high yield potential and yield stability in irrigated as well as in moderately drought stressed conditions (Rizza et al. 2004), while Tremois (drought susceptible) is a spring barley cultivar originated from France with low temperature tolerance and adapted to high input conditions (Francia et al. 2004; Tondelli et al. 2014). The DH population and two parents were planted at the research farms of Agricultural and Natural Resource Center of Zabol ($61^{o}41'$N $30^{o}54'$E, 483 m above sea level) Iran in 2015. Mean annual precipitation and mean annual temperature were 53 mm and 24^{o}C, respectively. The field trials were conducted using an alpha lattice design (11×11) with two replications. Each DH and parental lines were planted in two rows with plot size 0.5 × 2.5 m^2. Drought stress started after the first irrigation for germination. At this time, the irrigation of the stress variant was stopped till the soil reached 17.5 % of the maximal soil water capacity and for normal environment when the soil reaches the field capacity. Totally the plot with normal treatment (control) was irrigated 6 times, while stress treatment was irrigated only once. Agronomic and phenological traits like days to flowering (DTF), days to maturity (DTM), plant height (PH), number of nodes (NN), number of spikes/plant (Ns/P), no. of kernels per spike (KS), thousand kernel weight (TKW), main spike length (MSL), grain yield (GY), biological yield (BY), harvest index (HI) and the relative water content (RWC) were measured.

Data and QTL analysis

SAS 9.3 software was used to conduct the analysis of variance (ANOVA) of each data set. Before QTL analysis of each measured trait, the average of two replications was calculated. For QTL (quantitative trait loci) analysis, the linkage map of the 'Nure' and 'Tremois' population was used. This map included 543 markers spread over the 7 barley chromosomes. A total of 396 DArT, 18 STS-SNP and 10 SSR loci have been added to the Nure and Tremois molecular linkage map already available (Francia et al. 2004). The NT map now consist of 543 markers, spanning a total length of 1114 cM with an average resolution of one marker every 2.8 cM (Tondelli et al. 2014). QTLs with a and aa epistatic effects, as well as their environmental interactions (ae and aae) were identified using QTLNetwork program version 2.1 (Yang et al. 2008; Yang et al. 2007) with a mixed linear composite interval mapping method and with joint analysis of multi-environment phenotypic values. The LOD thresholds of QTLs were determined with a 1,000 permutation test at a 95% confidence level, with a 1 cM walking speed and a window size of 10 cM (Masoudi et al. 2015).

Results

Phenotypic variation and relationships between the traits

In the normal and stress environments, the Nure genotype was superior to Tremois for all measured traits, except the relative water content (Table 1). The differences between parents for all traits in both environments were significant. Parental genotypes are classified as early (Tremois) and late (Nure) according to the large differences between their maturity dates in all environments. The maturity date of the Tremois genotype was about 11 days earlier than the Nure genotype under well-watered condition. The stress environment in contrast to normal environment increase the duration of different plant growth stages (days to flowering and days to maturity) and this increase was higher for Nure genotype as compared with Tremois genotype. In the stress condition, all of the yield component traits decreased as compared to non-stress condition and these decreases were higher for Tremois genotype in contrast to the Nure genotype for most of the traits, except thousand kernel weight. Nure genotype had a higher duration of growth stages (days to flowering and days to maturity) and also had higher yield and yield component traits in contrast to Tremois genotype. Grain yield reduction in Nure (from 1461.51 to 1421.75 Kg/ha) under drought stress was less than the Tremois genotype (from 1095.44 to 865.86 Kg/ha); so the drought tolerant cultivar (Nure) may have some mechanisms which can produce higher biological yield and grain yield under lower water content, and had higher harvest index with lower reduction in harvest index. The Tremois genotype had higher relative water content in both environments but the increase in this trait was higher in the drought tolerant cultivar (Nure) under stress conditions as compared to the Tremois genotype.

The 118 DH population displayed a wide range of phenotypic variation among the measured traits. The coefficient of variation (CV) was higher than 10% for most of the traits in both the environments. All measured traits displayed environmental effects. The mean values of all yield and yield components traits among doubled haploid (DH) population were higher in well-watered environment than those in stress environment; however, the reverse was true for the traits related to days to different growth stages and RWC. A significant transgressive segregation in both directions and continuous variation of the frequency distribution among all measured traits due to their polygenic inheritance patterns (Table 1) was recorded. Significant genetic correlation was observed between several of the measured traits (Table 2). A significant correlation was observed between the yield and yield components under normal condition but positive correlations were found under drought stress condition between yield with thousand kernel weight, main spike length, biological yield and harvest index. Of these, the strongest correlation was between yield with harvest index and biological yield in both conditions. A significant negative correlation was observed between yield and yield components with traits related to days to different growth stages in both conditions.

Identification of additive QTLs and additive QTLs × environment interactions

By the combine analysis of the multi-environment phenotypic values under normal and stress conditions, we detected 33 QTLs for 9 traits on 7 chromosomes. All of these QTLs had only an effect explaining the phenotypic variation ranging from 0.04 to 10.05 % (Table 3). Three QTLs were detected for days to maturity; one of them on chromosome 3, which is co-localized with one of the DTMI and DTD QTLs and was responsible for 3.25 % of the phenotypic variation. Six QTLs were identified for plant height; one of them (on chromosome 2) is co-localized with one of the KS and MSL QTLs and was responsible for 3.43 % of the phenotypic variation. We found 4 QTLs for number of nodes; out of which one on chromosome 6 is co-localized with one of the NS/P and KS QTLs and explained 5.23 % of the phenotypic variation.

