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ORIGINAL PAPER

A new semi-dwarfing gene identified by molecular mapping of quantitative trait loci in barley

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Abstract Semi-dwarfing genes have been widely used in spring barley (*Hordeum vulgare* L.) breeding programs in many parts of the world, but the success in developing barley cultivars with semi-dwarfing genes has been limited in North America. Exploiting new semi-dwarfing genes may help in solving this dilemma. A recombinant inbred line population was developed by crossing ZAU 7, a semi-dwarf cultivar from China, to ND16092, a tall breeding line from North Dakota. To identify quantitative trait loci (QTL) controlling plant height, a linkage map comprised of 111 molecular markers was constructed. Simple interval mapping was performed for each of the eight environments. A consistent QTL for plant height was found on chromosome 7HL. This QTL is not associated with maturity and rachis internode length. We suggest the provisional name *Qph-7H* for this QTL. *Qph-7H* from ZAU 7 reduced plant height to about 3/4 of normal; thus, *Qph-7H* is considered a semi-dwarfing gene. Other QTLs for plant height were found, but their expression was variable across the eight environments tested.

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Introduction

Lodging resistance is a trait that helps in defining the adaptability of a cultivar. Lodging reduces not only barley yield and grain quality, but also indirectly affects malt quality (Day and Dickson 1958). Grain from lodged plants is often lighter in weight and lower in malt extract. In the Midwest, where a large proportion of the USA malting barley is grown, storms and excess rainfall can cause severe lodging problems.

Short-stature cultivars have been developed by cereal breeders worldwide to reduce lodging and increase grain yield. In the USA, the effort to develop short-stature genotypes has relied in part on the *sdw* gene, since the 1970s. However, the cultivars with this gene have not been widely accepted (Hellewell et al. 2000) and no cultivar with a semi-dwarfing gene has been recommended by the American Malting Barley Association, Inc. (Milwaukee, WI) as a malting barley cultivar in the USA. The reason for the poor acceptance of semi-dwarfs in six-rowed malting barley is the associations of the *sdw* gene with inferior malting quality traits, such as low test weight and percentage of plump kernels, and low yield (Foster and Thompson 1987; Rasmusson and Phillips 1997).

Plant height in barley appears to be controlled by many genes, including dwarfing, semi-dwarfing, and other plant height genes. Because dwarfing genes depress vigor and grain yield, they are not useful in breeding programs. Semi-dwarfing genes are useful and more common than dwarfing

genes (Mickelson and Rasmusson 1994; Zhang 2003). The principal semi-dwarfing genes used in barley improvement are semi-brachytic 1 (*uzu1*) (Tsuchiya 1972), semi-dwarf 1 (*sdw1*or *denso*) (Haahr and von Wettstein 1976), breviaristatum-e (*ari-e*) (Thomas et al. 1984), and short culm 1 (*hcm1*) (Swenson and Wells 1944).

The *uzu1* gene is located on the long arm of chromosome 3H (3HL) close to the centromere (Tsuchiya 1972) and it has been widely used in East Asia. The *sdw1* locus is also located on chromosome 3HL, but more distal from the centromere than *uzu1* (Barua et al. 1993). Three alleles at the *sdw1* locus [*sdw1.a* (Jotun), *sdw1.c* (*denso*), and *sdw1.d* (Diamant)] delay heading; yet, they have been used to reduce plant height in many semi-dwarf cultivars (Hellewell et al. 2000). The *sdw1* alleles have been successfully used in cultivar development in Europe (Hellewell et al. 2000), but they have not been incorporated into malting barley cultivars in the USA. The *ari-e* mutant in 'Golden Promise' has been used in several European cultivars and is located on chromosome 5HL (Thomas et al. 1984). The short culm1 gene (*hcm1*) has a similar effect on barley plant height as a semi-dwarfing gene, but it is not considered a true semi-dwarfing gene. The *hcm1* locus is reported to be located on chromosome 2HL near the centromere (Neatby 1929) and it is probably the only gene used to reduce plant height in six-rowed barley cultivars developed for the Upper Midwest of the USA (Franckowiak 2000). Additional semi-dwarfing genes have recently been found in landraces and cultivars, but they have not been localized in the genome yet (Mickelson and Rasmusson 1994; Zhang 2003).

The objective of this study was to identify and map quantitative trait loci (QTL) controlling plant height in the Chinese cultivar ZAU 7.

Materials and methods

Plant materials and trait evaluation

A recombinant inbred line (RIL) population was developed from a cross between ZAU 7 and ND16092. ZAU 7, released in 1997 by Zhejiang University, Hangzhou (China), is a short (short internodes, peduncle and dense spike), early maturing cultivar (http://www.seedsinfo.cn/PzJsMx.asp?ID=281). ND16092, selected from the cross ND13297/ND14701, is a tall, mid-maturing breeding line developed as a malting barley by the North Dakota State University two-rowed barley breeding program. The scheme for the development of the population and phenotyping of 160 lines is presented in Fig. 1. Phenotyping for heading date and plant height was done in the $F_{4:5}$ generation during the 2002–2003 winter in Hangzhou (China); in the $F_{4:6}$ generation during the 2003 summer at Casselton, Fargo, and Langdon, ND (USA); in the $F_{5:6}$ generation during the 2003 summer at Sidney, MT (USA) and during the 2003–2004 winter at Hangzhou (China); in the $F_{5:7}$ generation during the 2004 summer at Osnabrock, ND (USA); and in the $F_{7:8}$ generation during the 2004 summer at Sidney, MT (USA). Rachis internode length was phenotyped in the $F_{7:8}$ generation during the 2005–2006 winter at Leeston (New Zealand).

