QTL mapping of heading date and plant height in Barley cross "Azumamugi"×"Kanto Nakate Gold"

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Abstract

To identify quantitative trait loci (QTLs) controlling heading date and plant height, ninety nine F_{13} recombinant inbred lines (RILs) derived from barley cultivars Azumamugi × Kanto Nakate Gold cross were evaluated. The field trails were conducted at randomized complete block design with two and three replications in 2004 and 2005, respectively. Significant differences and transgrassive segregates were observed among lines for heading date and plant height. Composite interval mapping (CIM) was done based on linkage map constructed using 99 RILs and 100 markers including isozyme, morphological, STS and AFLP markers. A strong QTL controlling 26% phenotypic variation of heading date on chromosome 5HL was located near to the e07m25.3-e12m199.1 markers. The QTL had the same interval of the Sgh_2 locus. Allele inherited from Azumamugi parent in this locus decreased heading date. The QTL for heading date in the map interval of ABC261-ABG055 markers on chromosome 1HL could be identical with the eam8 locus and accounted for 11% of the phenotypic variation. New QTL for plant height was detected near to uzu1 locus on chromosome 3HL, explaining 52% of the phenotypic variation. The effect of allele transmitted from Azumamugi parent in this locus decreased plant height. The QTLs identified on chromosomes 1HL, 3HL and 7HS in relation to eam8, uzu1 and dsp1 genes showed pleiotropic effects on controlling heading date and plant height.

Keywords: *Composite interval mapping; Hordeum vulgare L.; Major genes; Pleiotropic effects; QTLs combination.*

INTRODUCTION

The relationship between heading date and plant height is particularly important in the grass family including barley, in which apical growth is terminated by flowering (Lin *et al*., 1995). Increased plant height is often correlated with late flowering. Heading date is an important factor in adapting cereal varieties to environment and in maximizing yield potential. The control of plant height can be used to reduce yield loss arising from lodging and to increase harvest index (Bezant *et al*., 1996). These are determined by the interaction of three genetic factors, vernalization response (sensitivity to temperature), photoperiodic response (sensitivity to short days) and earliness in the narrow sense (sensitivity to long days) (Takahashi and Yasuda, 1970; Hackett *et al*., 1992).

Heading date and plant height show continuous variation and they are controlled by quantitative trait loci (QTLs). The inheritance of these characters is complex and usually assumed to involve numerous genetic factors that interact with environmental conditions (Kjær *et al*., 1995). The advent and development of molecular markers in quantitative genetics greatly facilitates the study of complex quantitatively inherited traits by the construction of high density genome linkage maps for crops such as barley and has made it possible to dissect the poly genes for such traits into individual Mendelian factors (Xiao *et al*., 1996). Using molecular linkage maps and QTL mapping methods, it is possible to estimate the number of loci controlling genetic variation in a segregating population and to characterize these with regard to their map position in the genome, gene action, phenotypic effects, pleiotropic effects and epistatic interactions with other QTLs (Xiao *et al*., 1996; Zhu *et al*., 1999).

Several statistical methods are available to detect and locate QTL. The most popular analytical method

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is of flanking marker mapping, either by the log-likelihood approach of interval mapping or by multiple regressions (Lander and Botestein, 1989; Haley and Knott, 1992; Martinez and Curnow, 1992). Combining interval mapping with multiple regressions has been proposed to attempt to separate the effects of possible multiple linked QTL (Jenson, 1992; Zeng, 1994). Cofactors are used to reduce the effect of back ground noise or variation by taking into account the variation of these selected markers with the QTLs (Bezant *et al*., 1996).

The objectives of this study were to (1) identify QTLs controlling heading date and plant height (2) investigate correspondence between major genes and QTLs affecting the traits in a recombinant inbred lines population derived from the cross between two Japanese cultivars of barley.