Six QTLs were identified for number of spikes/plant; one of them (on chromosome 5) is co-localized with one of the HI QTLs and explained 3.53 % of phenotypic variation. We found six QTLs for number of kernel per spike; one of them (on chromosome 1) is co-localized with one of the NN, IL and Ns/P QTLs and was responsible for 4.22 % of phenotypic variation. The other one QTL for Ns/P identified on chromosome 2 is co-localized with one of the PH and MSL QTLs and subscribing for 9.23 % of the phenotypic variation.Further, we detected two QTLs for TKW; one of them (on chromosome 5) is co-localized with PH and HI QTLs and explained 3.3 % of the phenotypic variation.Two QTLs were detected for MSL; one of them (on chromosome 2) is co-localized with PH and KS QTLs and explains 10.05% of the phenotypic variation.We also identify 2 QTLs for RWC; one of them is on chromosome 4 and co-localized with one of the NN QTLs and the other (on chromosome 5) co-

Table 1. Phenotypic performance of relevant traits in the two parents and doubled haploid(DH) population under normal (N) and drought stress (S) environments

Trait	Treatment	Parent		RILs				
		Nure	Tremois	Mean	Min.	Max.	SD	CV (%)
Days to flowering (DTF) (d)	N	131.05	114.49	124.7	105.41	160.01	15.00	12.03
	S	139.08	118.05	125.94	109.42	159.99	14.79	11.74
Days to maturity (DTM) (d)	N	152.05	141.41	151.42	130.38	183.44	15.11	9.98
	S	156.15	144.01	152.65	134.40	190.56	14.66	9.60
Plant height (PH) (cm)	N	104.70	103.41	96.42	77.50	114.74	7.32	7.59
	S	102.49	90.44	89.24	67.17	104.59	7.55	8.46
number of nods (NN) (Number)	N	5.00	5.00	5.23	4.00	6.00	0.49	9.44
	S	5.00	5.00	5.16	3.00	6.00	0.52	10.05
number of spikes /plant(Ns/P) (Number)	N	7.08	6.52	6.19	3.01	9.48	1.17	18.85
	S	7.03	5.01	5.64	3.00	9.48	1.52	26.90
Kernels per spike (KS) (Number)	N	26.1.00	24.98	25.53	14.12	36.96	3.17	12.42
	S	25.61	24.94	23.83	16.28	33.15	3.29	13.83
Thousand kernel weight (TKW) (g)	N	44.56	41.40	39.79	25.47	48.37	5.04	12.66
	S	41.02	38.70	38.95	26.05	46.55	4.84	12.44
Main Spike length (MSL) (cm)	N	7.26	7.17	7.55	5.00	18.08	1.43	18.97
	S	6.85	6.75	6.73	4.67	9.43	1.07	15.94
Grain yield (GY) (g)	N	1461.51	1095.44	1298.00	495.87	1991.00	297.05	22.89
	S	1421.75	865.86	1236.00	430.06	2156.00	283.57	22.94
Biological yield (BY) (g)	N	3618.45	3436.44	3752.00	1765.00	5129.00	579.43	15.44
	S	3569.40	3306.46	3626.00	1712.00	5003.00	601.40	17.55
harvest index (HI)	N	0.41	0.32	0.35	0.15	0.53	0.07	21.23
	S	0.40	0.26	0.34	0.16	0.53	0.07	19.01
relative water content(RWC)	N	49.57	66.33	59.43	22.49	89.25	12.58	21.17
	S	57.99	67.08	60.56	39.86	81.99	8.15	13.47

Table 2. Correlation coefficients between different traits under normal (below the diagonal) and stress (above the diagonal) treatments

	DTF	DTM	PH	NN	Ns/P	KS	TKW	SL	GY	BY	HI	RWC
DTF		0.95**	0.36**	0.35**	–0.10	–0.16	–0.69**	–0.23*	–0.51**	–0.05	–0.54**	0.13
DTM	0.94**		0.39**	0.34**	–0.07	–0.16	–0.61**	–0.21*	–0.41**	0.04	–0.51**	0.13
PH	0.15	0.17		0.31**	0.06	0.26**	–0.17	0.16	0.07	0.34**	–0.21*	0.18*
NN	0.29**	0.37**	0.18		–0.08	0.13	–0.28**	–0.01	–0.09	0.15	–0.24**	0.13
Ns/P	–0.21*	–0.16	0.20*	–0.03		0.02	0.01	–0.13	–0.01	–0.01	0.001	0.03
KS	–0.24**	–0.17	0.39**	0.03	0.15		–0.02	0.54**	0.05	0.15	–0.06	0.14
TKW	–0.74**	–0.74**	–0.01	–0.29**	0.20*	0.06		0.06	0.55**	0.23	0.47**	0.03
MSL	–0.30**	–0.24	0.36**	–0.02	0.15	0.85**	0.15		0.18	0.19*	0.04	0.13
GY	–0.56**	–0.53**	0.17	–0.12	0.13	0.23*	0.59**	0.21*		0.47**	0.72**	–0.09
BY	–0.13	–0.10	0.47**	0.05	0.06	0.28**	0.24**	0.22**	0.59**		–0.24**	–0.08
HI	–0.58**	–0.59**	–0.22*	–0.18	0.11	0.03	0.54**	0.08	0.63**	–0.22*		0.01
RWC	0.19*	0.15	–0.20*	–0.06	–0.15	–0.07	–0.13	–0.09	–0.30	–0.34	–0.02	