Trial design was a randomized complete block design (RCBD) with two replicates except Hangzhou 2003, where it was a repeated augmented block design (ABD). Experimental units in the nurseries at Langdon, Osnabrock, and Hangzhou were hill plots spaced about 30-cm apart. Experimental units for the other sites were single 3-m rows spaced 30-cm apart. Plant height data (distance from soil surface to the tip of spikes, excluding awns), heading date (from sowing) and rachis internode length (average length over 10 adjacent rachis internodes) were recorded for individual hills or rows in the field experiments.

Molecular marker analysis

Ninety-three lines were selected at random for molecular marker analysis. Ten seeds ($F_{6:7}$) harvested from a single plant in each row at Sidney in 2003 were sown in pots in the greenhouse. Clean leaf tissue for DNA extraction was collected from all plants in each pot 25 days after sowing. The DNA extraction was conducted using the standard protocol of the MIDI method (Kleinhofs et al. 1993).

Simple sequence repeat (SSR) technology was used to identify differences between parental cultivars and to characterize the progeny. Parental and progeny DNA were screened for polymorphisms using polymerase chain reaction (PCR) methodology and published SSR sequences purchased from Integrated DNA Technologies (Coralville, IA) and from the Scottish Crop Research Institute (Ramsay et al. 2000). Simple sequence repeat primers that identified polymorphisms between parents were then employed for genotyping the entire mapping population. The PCR for the SSR analysis was done in a 10-µl reaction mixture containing 50 ng of template DNA, 0.3 µM of each primer, 200 µM of each dNTP, 2.5 mM of $MgCl_2$, 0.8 unit of *Taq* DNA polymerase, and 1× *Taq* buffer supplied with the enzyme using standard programs designed for different profiled SSR primer pairs. The buffer in the lower reservoir of the electrophoresis apparatus was mixed with ethidium bromide (Promega Corp.; Madison, WI) for visualization and PCR products were separated on 4–8% non-denaturing gels (Cambrex; East Rutherford, NJ). When target bands reached approximately the middle of the gel, the gel was scanned to obtain a photo.

Diversity Array Technology (DArT) markers (Wenzl et al. 2004) were also used in this study. The DArT marker analysis was conducted by Diversity Array Technology Ltd. (Canberra, Australia).

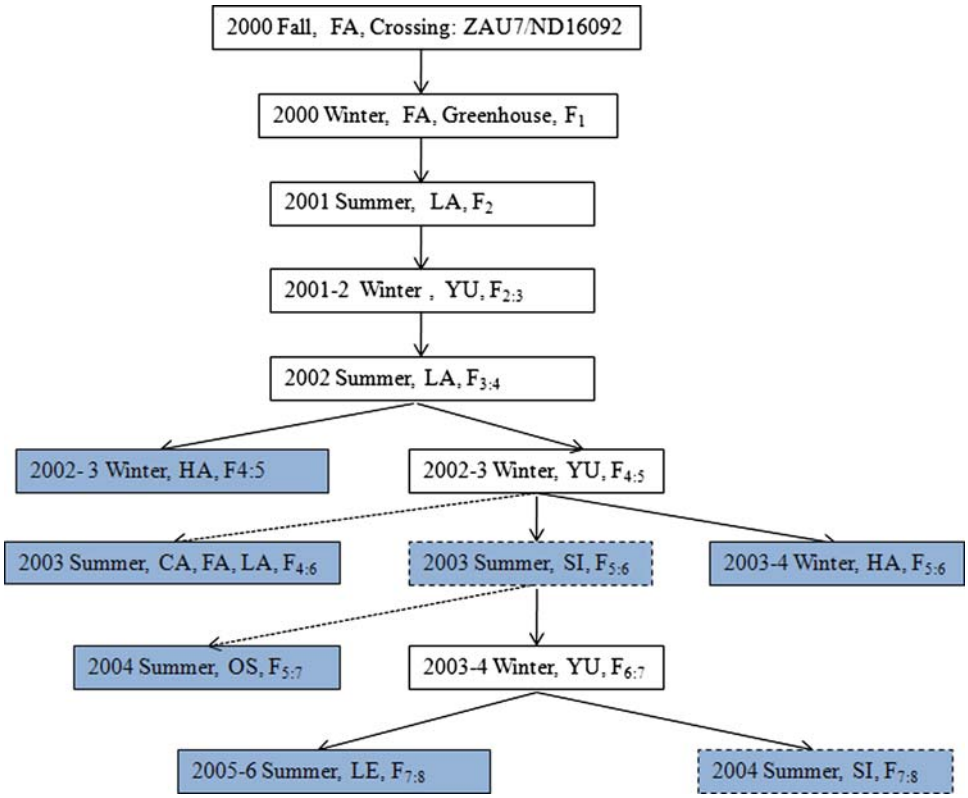

Fig. 1 Scheme for development of the population and phenotyping of 160 lines. **a** A *solid line* indicates the generation advance. **b** A *gray-colored box* indicates the environments for only phenotyping. **c**. A *gray-colored* and *dashed box* indicates the environments for both generation advance and phenotyping. **d**. A *solid arrow* indicates the seed from a single randomly selected plant. **e**. A *dashed arrow* indicates the seed from a bulked family. Environment locations: *CA* Casselton, *ND* (USA), *FA* Fargo ND (USA), *LA* Langdon, ND (USA), *OS* Osnabrock, ND (USA), *SI* Sidney, MT (USA), *HA* Hangzhou (China), *LE* Leeston (New Zealand)

Statistical and map analysis

All statistical analyses were done using PC-SAS (Cary, NC). Phenotypic data for parents and lines in the population from most environments were analyzed using a RCBD design. For Hangzhou 2003, the data were analyzed as a repeated ABD. Adjusted means were calculated for each entry in the repeated ABD, and these means were used to perform the analysis of variance across experiments as an RCBD. Within a year, each experiment at the location was considered a replicate. Standard deviations were calculated from the ANOVA. The *t* test ($P \leq 0.05$) was used for mean separation of parents.

