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Identification of QTLs for yield and yield components of barley under different growth conditions*

Da-wei XUE[1,2], Mei-xue ZHOU[3], Xiao-qin ZHANG[1,2], Song CHEN[2], Kang WEI[2], Fan-rong ZENG[2], Ying MAO[2], Fei-bo WU[2], Guo-ping ZHANG†‡[2]

([1]*College of Life and Environment Sciences, Hangzhou Normal University, Hangzhou 310036, China*)

([2]*Department of Agronomy, Zhejiang University, Hangzhou 310029, China*)

([3]*Tasmanian Institute of Agricultural Research, University of Tasmania, Kings Meadows, TAS 7249, Australia*)

†E-mail: zhanggp@zju.edu.cn

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Abstract: Waterlogging is a major abiotic stress limiting barley (*Hordeum vulgare* L.) yield and its stability in areas with excessive rainfall. Identification of genomic regions influencing the response of yield and its components to waterlogging stress will enhance our understanding of the genetics of waterlogging tolerance and the development of more tolerant barley cultivars. Quantitative trait loci (QTLs) for grain yield and its components were identified using 156 doubled haploid (DH) lines derived from a cross between the cultivars Yerong (waterlogging-tolerant) and Franklin (waterlogging-sensitive) grown under different conditions (waterlogged and well drained). A total of 31 QTLs were identified for the measured characters from two experiments with two growth environments. The phenotypic variation explained by individual QTLs ranged from 4.74% to 55.34%. Several major QTLs determining kernel weight (KW), grains per spike (GS), spikes per plant (SP), spike length (SL) and grain yield (GY) were detected on the same region of chromosome 2H, indicating close linkage or pleiotropy of the gene(s) controlling these traits. Some different QTLs were identified under waterlogging conditions, and thus different markers may have to be used in selecting cultivars suitable for high rainfall areas.

Key words: Barley (*Hordeum vulgare* L.), Waterlogging tolerance, Yield, Quantitative trait locus (QTL)
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1 Introduction

Barley (*Hordeum vulgare* L.) is an important cereal crop, ranking fourth in the world in terms of planted area after only wheat, rice and maize. Barley production is often influenced by abiotic stress caused, for example, by salinity, drought, frost or waterlogging. In southern China, waterlogging occurs frequently at the seedling and tillering stages, causing huge yield losses (Xiao *et al*., 2007).

Waterlogging tolerance in plants is a complex trait involving many morphological and physiological responses. The phenotypic characters associated directly with waterlogging tolerance are still unclear and controversial, although some researchers have noted that leaf chlorosis after waterlogging is associated with waterlogging tolerance (Hamachi *et al*., 1990; Wang *et al*., 1996; Zhou *et al*., 2007; Li *et al*., 2008). In recent years, there have been many investigations to determine the morphological, physiological, anatomical and metabolic responses to waterlogging in barley (Garthwaite *et al*., 2003; Pang *et al*., 2004; 2006; 2007a; 2007b; Xiao *et al*., 2005;

‡ Corresponding author

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Zhang *et al*., 2007). However, little progress has been made in mapping quantitative trait loci (QTLs) controlling waterlogging tolerance in barley (Setter and Waters, 2003). Li *et al*. (2008) identified 7 QTLs controlling waterlogging tolerance using two barley double haploid (DH) populations based on leaf chlorosis, plant survival and biomass reduction after waterlogging treatment. There have been no reports on QTL analysis of barley waterlogging tolerance based on major agronomic traits, such as plant height and yield components.

In practice, it is very difficult for breeders to control the multiple environmental factors operating in a field experiment over thousands of barley genotypes; thus selection in the natural environment is not very effective. Development of molecular markers associated with barley waterlogging tolerance could effectively avoid environmental effects. QTL analysis has proven to be very useful in identifying the genetic components of variation in important economic traits. A molecular marker closely linked to the target gene or QTL can act as a "tag" which can be used for indirect selection of the gene(s) in a breeding program (Babu *et al*., 2004). Numerous QTLs have been reported to affect plant height and yield components (Backes *et al*., 1995; Kjær and Jensen, 1996; Hori *et al*., 2003; Pillen *et al*., 2003; Sameri *et al*., 2006; von Korff *et al*., 2006; Baghizadeh *et al*., 2007), but none of them was identified under abiotic stress. To use molecular markers effectively for the selection of waterlogging tolerant barley cultivars, it is crucial to find QTLs controlling agronomic traits and yield components under waterlogged conditions.