* pd”0.05; ** pd”0.01

Table 3. QTLs with additive effects (a) and additive × treatment interaction effects (ae) under normal and stress treatments detected using QTLNetwork

Traits	Chr.[a]	QTLs	Marker interval	Site (cM)	Range (cM)	*a*	h^2 (*a*)
DTM	1H	QDTM-1H	BPB-1604-1H-BPB-0357-1H	39.9	33.0-43.1	3.06**	2.85
	3H	QDTM-3H	HVHDAC2_2-3H-BMAG0013-3H	123.7	123.0-131.7	3.45**	3.25
	7H	QDTM-7H	BPB-7004-7H-BPB-2718-7H	0.0	0.0-8.3	2.37**	2.04
PH	1H	QPH-1H	BPB-0357-1H-BPB-6621-1H	40.3	34.0-46.1	1.72**	1.98
	2H	QPH-2H	BPB-8737-2H-BPB-3653-2H	110.8	108.6-111.9	1.59**	3.43
	3H	QPH-3H	E39M61_198-3H-BPB-9207-3H	167.0	152.3-184.8	1.67**	1.89
	5H	QPH-5Ha	E35M61_289-5H-E42M38_149-5H	41.5	39.2-46.5	1.64**	1.06
	5H	QPH-5Hb	BMAG0222-5H-BPB-6195-5H	159.9	126.7-168.7	1.17**	2.65
	7H	QPH-7H	BPB-1209-7H-BPB-5260-7H	51.5	42.7-64.5	1.44**	0.44
NN	1H	QNN-1H	E41M38_448-1H-BMAG0211-1H	44.7	33.0-117.1	0.11**	3.95
	4H	QNN-4Ha	BPB-7275-4H-E39M61_181-4H	19.9	0.0-77.5	0.18**	3.82
	4H	QNN-4Hb	SNF2P-4H-BMY1-4H	147.2	114.7-149.5	-0.16**	2.8
	6H	QNN-6H	BPB-UNK3-6H-BPB-1724-6H	57.8	48.6-127.9	-0.08**	5.23
Ns/P	1H	Q Ns/P-1H	BPB-2260-1H-BPB-5550-1H	115.8	98.6-117.1	0.25**	0.61
	2H	Q Ns/P-2Ha	BPB-3677-2H-BMAC0273F-2H	79.7	74.4-100.3	0.5**	2.57
	2H	Q Ns/P-2Hb	BPB-8008-2H-BPB-9800-2H	146.4	140.0-152.6	0.15*	0.77
	4H	Q Ns/P-4H	E39M61_181-4H-BPB-9998-4H	57.9	54.9-69.4	-0.87**	2.83
	5H	Q Ns/P-5H	E42M38_190-5H-BPB-0486-5H	109.4	102.8-118.8	0.17*	3.53
	6H	Q Ns/P-6H	SCSSR05599-6H-DHN3_4_5_7-6H	103.1	99.8-113.6	-0.32**	1.54
KS	1H	QKS-1H	WMC1E8-1H-BPB-2260-1H	112.6	40.3-117.1	0.7**	4.22
	2H	QKS-2Ha	BPB-1212-2H-BPB-9682-2H	48.5	18.5-71.2	-0.72**	0.04
	2H	QKS-2Hb	BPB-8737-2H-BPB-3653-2H	110.8	109.6-111.9	1.27**	9.23
	3H	QKS-3H	BMAG0606-3H-HVHDAC2_2-3H	107.0	97.1-122.0	-0.7**	4.09
	5H	QKS-5H	BPB-9147-5H-BPB-8070-5H	168.7	162.9-183.5	-0.63**	2.47
	6H	QKS-6H	BPB-0597-6H-BPB-6002-6H	35.4	3.3-102.8	0.86**	1.93
TKW	5H	QTKW-5H	HVBPBF-5H-E42M38_640-5H	45.8	30.8-46.5	-0.73**	3.3
	7H	QTKW-7H	BPB-1209-7H-BPB-5260-7H	66.5	52.5-77.0	-0.68*	2.2
MSL	2H	QSL-2H	BPB-8737-2H-BPB-3653-2H	110.8	108.6-113.9	0.45**	10.05
	5H	QSL-5H	BPB-6195-5H-BPB-9147-5H	168.7	161.9-186.5	-0.24**	2.58
HI	5H	QHI-5Ha	E35M61_289-5H-E42M38_149-5H	41.5	33.8-46.5	-0.02**	2.99
	5H	QHI-5Hb	PSR637-5H-E39M61_229-5H	104.2	99.6-111.2	-0.01*	3.28
RWC	4H	QRWC-2H	BPB-7275-E39M61_181-4H	16.9	0-97.7	2.02*	1.63
	5H	QRWC-5H	E42M38_151-BPB-6603-5H	29.8	26/9-39.6	-1.68**	1.80

[a]Chromosome on which the QTL was located

localized with one of the PH, Ns/P, TKW and HI QTLs.