The skeletal genetic linkage map was constructed with Map Manager QTXb20 (Manly et al. 2001) using an LOD score of 3 (de la Pena et al. 1999; Zhu et al. 1999; Ma et al. 2000). Recombination values were converted to centimorgans using the Kosambi (1944) function. Assignment of markers to a chromosome and marker selection for the skeletal map was based on the common markers with those on published maps, primarily the DArT map for the Steptoe/Morex population of 94 doubled haploid lines (Wenzl et al. 2004) and the SSR map of Ramsay et al. (2000).

The computer program MQTL (Tinker and Mather 1995) was used to detect both QTL main effects and QTL × environment interactions. In this program, the test statistic (TS) is defined as $TS = n \times \ln (SS_{reduced}/SS_{full})$, where n is the number of individuals, and $SS_{reduced}/SS_{full}$ are the residual sum of squares for the reduced (model without the effect being tested model) and full models, respectively. Simple interval mapping (SIM) was conducted in this study. Because QTL × environment interactions were significant for all traits, QTL analyses were done for each individual environment. All QTL analyses were done in 1 cM steps. The type-I error rate was set at 5%. Thresholds for the type-I error rate of 5% were calculated at 5,000 iterations for the whole genome. The percentage of variation for a single QTL was calculated using the following formula $R^2 = 100[1-1/(\exp(TS/n)]$ (Tinker and Mather 1995).

It needs to be pointed out that phenotyping was done using seed from several generations, whereas genotyping was done using leaf tissue obtained from several plants from each $F_{6:7}$ family. The marker genotyping identified the families as nearly homozygous; however, it is possible that a small number of the families phenotyped from the earlier generations may have been segregating for the QTL. Nonetheless, this would have minimal to no affect on the results obtained.

Results

Trait characterization

Means, ranges and standard deviations for plant height, heading date, and rachis internode length of parents and the

Table 1 Means, ranges, and standard deviations (SD) for plant height (PH), heading date (HD), and rachis internode (RI) length of the parents and 93 recombinant inbred lines in various environments

Trait	Environments[a]	Parents		Recombinant inbred lines		
		ZAU 7	ND16092	Mean	Range	SD
PH (cm)	2003CA	46.1a[b]	68.3b	58.7	30.0−84.0	4.7
	2002-3HA	84.5a	99.3b	96.6	60.6–126.4	3.9
	2003FA	62.8a	92.9b	79.5	46.7–105.7	4.1
	2003LA	66.3a	97.1b	80.8	46.7–113.7	4.5
	2003SI	60.4a	95.6b	79.6	45.0–102.0	3.1
	2003-4HA	86.8a	114.8b	104.6	56.0–136.5	4.7
	2004OS	65.5a	89.1b	78.6	45.0–106.0	6.7
	2004SI	61.6a	88.3b	76.2	41.5–103.0	3.0
HD (number of the days after sowing to heading)	2003CA	38.5a	48.0b	45.5	34.5–58.5	1.8
	2002-3HA	130.8a	135.5b	135.7	118.4–149.5	1.8
	2003FA	50.5a	60.7b	57.0	47.0–66.0	1.2
	2003LA	56.6a	63.8b	62.1	52.7–73.7	1.4
	2003SI	49.1a	53.8b	52.6	47.0–64.5	0.9
	2003-4HA	125.1a	133.8b	129.9	106.0–144.0	2.1
	2004OS	60.2a	70.5b	66.8	55.5–78.0	2.7
	2004SI	50.4a	55.4b	52.7	48.0–58.5	1.0
RI (mm)	2005-6LE	3.3a	4.5b	4.0	2.5–5.2	0.23

[a] Environment locations: *2003CA* Casselton, ND (USA) in 2003, *2002-3HA* Hangzhou (China) in 2002–2003, *2003FA* Fargo, ND (USA) in 2003, *2003LA* Langdon, ND (USA) in 2003, *2003SI* Sidney, MT (USA) in 2003, *2003-4HA* Hangzhou (China) in 2004, *2004OS* Osnabrock, ND (USA) in 2004, and *2004SI* Sidney, MT (USA) in 2004, *2005-6LE* Leeston (New Zealand) in 2005–2006

[b] Means of parents within an environment followed by the same letter are not significantly different at $P \leq 0.05$ as determined by a *t* test

population from each environment are presented in Table 1. ZAU 7 was significantly shorter than ND16092 in all eight environments. Averaged across all environments, plant height of ZAU 7 and ND16092 were 66.8 and 93.2 cm, respectively. Mean plant height of the population across environments was 81.8 cm and standard deviations for the population ranged from 3.0 to 6.7. The plant height distribution is shown in Fig. 2.