The objectives of the current study were: (1) to identify QTLs for important characters such as plant height (PH), grains per spike (GS), spikes per plant (SP), kernel weight (KW), spike length (SL), and grain yield per plot (GY) using a barley DH population grown under different conditions; and (2) to compare QTLs identified from waterlogged trials with those identified from non-waterlogged trials.

2 Materials and methods

2.1 Plant materials

One hundred and fifty-six DH lines derived from a cross between the cultivars Yerong and Franklin were used in this study. Yerong is a waterlogging-tolerant, six-rowed feed barley, while Franklin is a waterlogging-sensitive, two-rowed malting barley (Li *et al*., 2008).

2.2 Plant growth conditions

The field experiment was conducted at the experimental farm on the Huajiachi Campus, Zhejiang University, Hangzhou, China (30°10′ N, 120°12′ E). Two experiments, Exp. 1 and Exp. 2, were conducted in the 2005–2006 and 2006–2007 barley growing seasons, respectively. The field was divided in half by making a ridge, which was encircled by plastic film to a depth of 50 cm to avoid water percolation between the two halves. The seeds of the DH lines and the two parents were sown early in November. Each plot consisted of 1 line with a length of 2 m. There was a gap of 0.25 m between plots. Fifty seeds were sown of each line. Prior to seeding, 70 kg/ha of nitrogen as urea and 180 kg/ha of potassium chloride were applied. Another 70 kg/ha of nitrogen was top-dressed at the 4-leaf stage. The experiments were laid out in a randomized complete-block design with three replications. The waterlogging treatment was imposed at the tillering stage (100 d after sowing) to one half of the field by pouring water into the plots to 2–3 cm above the soil surface and maintaining the water level by applying successive water supplements. After 12 d, the water in the waterlogged plots was drained out and the plants were allowed to grow to maturity. Normal agronomic practices were applied to the other half of the field which was used as the control.

2.3 Determination of yield and yield components

At maturity, PH, GS, SP, KW and GY were measured in Exp. 1. PH, GS, KW and SL were measured in Exp. 2.

2.4 Statistical and QTL analyses

A genetic linkage map was constructed using 496 diversity arrays technology (DArT) markers, 80 amplified fragment length polymorphism (AFLP) markers and 28 microsatellite markers (Wenzl *et al*., 2006; Li *et al*., 2008). Population distribution analysis was performed using SPSS 11.0 statistical software. QTL analysis for individual environments was performed using software QTLMAPPER 1.60, which was developed based on a mixed linear model (Wang

et al., 1999; 2003), to identify QTLs, with main effects. QTLs were determined using a threshold of $P<0.005$. A threshold of likelihood of odds (LOD) >2.5 was chosen for claiming a putative QTL. The nomenclature of McCouch *et al*. (1997) was used to describe the QTLs.

3 Results

3.1 Phenotypic variation

Table 1 shows the mean values of measured traits for the parents and the DH population. In Exp. 1, the KW of both parents was reduced by waterlogging stress while other traits were less affected. In the DH population, the mean values of nearly all the measured traits were reduced as a result of waterlogging. The biggest reduction was found for one of the yield components, SP, which was 24% lower under waterlogged conditions. Similar results were found in Exp. 2 with the waterlogging treatment, showing great effects on most of the traits measured in this experiment.