Identification of epistatic QTLs and epistatic QTLs × environment interactions

In the present study, 67 pairs of epistatic effects were detected across the 7 chromosomes of barley for 11 different traits. Five of them had only aae effects, explaining the observed phenotypic variation ranging from 0.01 to 13.9 % (Table 4).

Eight epistatic Qtls were identified for days to flowering. The parental type q1q1q2q2 and Q1Q1Q2Q2

Table 4. QTLs with epistatic effects (*aa*) and epistatic × treatment interaction effects (*aae*) under normal (e_1) and stress (e_2) treatments detected using QTLNetwork

Traits	Chr	QTL i	Marker interval	Site	Range (cM)	Chr	QTL j	Marker interval	Site	Range (cM)	aa	h^2(aa)
aae_1	aae_2	h^2(aae)										
DTF	2H	QDTF-2H	BPB-3536-2H-BPB-8302-2H	137.1	120.5-169.6	5H	QDTF-5H	E42M38_170-5H-BPB-4971-5H	197.5	184.5-197.5	-4.61**	5.4
	3H	QDTF-3Ha	TEL3S-3H-E42M38_230-6-3H	0.0	0.0-6.9	6H	QDTF-6Ha	BPB-3309-6H-BPB-4409-6H	52.6	49.8-56.2	4.14**	3.2
	3H	QDTF-3Ha	TEL3S-3H-E42M38_230-6-3H	0.0	0.0-6.9	6H	QDTF-6Hb	DHN3_4_5_7-6H-BPB-6477-6H	112.4	102.8-120.2	-2.72**	2.8
	3H	QDTF-3Hb	BPB-5864-3H-BPB-9640-3H	180.5	167.0-184.8	5H	QDTF-5H	BPB-5317-5H-SCSSR02306-5H	0.5	0.0-8.6	-3.24**	2.8
	5H	QDTF-5Ha	E42M38_149-5H-E35M61_117-5H	41.6	38.2-46.5	6H	QDTF-6H	BPB-3309-6H-BPB-4409-6H	52.6	49.8-56.2	2.1*	0.8
	5H	QDTF-5Hb	HVABI5-5H-BMAG0113F-5H	67.3	65.4-70.3	6H	QDTF-6H	BPB-3309-6H-BPB-4409-6H	52.6	49.8-56.2	-4.04**	0.7
	6H	QDTF-6H	DHN3_4_5_7-6H-BPB-6477-6H	112.4	102.8-120.2	7H	QDTF-7Ha	BPB-5260-7H-BMAC0273A-7H	74.3	64.5-77.0	4.28**	5
	6H	QDTF-6H	DHN3_4_5_7-6H-BPB-6477-6H	112.4	102.8-120.2	7H	QDTF-7Hb	BPB-1360-7H-BPB-5091-7H	33.4	33.2-49.5	-1.87*	0.4
DTM	1H	QDTM-1Ha	BPB-8973-1H-HOR1-1H	7.1	0.0-22.0	1H	QDTM-1H	BPB-1541-1H-COR18-1H	56.1	51.5-61.1	-3.41**	1.6
	1H	QDTM-1Hb	E39M61_247-1H-HV347D22_	76.2	62.6-76.6	5H	QDTM-5Ha	BPB-3138-5H-BPB-6179-5H	172.8	162.9-181.0	2.4**	2.6
	1H	QDTM-1Hc	BPB-6343-1H-BPB-8081-1H	87.5	85.2-88.5	3H	QDTM-3H	BPB-1264-3H-BPB-9402-3H	14.2	4.0-20.9	-2.98**	1.3
	2H	QDTM-2Ha	BPB-2219-2H-HVCEN_EPS2-2H	78.3	77.1-83.9	7H	QDTM-7H	BPB-7004-7H-BPB-2718-7H	0.0	0.0-8.3	-3.42**	1.8
	2H	QDTM-2Hb	EBMAC0415-2H-HVM54-2H	134.7	130.5-143.8	4H	QDTM-4H	BPB-9820-4H-ZCCT-H_VRN-H2-4H	143.9	123.7-149.5	-6.01**	11.4
	2H	QDTM-2Hb	EBMAC0415-2H-HVM54-2H	134.7	130.5-143.8	5H	QDTM-5Hb	SCSSR02306-5H-TC138581_LOS2-5H	7.6	3.5-10.6	-2.71**	3
	2H	QDTM-2Hc	BPB-7455-2H-BPB-6296-2H	174.5	164.6-174.5	5H	QDTM-5Hc	BPB-7627-5H-HVABI5-5H	65.4	51.4-69.3	3.13**	2.2
	5H	QDTM-5H	SCSSR02306-5H-TC138581_LOS2-5H	7.6	3.5-10.6	6H	QDTM-6H	BPB-3927-6H-BPB-0396-6H	38.5	35.5-47.0	3.83**	1.7
PH	2H	QPH-2H	BPB-8737-2H-BPB-3653-2H	110.8	108.6-111.9	5H	QPH-5H	E35M61_289-5H-E42M38_149-5H	41.5	39.2-46.5	1.46**	3.
	1H	QPH-1Ha	COR18-1H-BPB-7899-1H	61.2	56.1-62.6	3H	QPH-3H	E39M61_198-3H-BPB-9207-3H	167.0	152.3-184.8	-1.59**	4.6
	1H	QPH-1Hb	BPB-0589-1H-BPB-8112-1H	111.9	105.6-115.6	7H	QPH-7Ha	BPB-2718-7H-BPB-6170-7H	0.0	0.0-2.9	-1.54**	4.7
	2H	QPH-2H	BPB-5460-2H-BPB-5619-2H	154.9	153.6-155.5	7H	QPH-7Ha	BPB-2718-7H-BPB-6170-7H	0.0	0.0-2.9	-1.05**	1.9
	6H	QPH-6H	BPB-0396-6H-BPB-2464-6H	42.1	31.4-47.0	7H	QPH-7Hb	BPB-0578-7H-BMAG0007-7H	12.8	11.5-14.3	1.67**	3.1
NN	4H	QNN-4H	SNF2P-4H-BMY1-4H	147.2	114.7-149.5	6H	QNN-6Ha	BPB-UNK3-6H-BPB-1724-6H	57.8	48.6-127.9	0.16**	6
	1H	QNN-1H	E41M38_448-1H-BMAG0211-1H	44.7	33.0-117.1	3H	QNN-3H	BPB-7448-3H-TC-MYB1-3H	26.9	20.9-27.6	-0.1**	3.2
	2H	QNN-2H	BPB-4768-2H-BPB-6047-2H	147.2	120.5-152.3	5H	QNN-5H	SCSSR02306-5H-TC138581_LOS2-5H	11.6	0.0-15.0	-0.07*	1.9
	5H	QNN-5H	BPB-2273-5H-E42M32_184-4-5H	38.2	36.4-40.6	6H	QNN-6Hb	BPB-3927-6H-BPB-0396-6H	40.5	36.5-42.1	0.1**	4.8
KS	2H	QKS-2H	BPB-1212-2H-BPB-9682-2H	48.5	18.5-71.2	2H	QKS-2H	BPB-8737-2H-BPB-3653-2H	110.8	109.6-111.9	-0.54**	2.1
TKW	1H	QTKW-1Ha	BPB-7112-1H-BPB-7043-1H	3.2	0.0-20.0	5H	QTKW-5Ha	BMAG0223-5H-MWG583-5H	80.7	78.3-89.7	0.9**	1.2
	1H	QTKW-1Hb	E41M38_448-1H-BMAG0211-1H	44.7	43.4-48.3	2H	QTKW-2H	BPB-1072-2H-HVBM3-2H	73.4	71.2-78.1	-1.73**	4.6
	1H	QTKW-1Hc	BMAG0382-1H-BPB-3992-1H	80.1	80.1-83.1	5H	QTKW-5Hb	PSR637-5H-E39M61_229-5H	105.2	99.8-107.6	-0.87**	2.1
	1H	QTKW-1Hc	BMAG0382-1H-BPB-3992-1H	80.1	80.1-83.1	2H	QTKW-2H	BPB-1072-2H-HVBM3-2H	73.4	71.2-78.1	1.12**	0.9