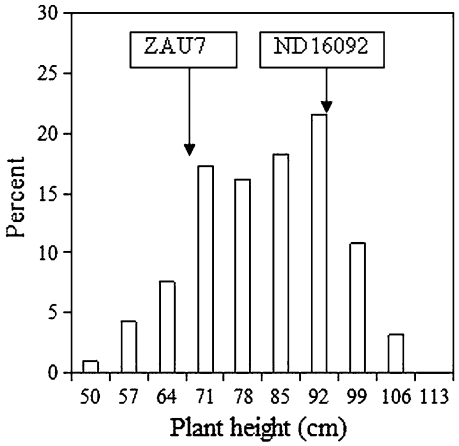

Fig. 2 Frequency distribution for mean plant heights of 93 recombinant inbred lines from the cross of ZAU 7/ND16092 over eight environments in the USA and China

Linkage map

A total of 455 molecular markers, including 428 DArT and 27 SSR markers, identified polymorphisms between ZAU 7 and ND16092. Because many markers co-segregated or were very closely linked, they did not provide much additional information. These markers were dropped from the analysis. A total of 111 markers were used to generate the linkage map (Fig. 3). This map is composed of 101 DArT markers and 10 SSR markers. The total map distance was 1,157.5 cM with two-locus intervals ranging from 3.8 to 41.9 cM. The average distance of two-locus intervals was 10.4 cM.

QTL for plant height

For convenience, plant height, heading date, and rachis internode length QTLs are simply designated with the acronym PH, HD, and RI, respectively, followed by a sequential number from chromosome 1H to 7H and from the top of the short arm to the bottom of the long arm of a chromosome. The order of discussion of the QTL is based on the number of environments where the QTL was detected. The QTLs detected in the most environments are discussed first.

A total of seven putative QTLs for plant height, designated PH-1 to PH-7, were found in the ZAU7/ND16092

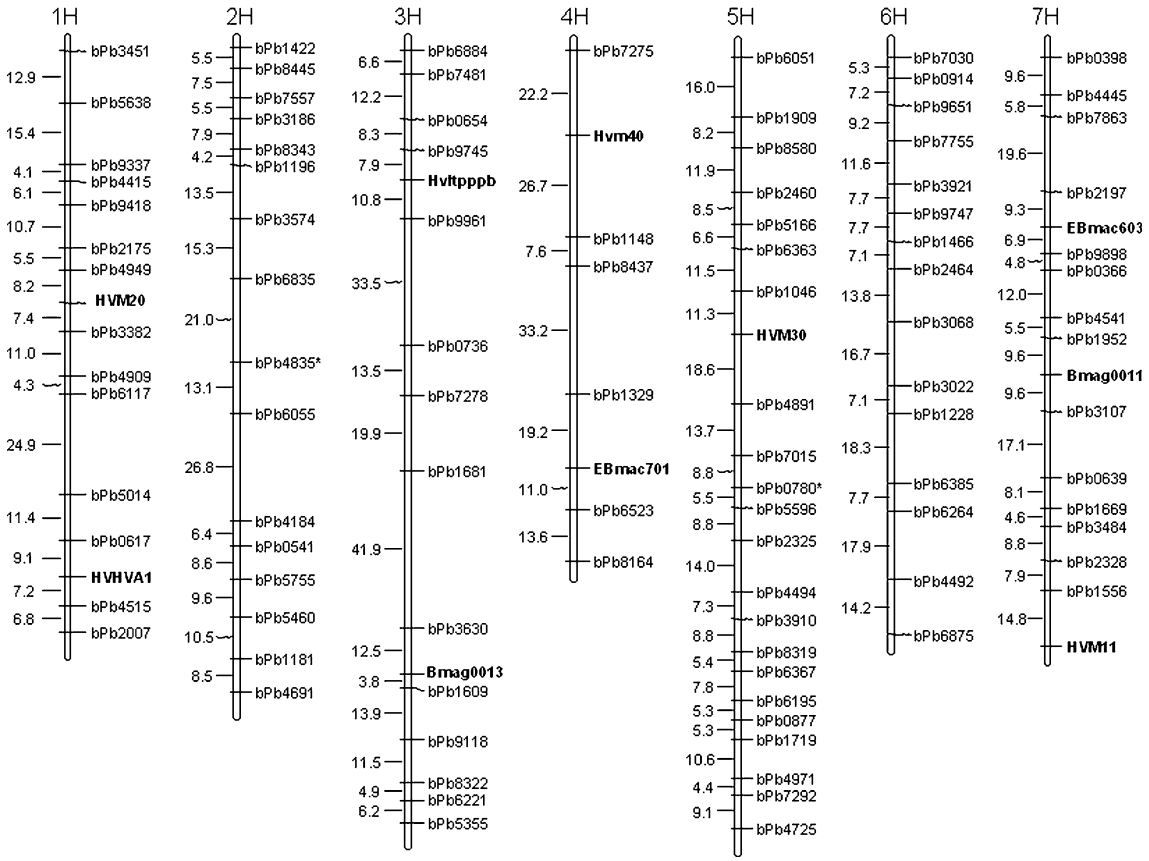

Fig. 3 The linkage map generated for the ZAU 7/ND16092 recombinant inbred line population ($F_{6:7}$). Markers in *bold font* are SSR markers. New DArT markers mapped in this population are *highlighted* with the *symbol**

population in the eight environments. QTLs were distributed across all chromosomes except 1H, 3H and 4H (Table 2). The number of environments where a putative QTL was detected varied from 2 to 8. The percentage of the phenotypic variation explained by each QTL ranged from 13 to 46% for a single locus. Significant interactions among the QTLs for plant height were not found.

QTL PH-7 was identified in all eight environments and it explained a phenotypic variation from 30 to 46%. This was larger than any other QTL for plant height over the eight environments. The allele from ZAU 7 at this locus reduced plant height. In the eight environments, coefficients of the additive effect for PH-7 ranged from −14.6 to −22.1. The QTL PH-7 is located between markers bPb1669 and Hvm11 in chromosome 7HL. The peak was flanked by markers bPb2328 and bPb1556 and was close to the end of the long arm. The closest marker to the TS peak was bPb2328 in all eight environments, which was 1–5 cM proximal from the peak.