The two parents differed greatly in the traits measured in the two experiments. In general, the six-rowed barley, Yerong, had higher KW and yield, more GS, higher PH, but shorter SL and less SP than the two-rowed barley, Franklin. In the DH lines, all phenotypic traits showed a continuous normal distribution with skew values ranging from −0.52 to 0.66 (Table 1), indicating that these characters were quantitatively inherited. In addition, transgressive segregation in both directions was observed for all characters under both control and waterlogging treatments. Unlike the parents, the average KW of two-rowed DH lines was much higher than that of six-rowed DH lines, being 7.7 g higher in Exp. 1 and 13.99 g higher in Exp. 2. In Exp. 1, the average GY of two-rowed

Table 1 Phenotypic values of yield and yield components in a DH population and its two parent cultivars, Yerong and Franklin, under control and waterlogged conditions in two experiments

	Exp. 1									
	KW (mg)		GS		SP		PH (cm)		GY (g)	
	C	W	C	W	C	W	C	W	C	W
Patient										
Yerong	45.70	39.85	35.7	39.7	9.4	8.5	70.3	69.5	140.8	146.2
Franklin	34.56	33.65	15.7	14.9	14.2	14.1	66.3	69.8	29.4	27.9
DH population										
Two-row line mean	40.91	40.78	22.0	19.7	13.3	9.6	73.0	69.7	84.3	67.6
Six-row line mean	33.21	31.68	37.6	36.5	12.2	9.2	70.1	70.4	109.1	95.5
All lines										
Mean	35.8	34.8	31.9	30.4	12.6	9.3	71.1	70.1	99.5	85.9
Range	16.0–57.4	20.3–59.7	13.6–57.7	5.9–59.9	3.8–22.4	1.5–15.3	58.0–90.8	61.1–76.6	26.0–220.1	7.2–204.0
Skewness	0.45	0.58	0.25	0.39	0.42	0.05	0.26	−0.52	0.42	0.52

	Exp. 2							
	KW (mg)		GS		SL (cm)		PH (cm)	
	C	W	C	W	C	W	C	W
Patient								
Yerong	53.58	49.05	46.3	43.0	7.1	6.4	112	92
Franklin	36.49	33.61	25.6	24.3	9.1	7.7	109	81
DH population								
Two-row line mean	49.21	47.97	24.5	23.2	8.1	7.5	100	82
Six-row line mean	35.22	34.55	40.7	36.8	6.9	5.9	101	77
All lines								
Mean	40.5	40.0	34.8	31.6	7.4	6.6	100.8	78.8
Range	25.9–68.1	22.0–64.6	15.3–57.0	16.8–54.4	3.9–11.4	3.1–11.6	84–120	57–99
Skewness	0.66	0.39	0.26	0.45	0.48	0.61	0.04	−0.13

KW: kernel weight; GS: grains per spike; SP: spikes per plant; PH: plant height; SL: spike length; GY: grain yield; C: control; W: waterlogging

DH lines showed greater reduction (24.7%) due to waterlogging than that of six-rowed DH lines (14.2%) (Table 1).

3.2 QTL analysis

A total of 32 QTLs were identified for the measured characters from the two years and the two growth environments. Some of the QTLs identified from different environments were at the same position (Table 2). QTLs were mapped on all seven chromosomes with the majority being on 2H (Fig. 1). In the genetic map of this population, 1H and 2H were each separated into two groups with the gap between the two groups being more than 20 cM.

The QTLs controlling KW were located on chromosome 2H. In Exp. 1, only one QTL was found on chromosome 2H in the control trial, and only 6.54% of the phenotypic variation was determined by this QTL. Under waterlogged conditions, two QTLs were identified. One of them was in a similar position to that found in the control trial and another one showed greater effect. Similar QTLs were found in-Exp. 2. One more minor QTL was found on chromosome 6H (Table 2 and Fig. 1). For all the QTLs, the alleles from Franklin increased KW.

The QTLs controlling GS were located mainly on chromosome 2H with Yerong alleles contributing to more grains. Some minor QTLs were also identified

Table 2 QTLs for agronomic traits detected in a DH population derived from Yerong×Franklin and grown in different environments