	2H	QTKW-2Ha	BPB-7626-2H-BPB-9220-2H	12.8	5.6-46.7	7H	QTKW-7H	BMAC0156-7H-BPB-0375-7H	121.6	121.6-127.6	0.88**	1.8
	2H	QTKW-2Hb	BPB-1154-2H-HVCSG-2H	147.3	139.0-151.3	6H	QTKW-6Ha	BMAC0040-6H-BPB-2054-6H	124.2	114.9-124.4	-0.96**	2.3
	3H	QTKW-3Ha	E42M38_230-6-3H-BPB-1264-3H	7.9	0.0-27.6	6H	QTKW-6Hb	BPB-1724-6H-SCSSR05599-6H	98.8	83.8-113.4	1.62**	13.9
	3H	QTKW-3Hb	BPB-1481-3H-BPB-4564-3H	148.0	140.4-151.8	6H	QTKW-6Hc	BPB-5515-6H-BPB-7644-6H	135.7	129.7-136.2	1.11**	2.7
	4H	QTKW-4H	BPB-0610-4H-BPB-9820-4H	86.7	67.4-120.7	5H	QTKW-5Hc	BPB-9244-5H-BPB-7360-5H	201.8	187.5-202.3	1.4**	4.3
	5H	QTKW-5H	HVBPBF-5H-E42M38_640-5H	45.8	30.8-46.5	5H	QTKW-5Hd	BPB-2580-5H-BPB-5379-5H	139.7	134.7-139.8	0.71**	0.2
MSL	2H	QSL-2H	BPB-8737-2H-BPB-3653-2H	110.8	108.6-113.9	5H	QSL-5Ha	BPB-6195-5H-BPB-9147-5H	168.7	161.9-186.5	-0.21**	2.2
	2H	QSL-2H	BPB-8737-2H-BPB-3653-2H	110.8	108.6-113.9	5H	QSL-5Hb	BPB-0091-5H-BPB-0351-5H	17.9	16.5-38.2	0.23**	2.6
GY	1H	QGY-1Ha	BPB-0405-1H-HOR2-1H	0.0	0.0-5.2	6H	QGY-6H	BMAC0040-6H-BPB-2054-6H	120.2	102.8-124.2	-55.1**	8
	1H	QGY-1Hb	BPB-2183-1H-BMAC0399-1H	13.6	10.6-14.4	1H	QGY-1H	BMAG0382-1H-BPB-3992-1H	80.1	80.1-86.2	58.03**	4.1
	1H	QGY-1Hb	BPB-2183-1H-BMAC0399-1H	13.6	10.6-14.4	5H	QGY-5Ha	BMAG0223-5H-MWG583-5H	86.7	78.3-90.0	57.04**	4.5
	1H	QGY-1Hc	BMAG0211-1H-E41M38_206-1H	46.1	32.0-54.6	5H	QGY-5Hb	BPB-5766-5H-HVM06-5H	202.3	190.5-202.3	51.66**	2.3
	1H	QGY-1Hd	WMC1E8-1H-BPB-2260-1H	113.6	107.6-117.1	3H	QGY-3H	E42M38_230-6-3H-BPB-1264-3H	7.9	2.0-16.2	55.22**	3.5
	2H	QGY-2H	BMAC0134-2H-BPB-7354-2H	3.1	0.0-5.5	2H	QGY-2H	E42M32_378-2H-EBMAC0415-2H	129.5	122.5-134.7	50.62**	6.3
	4H	QGY-4Ha	BPB-7275-4H-E39M61_181-4H	47.9	29.9-52.9	7H	QGY-7Ha	BPB-8539-7H-BPB-9104-7H	99.2	94.0-106.3	84.79**	8.4
	4H	QGY-4Hb	BPB-9998-4H-BPB-5408-4H	75.4	71.4-75.4	7H	QGY-7Hb	BPB-0889-7H-BPB-0917-7H	110.6	107.7-110.9	-69.97**	6.5
	5H	QGY-5H	BPB-6568-5H-BPB-6183-5H	26.3	19.3-26.7	6H	QGY-6H	MWG634B-6H-BPB-0597-6H	33.8	31.4-35.4	-52.75**	5.6
BY	1H	QBY-1Ha	E41M38_210-1H-BMAC0032-1H	46.3	40.3-50.3	3H	QBY-3H	BPB-1264-3H-BPB-9402-3H	8.2	0.0-16.2	87.12*	4.3
	1H	QBY-1Hb	BPB-9108-1H-BPB-6343-1H	86.2	76.6-98.6	4H	QBY-4H	BMY1-4H-BPB-4765-4H	149.5	142.9-149.5	-95.27**	0