Because PH-7 was associated with the largest effect on plant height, a frequency distribution analysis was conducted for the RIL population, with each of the alleles of bPb2328, the marker closest to the QTL. The frequency distribution for plant height of lines with the maternal and paternal alleles at bPb2328 appeared normal, but the means were different (Fig. 4). This indicates that PH-7 is the primary factor controlling variation in plant height in the ZAU 7/ND16092 population. The difference between ZAU 7 and ND16092 alleles (Fig. 4) is about 20 cm, which is consistent with the results of the SIM QTL analysis where the coefficient of additive effects was about a 20-cm change in plant height for two-allele replacement (Table 2). Because the peak of taller plants is located around 90 cm, PH-7 reduced plant height by approximately 25%.

The QTL PH-1 was detected in the six North Dakota and Montana environments where the population was tested. PH-1 was located between markers bPb1196 and bPb6835 in chromosome 2HS, with a peak near bPb3754. In the six environments, the phenotypic variation explained by this QTL ranged from 13 to 18%. The allele from ZAU 7 at this locus reduced plant height. In the individual location analyses, coefficients for the additive effect of the QTL PH-1 varied from −9.8 to −15.0.

The QTL PH-2 was identified in five out of six environments in North Dakota and Montana. The QTL was located between markers bPb4184 and bPb4691 in chromosome

Table 2 Significant QTL for plant height (PH), heading date (HD), and rachis internode (RI) length found by simple interval mapping using recombinant inbred lines of the ZAU7/ND16092 cross

QTL	Chr	Interval	CMP	2003CA		2002-3HA		2003FA		2003LA		2003SI		2003-4HA		2004OS		2004SI		2005-6LE	
				R^2 (%)	A	R^2 (%)	A	R^2 %	A	R^2 (%)	A	R^2 (%)	A	R^2 (%)	A	R^2 (%)	A	R^2 (%)	A	R^2 (%)	A
Plant height (cm)																					
PH-1	2H	BPb1196–bPb6835	BPb3574	13	−9.8			17	−13.7	14	−13.0	14	−13.0			18	−15.0	13	−13.0		
PH-2	2H	BPb4184–bPb4691	BPb5460	19	−11.6			21	−13.4	25	−16.3	23	−15.5					25	−16.9		
PH-3	5H	BPb5596–bPb8319	BPb4494			18	−16.1	18	−13.0			14	−12.1	24	−16.9	17	−15.2				
PH-4	6H	bPb0914–bPb9747	bPb9651					19	−12.9			16	−12.0			14	−11.8	15	−11.9		
PH-5	6H	bPb1228–bPb4492	bPb6264					16	−11.8			16	−12.6			22	−15.3	21	−14.4		
PH-6	7H	bPb4541–bPb3107	Bmag11			13	−12.6							17	−16.0						
PH-7	7H	bPb1669–Hvm11	bPb2328	32	−14.6	30	−19.3	42	−19.3	38	−19.2	46	−21.3	35	−22.1	41	−20.6	42	−21.0		
Multi-locus				57		41		66		63		68		51		57		66			
Heading date (number of the days after sowing to heading)																					
HD-1	1H	bPb0617–bPb4515	Hvhva1			15	6.8							15	7.3						
HD-2	2H	bPb7557–bPb6835	bPb1196	38	−8.6			36	−6.7	41	−7.1	43	−6.6			35	−7.6	33	−3.4		
HD-3	5H	bPb0780–bPb8319	bPb4494			35	−12.4							42	−13.5						
Multi-locus				38		39		36		41		43		51		35		33			
Rachis internode length (mm)																					
RI-1	2H	bPb6055–bPb4691	bPb5755																	66	−1.3
RI-2	3H	bPb3630–bPb9118	Bmag013																	17	−0.6
Multi-locus																				67	

Chr chromosome, *CMP* the closer marker to a peak, Environment locations: *2003CA* Casselton, ND (USA) in 2003, *2002-3HA* Hangzhou (China) in 2002–2003, *2003FA* Fargo, ND (USA) in 2003, *2003LA* Langdon, ND (USA) in 2003, *2003SI* Sidney, MT (USA) in 2003, *2003-4HA* Hangzhou (China) in 2004, *2004OS* Osnabrock, ND (USA) in 2004, and *2004SI* Sidney, MT (USA) in 2004, *2005-6LE* Leeston (New Zealand) in 2005–2006, *A* additive effect of two ZAU 7 alleles

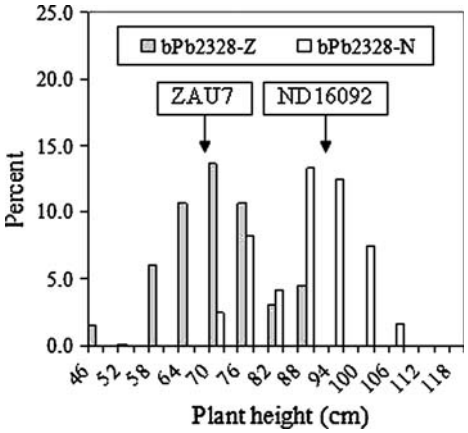

Fig. 4 The frequency distribution for plant height (cm) of lines with ZAU 7 (*Z*) and ND16092 (*N*) alleles at marker bPb2328 based on the means over eight environments

2HL, with a peak near bPb5460 and close to the tip of the long arm. The closer marker to the TS peak was bPb5460. In the five environments where the QTL was detected, PH-2 explained from 19 to 25% of the phenotypic variation. The allele from ZAU 7 reduced plant height. Coefficients of the additive effect for PH-2 ranged from −11.6 to −16.9.