Traits	QTL[a]	Chr.[b]	Marker interval	LOD[c]	Add.[d]	R^2 (%)[e]
Exp. 1-control						
Kernel weight	KWc1.1	2H	bPb-6088-bPb-5440	2.79	−1.92	6.54
Grains per spike	GSc1.1	2H	bPb-9754-bPb-3653	13.22	7.71	50.86
	GSc1.2	7H	bPb-9601-bPb-9898	6.17	2.84	6.91
Spikes per plant	SPc1.1	2H	bPb-7124-bPb-9258	5.31	−1.04	10.91
	SPc1.2	6H	bPb-1009-bPb-7323	5.12	−1.02	10.49
Plant height	PHc1.1	1H	bPb-9108-bPb-3992	2.91	1.37	5.61
	PHc1.2	2H	bPb-6881-bPb-3056	6.47	−2.04	12.40
Grain yield	GYc1.1	2H	bPb-4040-bPb-6088	6.94	15.52	15.94
Exp. 1-waterlogging						
Kernel weight	KWw1.1	2H	bPb-4040-bPb-6088	4.48	−2.13	6.82
	KWw1.2	2H	bPb-1772-bPb-8737	7.34	−3.31	16.59
Grains per spike	GSw1.1	2H	Bmac0093-bPb-4040	11.53	7.20	35.35
	GSw1.2	2H	bPb-1772-bPb-8737	6.29	4.22	12.18
	GSw1.3	7H	bPb-9601-bPb-9898	7.35	3.64	9.06
Spikes per plant	SPw1.1	7H	bPb-0182-bPb-3484	3.31	−0.65	8.13
Plant height	–	–	–	–	–	–
Grain yield	GYw1.1	2H	bPb-6088-bPb-5440	2.85	8.90	4.74
	GYw1.2	7H	Ebmac0603-bPb-9601	7.45	22.53	30.43
Exp. 2-control						
Kernel weight	KWc2.1	2H	bPb-6088-bPb-5440	11.56	−3.78	17.77
	KWc2.2	6H	Bmag0500-bPb-3202	4.46	−5.85	6.00
Grains per spike	GSc2.1	2H	bPb-6088-bPb-5440	4.09	3.20	9.40
	GSc2.2	2H	bPb-1772-bPb-8737	7.22	4.56	19.13
Spike length	SLc2.1	2H	bPb-6088-bPb-5440	7.76	−0.45	12.97
	SLc2.2	2H	HVM54-bPb-1103	7.05	0.41	10.97
	SLc2.3	4H	bPb-8164-bPb-9859	3.64	−0.29	5.50
Plant height	–	–	–	–	–	–
Exp. 2-waterlogging						
Kernel weight	KWw2.1	2H	bPb-6088-bPb-5440	9.10	−4.56	27.35
	KWw2.2	2H	bPb-1772-bPb-8737	3.94	−2.26	6.78
Grains per spike	GSw2.1	2H	Bmac0093-bPb-4040	5.63	7.15	55.34
	GSw2.2	2H	bPb-1772-bPb-8737	4.76	2.76	8.22
	GSw2.3	5H	bPb-2425-bPb-9476	6.18	−3.04	10.02
Spike length	SLw2.1	2H	bPb-6088-bPb-5440	11.16	−0.53	17.44
	SLw2.2	2H	bPb-2481-bPb-8274	8.74	−0.46	13.05
	SLw2.3	3H	bPb-1681-bPb-6722	7.74	−0.48	14.37
Plant height	PHw2.1	6H	bPb-9082-bPb-9835	5.52	2.63	9.74

[a] Individual QTLs are designated with the abbreviation of the trait, treatment, experiment number and QTL number; [b] Chromosome number; [c] Maximum-likelihood LOD score for the QTL calculated by QTLMAPPER 1.60; [d] Additive effect. The positive or negative value indicates that allele from Yerong or Franklin increases the trait score, respectively; [e] Variation explained by the putative QTL