	1H	QBY-1Hc	BPB-0589-1H-BPB-8112-1H	111.9	105.6-117.1	4H	QBY-4H	BMY1-4H-BPB-4765-4H	149.5	142.9-149.5	127.55**	2.5
	2H	QBY-2H	BPB-7626-2H-BPB-9220-2H	15.8	5.6-34.2	5H	QBY-5Ha	BPB-6603-5H-BPB-9317-5H	36.0	20.3-38.2	87.72*	2.3
	3H	QBY-3H	TC-MYB1-3H-BPB-9878-3H	34.6	27.6-42.6	5H	QBY-5Hb	HVABI5-5H-BMAG0113F-5H	66.3	60.4-70.3	109.29**	3.9
	4H	QBY-4H	MWG634-4H-BPB-8569-4H	0.0	0.0-20.9	5H	QBY-5Hc	BPB-6603-5H-BPB-9317-5H	36.0	20.3-38.2-45.44 n.s 93.29*	-94.92*	0.9 0.017
	6H	QBY-6H	BMAC0040-6H-BPB-2054-6H	120.2	117.4-124.4	7H	QBY-7Ha	SCSSR04056-7H-BPB-0328-7H	140.4	134.4-140.4-35.99 n.s -96.31*	95.55*	0.2 0.031
	6H	QBY-6H	BMAC0040-6H-BPB-2054-6H	120.2	117.4-124.4	7H	QBY-7Hb	HVACX1-7H-BPB-4064-7H	0.9	0.0-3.0	-79.454*	0.3
	7H	QBY-7H	BPB-9237-7H-TC147474_FRY1-7H	19.1	19.1-28.1	7H	QBY-7Hc	E41M38_231-7H-BPB-1669-7H	89.0	84.0-100.2	-100.43**	3.8
HI	1H	QHI-1H	HVZFP16-1-1H-BPB-9418-1H	15.0	6.1-29.0	1H	QHI-1H	BPB-7609-1H-BPB-9116-1H	62.6	51.5-64.6	0.020**	5.5
	2H	QHI-2Ha	BPB-4261-2H-BPB-2501-2H	50.8	41.7-55.2	6H	QHI-6Ha	BPB-3919-6H-BPB-8735-6H	140.4	137.8-140.4	-0.014**	6.3
	2H	QHI-2Ha	BPB-4261-2H-BPB-2501-2H	50.8	41.7-55.2	5H	QHI-5Ha	HVABI5-5H-BMAG0113F-5H	70.3	55.4-70.8	0.014**	4.2
	2H	QHI-2Hb	BMAG0125-2H-PAU-2H	102.3	91.2-107.6	3H	QHI-3H	WCA11A2-3H-E41M38_307-3H	55.4	45.1-58.7	-0.016**	3.5
	2H	QHI-2Hc	BPB-1986-2H-BPB-3102-2H	166.6	148.3-174.5	5H	QHI-5Hb	BPB-8070-5H-BPB-3138-5H	169.7	168.7-183.0	-0.01*	0.2
	5H	QHI-5H	E35M61_289-5H-E42M38_149-5H	41.5	33.8-46.5	6H	QHI-6Hb	BPB-1009-6H-BPB-3554-6H	7.5	7.3-41.5	-0.02**	3.7
RWC	1H	QRwc-1Ha	BPB-8973-HOR1-1H	7.1	0-9.1	5H	QRwc-5H	SCSNP02737-HVCBF4-5H	92.6	84.7-99.8	-2.21**	3.4
	1H	QRwc-1Hb	E39M61_346-BPB-3201-1H	117.1	112.6-117.1	5H	QRwc-5H	SCSNP02737-HVCBF4-5H	92.6	84.7-99.8 1.662*	-0.004ns -1.736*	0 0.025
	2H	QRwc-2H	BPB-0485-BPB-6466-2H	0.6	0-12.8	3H	QRwc-3H	BPB-8021-BPB-2420-3H	152	146.2-159.4 -1.593*	0.04ns 1.602*	0 0.042
	4H	QRwc-4H	BPB-0610-BPB-9820-4H	121.7	101.7-141.9	7H	QRwc-7Ha	BPB-9104-E38M50_220-7H	104.3	98.2-109.7 3.083*	1.47ns -3.076*	0 0.03
	5H	QRwc-5H	BMAG0222-BPB-6195-5H	161.9	157.6-168.7	7H	QRwc-7Hb	BPB-6214-E41M38_412-7H	77.1	62.5-90	1.82**	3.1