The QTL PH-3 was identified in five out of eight environments, two in China and three in the USA. The QTL was located between markers bPb5596 and bPb8319 on chromosome 5HL, with the TS peak near bPb4494. In the five environments, where the QTL was detected, the phenotypic variation explained ranged from 14 to 24%. The allele from ZAU 7 reduced plant height. Coefficients of the additive effect for PH-3 varied from −12.1 to −16.9 in the analyses of the five environments where the QTL was detected.

The QTL PH-4 was detected in four of eight environments in the USA. The QTL PH-4 mapped between the markers bPb0914 and bPb9747 on chromosome 6HS, with the TS peak near bPb9651. The QTL PH-4 explained from 14 to 19% of the phenotypic variation where the QTLs were detected. The alleles from ZAU 7 at these loci reduced plant height. Coefficients of the additive effect for PH-4 ranged from −11.8 to −12.9.

The QTL PH-5 was also detected in four of eight environments in the USA. The QTL PH-5 was located between the markers bPb1228 and bPb4492 on chromosome 6HL. The QTL PH-5 accounted for 16–22% of the variation in the locations where the QTLs were detected. The alleles from ZAU 7 at these loci reduced plant height. Coefficients of the additive effect for PH-5 varied from −11.8 to −15.3.

The QTL PH-6 was detected only in the two Hangzhou environments. It was located between the markers bPb4541 and bPb3107 on chromosome 7HL, near the marker Bmag11. In the two environments, the QTL PH-6 explained 13 and 17% of the phenotypic variation. The allele from ZAU 7 at this position reduced plant height. Coefficients of the additive effect for PH-6 were –12.6 and –16.0. We speculated that the QTL may be affected by day-length, since this environment had short days because the plants were grown over the winter; however, no QTL for heading date was found in the same region.

QTL for heading date

The QTL HD-1 was detected in two environments only under short-day conditions (Table 2). It was located between markers bPb0617 and bPb4515 on chromosome 1HL. This QTL explained 15% of the phenotypic variation when the population was grown at Hangzhou in 2002–2003 and 2003–2004. The allele from ZAU 7 increased the number of days from sowing to heading. The coefficients for the additive effect for HD-1 were 6.8 and 7.3.

The QTL HD-2 (likely *Eam1 or Ppd-H1*) was identified in six environments only under long-day conditions. It was mapped between markers bPb7557 and bPb6835. This QTL explained 33–43% of the phenotypic variation. The allele from ZAU 7 at this locus reduced the number of days from sowing to heading. The coefficients for the additive effect of HD-2 ranged from −3.4 to −8.6.

The QTL HD-3 (likely *Vrn-H1*) was detected in two environments only under short-day conditions. It was located between markers bPb0780 and bPb8319 on 5HL. This QTL explained 35 and 42% of the phenotypic variation when the population was grown at Hangzhou in 2002–2003 and 2003–2004, respectively. The allele from ZAU 7 reduced the number of days from sowing to heading. The coefficients for the additive effect for HD-3 were −12.4 and −13.5.

QTL for rachis internode length

Two QTLs for rachis internode length were identified. The QTL RI-1 was located between the markers bPb6055 and bPb4691 on chromosome 2HL. This QTL explained 66% of the phenotypic variation. The allele from ZAU 7 shortened the rachis internode. The coefficient for the additive effect for RI-1 was −1.3.

The QTL RI-2 was located between the markers bPb3630 and bPb9118 on chromosome 3HL. This QTL explained 17% of the phenotypic variation. The allele from ZAU 7 also shortened the rachis internode. The coefficient for the additive effect for RI-1 was −0.6.

Discussion

The total chromosome length in this map is close to that of the Steptoe/Morex map developed using primarily DArT

markers (Wenzl et al. 2004). The marker order and relative positions for SSR markers are consistent with the previously published maps (Ramsay et al. 2000; Dahleen et al. 2003; Wenzl et al. 2006).

Plant height is one of most important traits for barley. A lot of work on molecular mapping of plant height has been done, since 1990s (Hayes et al. 1993; Hayes and Iyambo 1994; Backes et al. 1995; Peighambari et al. 2005; Sameri et al. (2006). Using North American barley germplasm, Hayes et al. (1993) detected QTL for plant height on chromosome 1H, 2HS, 2HL, 3HL, 4HS, 4HL, 6HL, and 7HS. In a doubled haploid population derived from a cross between two winter barley cultivars Igri and Danilo, QTL for plant height were found on chromosomes 4HL, 6HL and 5H (Backes et al. 1995). In another doubled haploid population derived from the cross Steptoe/Morex, a consistent QTL for plant height was found on chromosome 3H in two separate studies (Hayes and Iyambo 1994; Peighambari et al. 2005). In an RIL population derived from a cross between Azumamugi (6-rowed winter cultivar) and Kanto Nakate Gold (a 2-rowed spring cultivar), Sameri et al. (2006) identified one QTL on chromosome 3HL (likely *Uzu1*locus) and one QTL on 7HL (likely *dsp1*locus). However, the QTL on 7HL explained only 7% of the plant height phenotypic variation. In mapping QTL for *Fusarium* head blight resistance along with plant height, de la Pena et al. (1999) identified one QTL for plant height on chromosome 7HL in one of the four environments tested, where it explained 13.6% of the plant height phenotypic variation. More recently, Sameri et al. (2009) found a QTL for reduced culm internode length on chromosome 7HL in the same region. However, it explained only 19.1% of the phenotypic variation in plant height, on average, in two environments. This value is less than half of the average (42.2%) for the semi-dwarfing gene *uzu1* that is also present in the same population. Thus, it is unclear whether the QTL they found on chromosome 7H is the semi-dwarfing gene identified in our study. Additional research, such as an allelism test would need to be done to determine whether there are actually two linked loci or a single locus in chromosome 7H contributing to the semi-dwar phenotype.