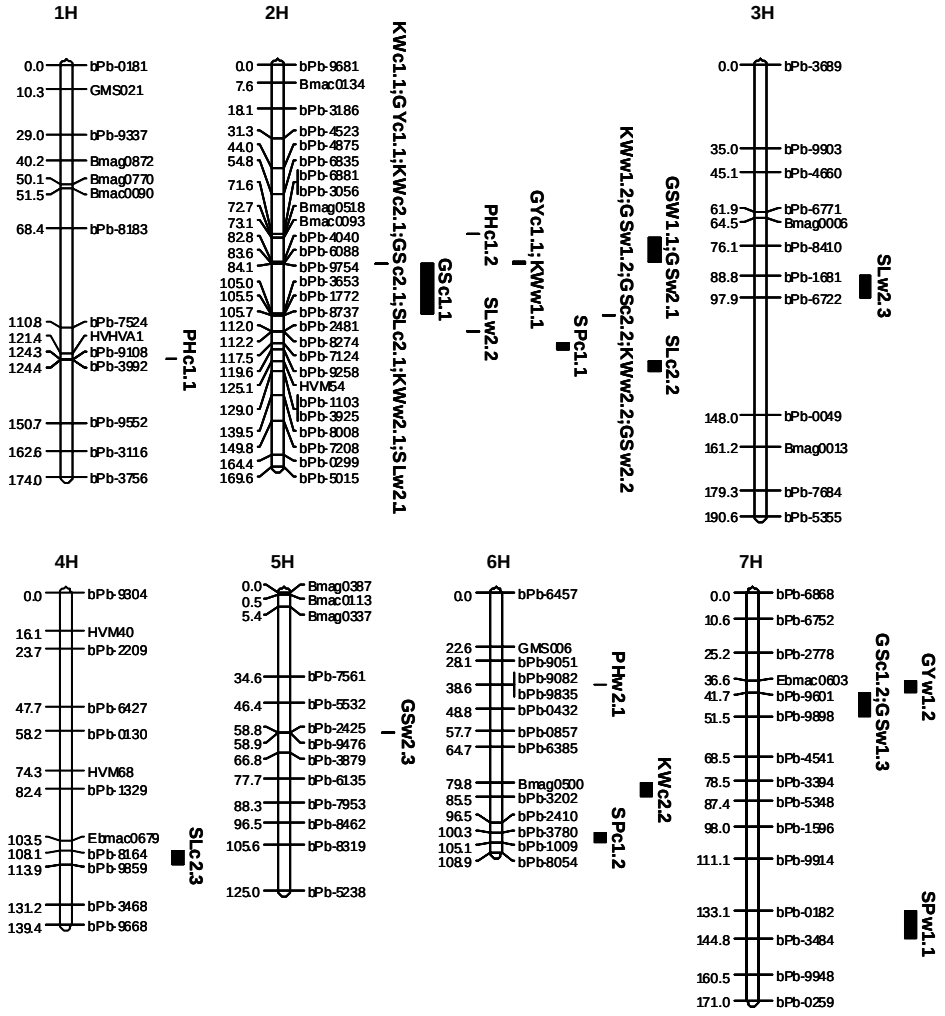

Fig. 1 QTLs identified for different traits in the DH population derived from Yerong×Franklin. Only SSR markers and a few DArT markers (prefix bPb-) are shown in the map. For detailed map, please refer to Li *et al*. (2008)

from different experiments, all determining less than 10% of the genetic variation. In both the control and waterlogged conditions of Exp. 1, a minor QTL was located on chromosome 7H with the Franklin allele also contributing a positive effect. The minor QTL identified in the waterlogged trial of Exp. 2 was located on chromosome 5H and the Franklin allele contributed a negative effect.

Some QTLs were identified for SP from different growth conditions in Exp. 1. Under the control conditions, two QTLs for this trait were located on chromosomes 2H and 6H, respectively, while under waterlogged conditions, only one QTL was found, located on chromosome 7H. For all the QTLs identified, the Franklin allele contributed a negative effect, reducing the number of SP.

SL was measured only in Exp. 2. Three QTLs were found for this trait in both the control and waterlogged trials. Of the two QTLs on chromosome 2H, one was in the same position (84 cM) in both treatments. The other was at 140 cM in the control, with the Yerong allele being positive, and at a slightly different position (124 cM) under waterlogging, with the Yerong allele being negative. The third QTL was located on chromosome 4H with the Franklin allele being negative in the control and on chromosome 3H with the Yerong allele being negative under waterlogged conditions.