*, ** pd"0.05, 0.01 respectively

showed increased DTF due to QDTF-6H/ QDTF-7Ha and QDTF-3Ha/QDTF-6Ha epistatic interactions, respectively. Similarly eight epistatic Qtls were detected for days to maturity. The QDTM-2Hb/ QDTM-4H epistasis decreased DTM by 6 days in the recombination type q1q1Q2Q2. We found five epistatic interactions for plant height. The parental type Q1Q1Q2Q2 resulted in increased HI in the QPH-2H/ QPH-5H and QPH-6H/ QPH-7Hb epistatic interactions. Ten epistatic Qtls were identified for TKW. The parental type Q1Q1Q2Q2 in the QTKW-1Ha/ QTKW-5Ha, QTKW-1Hc/QTKW-2H, QTKW-2Ha/ QTKW-7H, QTKW-3Ha/QTKW-6Hb, QTKW-3Hb/ QTKW-6Hc, QTKW-4H/QTKW-5Hc epistasis and q1q1q2q2 in the QTKW-5H/QTKW-5Hd epistatic interactions displayed increased TKW. For grain yield, 9 epistatic Qtls were detected. The QGY-4Ha/QGY-7Ha epistasis increased SY by 84.79 (g) in the parental type Q1Q1Q2Q2. Another nine epistatic Qtls were detected for biological yield. The parental type Q1Q1Q2Q2 showed increased BY due to the epistatic interactions between QBY-1Ha/ QBY-3H, QBY-1Hc/ QBY-4H, QBY-2H/QBY-5Ha and QBY-3H/QBY-5Hb.

Discussion

Drought tolerance and association between the traits

Drought stress conditions caused the reduction in measured traits except days to different growth stages. Stress conditions caused a delay in days to different growth stages in both parents and RILs. These findings are in agreement with the previous findings (Farooq et al. 2011; Ogrodowicz et al. 2017). The effects of drought on vegetative growth duration are not consistent. Water deficit can decrease the growth duration and caused a large reduction of yield due to accelerated transition of plants from vegetative to generative phase (Desclaux and Roumet 1996; McMaster and Wilhelm 2003). It has been observed in the present study that drought stress reduced the number of kernels per ear, the thousand kernel weight and the number of tillers/plant, which resulted in a decrease in grain weight per plant. Lower number of grains formed in spikes may be due to lower pollen viability during water stress. Grain yield reduction caused by drought stress has been reported by several researchers (Mäkelä and Muurinen 2012; Miko³ajczak et al. 2016) earlier. It has been shown that plant height is negatively correlated with grain weight per plant under water shortage, especially when it occurs at later stage of plant growth (Simane et al. 1993; Van Ginkel et al. 1997). However, we did not find significant genetic correlation between grain yield and plant height and number of nodes in both the environments.

Association between additive, epistatic and QTL×environment (Q×E) QTLs

Among the 33 additive QTLs detected with the QTLNetwork program in the present study, all of them had additive and digenic effects. None of the 33 additive QTLs and five out of the 67 epistatic Qtls exhibited significant Q×T interactions. The majority of main effects were detected on chromosome 5H, and were affected primarily PH, Ns/P, KS, TKW, MSL and HI. QTLs for most of the marker main effects for different growing stages did not coincide with a QTL for yield and its component. This indicates that the loci for different growing stages have not influenced yield, which is also reflected in the low correlation between different growing stages and yield. This finding was in good agreement with Von Korff et al. (2008). In the present study we found additive QTLs for plant height on most of the chromosomes, except 4H. We also detected five pairs of epistatic QTLs for plant height without interaction with environments. The most significant additive QTL for plant height was found on 2H in the region of BPB-8737-2H-BPB-3653-2H. Close to it, QTLs for the number of kernels per spike and the length of main spike were also located. In most the cases these QTLs exhibited strong effects on the traits, hence this interval seems to be important for the analysis of genetic determination of the observed traits. Several reports have considered this 2H region as a hot-spot (Mansour et al. 2014; Wang et al. 2010b). In barley, plant height is conditioned by several dwarfing and semi-dwarfing genes (Araus et al. 2008; Kuczyñska et al. 2013).