To be useful for MAS, QTL must have a sufficient allelic effect and be consistently expressed across multiple environments. Although it is hard to give a definitive number, we suggest a threshold of a QTL being significant in 75% of environments should be adopted before MAS is considered. In addition, the total number of the environments where QTL analysis is carried out should be sufficient.

In our study, although seven QTL for plant height were detected in the population from the cross ZAU 7/ND16092, only PH-7 was found in all eight environments (Table 2). We suggest the provisional name *Qph-7H* for this QTL. This QTL had the largest effect on plant height in all environments, nearly twice as much as the other plant height QTL. The mean variation explained by the QTL was 38% over the eight environments. The frequency distribution also indicates that PH-7 is the primary QTL controlling variation in plant height in the ZAU 7/ND16092 population. Because no QTL for maturity or rachis internode length were found on chromosome 7H, PH-7 is not associated with either of these traits. Therefore, the PH-7 is the semi-dwarfing gene in ZAU 7.

Utilization of barley cultivars with short stature has greatly increased barley yields, particularly in Asia and Europe. The semi-dwarfing gene *uzu1* gene is common in cultivars grown in Japan and Korea (Zhang and Zhang 2003), while the *sdw1* (or *denso*) gene has been incorporated into European barley cultivars (Hellewell et al. 2000). The *uzu1* and *sdw1* genes have not used in malting barley cultivars in the Upper Midwest of the USA because of their undesirable pleiotropic effects on other traits, such as reduced test weight, percentages of plump kernels, and yield (Foster and Thompson 1987; Rasmusson and Phillips 1997). In addition, *sdw1* delays heading while *uzu1* shortens leaf, culm, spike, awn, and kernel length and is temperature sensitive. Since 1950, most barley cultivars developed for China have short stature controlled by five unmapped semi-dwarfing genes (Zhang and Zhang 2003).

Based on the chromosome location, the semi-dwarfing gene in ZAU 7 is different from those previously discovered, including *uzu1*, *sdw1*, and *hcm1*. These three genes, so far, have not been used successfully to improve malting barley cultivars in stature in North America. The semi-dwarfing gene found in ZAU 7 provides breeders in North America with a new gene to reduce plant height. Because the gene is located on chromosome 7HL far away from the centromere, it should be easier to recover the desirable recombinants than when using the *uzu1*, *sdw1*, and *hcm1* genes that are close to chromosomal centromeres. Quite often when breeders wish to reduce plant height using semi-dwarfing genes, not every individual grown in the field having a semi-dwarfing gene can be easily identified due to the effects from other loci controlling plant height or environmental effects. However, molecular markers may help with the selection. To facilitate marker-assisted selection, two flanking DArT markers need to be converted into STS markers. STS markers that flank the QTL would make selection for semi-dwarf plants more efficient and effective.

The allele of ZAU 7 at PH-1 may have an effect on heading date. In the QTL analysis for heading date, the QTL HD-2 was found close to the plant height QTL PH-1 and both were identified only in the North Dakota and Montana environments (Table 2). However, the heading date QTL showed greater variation than could be accounted for by PH-1, which suggests that PH-1 might actually result from the pleiotropic effect of a photoperiod-sensitive gene for

heading date, the *Eam1* maturity gene. The *Eam1* gene has little effect on heading date under short-day conditions. The *Eam1* gene did not affect the heading date in the Hangzhou experiments because the ZAU 7/ND16092 population was grown in winter under short-day conditions. A reduction in plant height caused by early maturity genes has been reported in other studies (Karsai et al. 1997; Ma et al. 2000).

The PH-2 and RI-1 QTL map to the same region of chromosome 2H. This indicates that the PH-2 may have effect on rachis internode length, where the allele of ZAU 7 reduces the rachis internode length. However, the rachis internode length QTL showed much greater phenotypic variation than could be accounted for by QTL PH-2, suggesting that QTL RI-1 might have effect on PH-2 instead.

References

Backes G, Graner A, Foroughi-Wehr B, Fischbeck G, Wenzel G, Jahoor A (1995) Localization of quantitative trait loce (QTL) for agronomic important characters by the use of a RFLP map in barley (*Hordeum vulgare* L.). Theor Appl Genet 90:294–302

Barua UM, Chalmers KJ, Thomas WTB, Hackett CA, Lea V, Jack P, Forester BP, Waugh R, Powell W (1993) Molecular mapping of genes determining height, time to heading, and growth habit in barley (*Hordeum vulgare*). Genome 36:1080–1087

Dahleen LS, Agrama HA, Horsley RD, Steffenson BJ, Schwarz PB, Mesfin A, Franckowiak JD (2003) Identification of QTLs associated with Fusarium head blight resistance in Zhedar 2 barley. Theor Appl Genet 108:95–104

Day AD, Dickson AD (1958) Effect of artificial lodging on grain and malt quality of fall-sown irrigated barley. Crop Sci 50:338–340

de la Pena RC, Smith KP, Capettini F, Muehlbauer GJ, Gallo-Meagher M, Kill-Macky R, Somers DA, Rasmusson DC (1999) Quantitative trait loci associated with resistance to *Fusarium* head blight and kernel discoloration in barley. Theor Appl Genet 99:561–569

Foster AE, Thompson AP (1987) Effects of a semidwarfing gene from Jotun on agronomic and quality traits of barley, pp 979–982. In: Yasuda S, Kanishi T (ed) Barley genet. V. Proceedings of international barley genetics symposium. 5th Okayama, Japan. 6–11 October 1986, Sanyo Press Co., Okayama, Japan