There was no obvious difference in PH between the two parents. No QTL was identified in Exp. 1 under waterlogging or in Exp. 2 in the control environment. In the control treatment of Exp. 1, two QTLs

were found for PH. One was located on chromosome 1H at the interval of bPb-9108-bPb-3992 and one in chromosome 2H flanked by bPb-6881-bPb-3056. Under the waterlogging treatment in Exp. 2, the QTL on chromosome 6H was located between the two markers bPb-9082 and bPb-9835.

For GY, one QTL on chromosome 2H was identified in both the control and waterlogging treatments in Exp. 1. Another QTL on chromosome 7H was identified for GY under waterlogged conditions, which determined 15% of yield variation.

4 Discussion

The two parents differed considerably in most measured characters when grown in the different environments. The mean values of the population were close to the mid-parental values for all characters in both experiments (Table 1). Although the phenotypic distributions of the DH population were normal, transgressive segregation was observed in both directions for all characters, indicating that neither of the parents carried all the positive or all the negative alleles. The significant variation and the normal distribution of all characters measured in this study suggest the suitability of this population for QTL analysis.

In the past decade, with the development of molecular marker technologies, QTL analysis has been widely used to detect yield and related characters and a great number of QTLs have been mapped on all 7 chromosomes of barley using different genetic populations (Hayes *et al*., 1993; Backes *et al*., 1995; Thomas *et al*., 1995; Kjær and Jensen, 1996; Tinker *et al*., 1996; Bezant *et al*., 1997; Powell *et al*., 1997; Mather *et al*., 1997; Yin *et al*., 1999; Zhu *et al*., 1999; Marquez-Cedillo *et al*., 2001; Baum *et al*., 2003; Pillen *et al*., 2003; Li *et al*., 2005; 2006; Sameri *et al*., 2006). However, no QTLs for agronomic traits and yield components have been mapped in barley under waterlogging stress to dissect the genetic mechanism of waterlogging tolerance. In the present study, many QTLs were identified for some important agronomic traits and yield components under different growing conditions, i.e., normal and waterlogged. The majority of the QTLs were on chromosome 2H (Fig. 1) in the region where the gene controlling row-type is located (Li *et al*., 2008). Not surprisingly, the QTLs controlling GS and KW were co-located with the QTL for row-type, with the six-rowed barley cultivar Yerong contributing a positive effect for GS and the two-rowed barley cultivar Franklin contributing a positive effect on KW. Some QTLs controlled more than one trait. The QTL located on chromosome 2H at the position of around 84 cM was responsible for KW, GS, SL and GY. The results indicated that QTLs in the same region of a chromosome controlling different traits could be closely linked or pleiotropic. One or more QTLs were also found on the rest of the chromosomes including one on 3H and one on 4H for SL, one on 5H for GS, two on 6H for SP and KW, respectively, and four on 7H for GS, SP and GY, respectively.

Barley shows wide genetic diversity for waterlogging tolerance (Takeda and Fukuyama, 1986; Qiu and Ke, 1991; Fufa and Assefa, 1995; Setter *et al*., 1999; Pang *et al*., 2004; 2006; 2007a; 2007b; Zhou *et al*., 2007; Li *et al*., 2008). The identification of QTL for yield and related characters under waterlogging stress will be of great interest to plant breeders in developing barley cultivars with waterlogging tolerance. In this study, some QTLs were found to be affected by the growth conditions. The QTL for GS on chromosome 7H was found only in Exp. 1. A QTL for GS on chromosome 5H was found only under waterlogged conditions in Exp. 2. For PH, two QTLs were identified in the control treatment of Exp. 1, while under waterlogged conditions, the differences in PH between different DH lines were very small (Table 1) and no QTLs were identified. In contrast, a QTL for PH was found under waterlogging but not in the control. For SP, two QTLs on chromosomes 2H and 6H, respectively, were found in the control treatment while only one on chromosome 7H was found under waterlogged conditions.

The use of marker assisted selection (MAS) in combination with traditional field selection could significantly enhance barley breeding for waterlogging tolerance. However, as shown in this experiment, some different markers should be used for selecting cultivars which have superior agronomic traits and yield components when grown in high rainfall areas. As the genetics and expression of the characters related to waterlogging tolerance are quite complex, more studies are need involving more populations and environments.

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