The association between the reduced plant height (caused by sdw1/denso) and other traits, including grain yield, was recorded in numerous studies, although the results are not consistent. For example, Thomas et al. (1991) and Hellewell et al. (2000) observed decreased yield, whereas Yin et al. (1999) and Jia et al. (2011) noticed increased yield of semi-dwarf plants. However, in the present study, QTLs for yield identified on 1H (BMAG0211-1H-E41M38_206-1H) and 6H (MWG634B-6H-BPB-0597-6H) were linked to plant height QTL.

We found a QTL for plant height on chromosome 7H (BPB-1209-7H-BPB-5260-7H) which was co-located with thousand kernel weight. Wang et al. (2014) also found an important QTL for height on 7H (QPh.NaTx-7H) which consistently expressed in all of the environments and determined 23% of the phenotypic

variation. Several studies also reported QTL on 7H but this QTL was either located in different positions of the chromosome or no obvious evidence of a major gene (Yu et al. 2010). Qi et al. (1998) identified a major QTL for plant height on 7H and the position is similar to that identified in this experiment. Two additive QTLs were identified for spike length on chromosomes 2H and 5H. We also identified two pairs of epistatic QTLs on 2H and 5H without interaction with environments. Results obtained by earlier researchers have shown that loci associated with the length of spikes are placed on all the barley chromosomes (Baghizadeh et al. 2007; Wang et al. 2010a).

Six additive QTLs were found for number of grains per spike on all barley chromosomes except 4H and 7H. An epistatic QTL was also detected for number of grains per spike on chromosome 2H without interaction with environments. For grain number per plant (GP) and grain number per spike (GS), a common QTL on chromosome 2H (Wang et al. 2016) was identified. The QTLs affecting the number of grains per spike on chromosome 2H have been reported previously (Mehravaran et al. 2014; Ogrodowicz et al. 2017; Peighambari et al. 2005). QTLs for grain number per plant are also reported to be located on chromosomes 1H (Pillen et al. 2003), 2H (Baghizadeh et al. 2007; Islamovic et al. 2013), 3H and 4H (Teulat et al. 2001). Schmalenbach et al. (2009) detected eight QTL for number of grains per ear on chromosomes 1H, 2H, 3H, 4H and 7H in wild barley introgression lines. These findings have indicated that a number of grains per plant or per spike are well distributed across the barley chromosomes and hence it will be difficult to combine all QTLs in a single background through simple breeding methodology. In such cases a molecular approach combined with backcrossing may be a suitable strategy for increasing grain number.

We detected 2 additive QTLs for thousand kernel weight on chromosomes 5H and 7H. In addition, 10 pairs of epistatic QTLs for thousand kernel weight were also identified of which none of them had interaction with environment. Li et al. (2006) identified a QTL for the 1000-grain weight on chromosome 2H at Bmag0692 (which we mapped close to region B). Pillen et al. (2003) reported 12 QTLs for TGW located on four chromosomes, and three of them on 2H, whereas Ren et al. (2010) identified only two QTLs for 1000-grain weight on chromosomes 2H (Bmag0518) and 7H (GMS46). Thousand kernel weight (TKW) is one of the major yield components having a direct effect on final yield and previously reported on seven linkage groups (Baghizadeh et al. 2007; Schmalenbach et al. 2009; Wang et al. 2010a).

In the present study, we did not find any additive QTLs for grain yield, but we found nine epistatic QTLs on all of the barley chromosomes. None of them had interaction with environments. Several yield-related QTLs have been mapped to the short arm of chromosome 2H, including plant height (Karsai et al. 1997), number of seeds per spike (Kjaer et al. 1991) and number of tillers per plant (Eshghi et al. 2011). The number of QTLs associated with grain yield detected in other studies varies, depending on the studied populations and environmental conditions. Peighambari et al. (2005) found only one QTL for grain yield on chromosome 2H. However, in their study QTLs for yield components were detected also on chromosomes 1H and 5H. Three QTLs for grain yield were detected by Comadran et al. (2011). One of those was located in the centromeric region of chromosome 2H and the other two were detected on the long arm of chromosome 7H. Mansour et al. (2014) reported four QTLs for grain yield located on chromosomes 1H, 2H.1, 5H.3, and 7H. Mansour et al. (2014) found the most significant QTL for grain yield located in linkage group 5H.3, at the Vrn-H1 locus. Other studies QTLs for grain yield were identified on almost all barley chromosomes (Islamovic et al. 2013; Mansour et al. 2014; Mehravaran et al. 2014; Ogrodowicz et al. 2017; Schmalenbach et al. 2009). In conclusion, the results from the present study show that most of the detected QTLs in two diverse conditions did not have interactions with the environment. However, no additive QTLs for grain yield was detected but we found nine epistatic QTLs of which none of them had interaction with environments and the result showed that chromosome 1H was more involved than other chromosomes in this trait. The identified QTLs could be used in marker-assisted selection (MAS) and gene pyramiding to develop a drought tolerant barley with high yield.

Authors' contribution

Conceptualization of research (BAF, RA); Designing of the experiments (BAF, RA, NM, SSP); Contribution of experimental materials (BAF, RA); Execution of field/lab experiments and data collection (HB, SSP); Analysis of data and interpretation (HB, NM, BM); Preparation of manuscript (HB, BAF, BM).

Declaration

The authors declare no conflict of interest.

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