Franckowiak JD (2000) Notes on plant height in six-rowed barley and FHB resistance. In Proceedings of the Eighth International Barley Genetics Symposium (Adelaide University, Waite Campus, Glen Osmond, South Australia 5064, 2000), vol 2., pp 107–109

Haahr V, von Wettstein D (1976) Studies of an induced, high-yielding dwarf-mutant of spring barley. In: Proceedings of the third international barley genetics symposium (Garching, Verlag Karl Thiemig, München, 1975), pp 215–218

Hayes PM, Iyambo OE (1994) Summary of QTL effects in the Steptoe × Morex population. Barley Genet Barley Genet Newslett 23:94–143

Hayes PM, Liu BH, Knapp SJ, Chen F, Jones B, Blake T, Franckowiak J, Rasmusson D, Sorells M, SE U, Wesenberg D, Kleinhofs A (1993) Quntitative trait locus effects and environmental interaction in a sample of North Americal barley germplasm. Theor Appl Genet 87:392–401

Hellewell KB, Rasmusson DC, Gallo-Meagher M (2000) Enhancing yield in semidwarf barley. Crop Sci 40:352–358

Karsai I, Meszaros K, Hayes PM, Bedo Z (1997) Effects of loci on chromosomes 2 (2H) and 7 (5H) on developmental patterns in barley (*Hordeum vulgare* L.) under different photoperiod regimes. Theor Appl Genet 94:612–618

Kleinhofs A, Kilian A, Saghai Maroof M, Biyashev R, Hayes P, Chen F, Lapitan N, Fenwick A, Blake T, Kanazin V, Ananiev E, Dahleen L, Kudrna D, Bollinger J, Knapp S, Liu B, Sorrells M, Heun M, Franckowiak J, Hoffman D, Skadsen R, Steffenson B (1993) A molecular isozyme and morphological map of the barley *(Hordeum vulgare*) genome. Theor Appl Genet 86:705–712

Kosambi DD (1944) The estimation of map distances from recombination values. Ann Eugen 12:172–175

Ma Z, Steffenson BJ, Prom LK, Lapitan NLV (2000) Mapping of quantitative trait loci for Fusarium head blight resistance in barley. Phytopathology 90:1079–1088

Manly KF, Cudmore RH, Meer JM (2001) Map Manager QTX, cross-platform software for genetic mapping. Mamm Genome 12:930–932

Mickelson HR, Rasmusson DC (1994) Genes for short stature in barley. Crop Sci 34:1180–1183

Neatby RW (1929) An analysis of the inheritances of quantitative characters and linkage in barley. Sci Agric 9:701–718

Peighambari SA, Samadi BY, Nabipour A, Charmet G, Sarrafi A (2005) QTL analysis for agronomic traits in a barley doubled haploids population grown in Iran. Plant Sci 69:1008–1013

Ramsay L, Macaulay M, Degli-iavnissevich S, Maclean K, Cardle L, Fuller J, Edwards KJ, Tuvesson S, Morgante M, Massari A (2000) A simple sequence repeat-based linkage map of barley. Genetics 156:1997–2005

Rasmusson DC, Phillips RL (1997) Plant breeding progress and genetic diversity from de novo variation and elevated epistasis. Crop Sci 37:303–310

Sameri M, Takeda K, Komatsuda T (2006) Quantitative trait loci controlling agronomic traits in recombinant inbred lines from a cross of oriental- and occidental-type barley cultivars. Breed Sci 56:243–252

Sameri M, Nakamura S, Nair SK, Takeda K, Komatsuda T (2009) A quantitative trait locus for reduced culm internode length in barley segregates as a Mendelian gene. Theor Appl Genet 118:643–652

Swenson SP, Wells DG (1944) The linkage relations of four genes in chromosome I of barley. J Am Soc Agron 36:429–435

Thomas WBT, Powell W, Wood W (1984) The chromosomal location of the dwarfing gene present in golden promise. Heredity 53:177–183

Tinker NA, Mather DE (1995) MQTL: software for simplified composite interval mapping of QTL in multiple environments. J Agric Genom 1 http://wheat.pw.usda.gov/jag/papers95/paper295/jqtl16r2.html. Cited 16 July 2009

Tsuchiya T (1972) Genetics of *uz*, *uz2* and *uz3* for semi-brachytic mutations in barley. Barley Genet Newslett 2:87–90

Wenzl P, Carling J, Kudrna D, Jaccoud D, Hutter E, Kleinhofs A, Kilian A (2004) Diversity arrays technology (DArT) for whole-genome profiling of barley. Proc Natl Acad Sci USA 101:9915–9920

Wenzl P, Li H, Carling J, Zhou M, Raman H, Paul E et al (2006) A high-density consensus map of barley linking DarT markers to SSR, RFLP, and STS loci and agricultural traits. BMC Genomics 7:206

Zhang J (2003) Inheritance of plant height and allelism tests of the dwarfing genes in Chinese barley. Plant Breed 122:112–115

Zhang J, Zhang W (2003) Tracing sources of dwarfing genes in barley breeding in China. Euphytica 131:285–292

Zhu H, Gilchrist L, Hayes PI, Kleinhofs A, Kudrna D, Liu Z, Prom L, Steffenson B, Toojinda T, Vivar H (1999) Does the function follow form? Principal QTLs for *Fusarium* head blight (FHB) resistance are coincident with QTLs for inflorescence traits and plant height in a doubled-haploid population of barley. Theor Appl Genet 99:1221–1232