MATERIALS AND METHODS

Plant materials and trait evaluations: We used ninety nine F_{13} recombinant inbred lines of barley derived via single seed descent method from F_2 plants of Azumamugi (AZ) × Kanto Nakate Gold (KNG) cross (T. Komatsuda, unpublished data), in field condition at National Institute of Agrobiological Sciences, Tsukuba, Japan. AZ is six-rowed Japanese, winter barley and KNG is two-rowed Japanese, spring cultivar. The RILs used in this study were produced to identify the QTLs for shoot differentiation in barley (Komatsuda *et al*., 1989; Mano and Komatsuda, 2002). Also the population showed variation for important agronomic traits including heading date and plant height. AZ parental line showed lower value for plant height, whereas KNG line had higher value for heading date (Shahinnia *et al*., 2005). The field trails were conducted at randomized complete block design with two replications in 2004 and three replications in 2005 at Isfahan University of Technology Research Station, Isfahan, Iran (32° 32′ N, 51° 32′ E). The experimental plots consisted of four row plots, 2m × 0.8 m with 4 cm within row spacing. Two-hundred kg/ha ammonium phosphate as fertilizer before planting and 250 kg/ha urea at tillering stage were used.

Heading date was recorded when an estimated 50% of the spikes in each plot had completely emerged from the boot. Plant height was measured from the base of the culms to the tip of the spike (awn excluded). Data were recorded for 10 randomly plants in the center rows of each plot with considering 0.5 m border to omit bordering effect.

Statistical analysis*:* Analysis of variance was performed for data obtained from 2-year experiments using the general linear model (GLM) procedure of the SAS software (SAS Institute, 2000). Heritability (h^2) was calculated from variance components according to Kearsey and Pooni (1996).

Molecular linkage map and QTL analysis: For the QTL analysis the genetic base map covering 925.6-cM containing 100 markers including 2 isozyme, 2 morphological, 34 STS and 62 AFLP markers (Mano *et al*., 2001; Mano and Komatsuda, 2002) was used to obtain a density of 5 to 10-cM intervals without the clustering markers. Map distances were estimated based on Kosambi's map function (Kosambi, 1944) and the map was constructed using MAPMAKER 3.0 (Lander *et al*., 1987; Lincoln *et al*., 1992).

QTL analysis was performed using phenotypic data for the mean values of the traits evaluated in 2004 and 2005. Initially, single marker analysis (SM) was performed for each trait to identify markers associated with variation for traits using MAPMAKER/QTL ver.1.1b (Lander and Botestein, 1989). Further evaluation was carried out by composite interval mapping (CIM) with a 15-cM window and a maximum of 15 marker cofactors per model using Windows QTL Cartographer version 2.0 (Wang *et al*., 2004). Tests were performed at 1-cM intervals, and cofactors were selected by forward-backward stepwise regression (Model 6). Genome wide, trait specific, threshold values (α= 0.05) of the likelihood ratio (LR) test statistic for declaring the presence of a QTL was estimated from 2000 permutation test by random sampling of phenotypic data (Churchill and Doerge, 1994; Doerge and Churchill, 1996). The phenotypic variation explained by a QTL (R^2) conditioned by the CIM cofactors included in the model was calculated at the most likely QTL position. The additive effect of an allelic substitution at each QTL was also obtained. The LOD peak of each significant QTL was considered as the QTL location on the linkage map.

RESULTS

Phenotypic variations and heritability of traits: Pooled analysis of variance across 2 years (Table 1) confirmed the presence of highly significant differences among lines for heading date and plant height. The environmental effect was small, but the genotypic variance was large for both traits; thus, high heritability estimated for heading date and plant height (93%** and 90%** respectively). According to the frequency

distribution of phenotypes (Fig. 1), transgressive segregates were observed for heading date and plant height. AZ parental line had the lower value for heading date and plant height compared to KNG line. Also, the climatic condition of 2004 growing season was warmer and dryer than 2005. This may explain the earlier heading date and shorter plant height in 2004.

Table 1. Pooled analysis of variance across 2 years for heading date and plant height evaluated in the RILs derived from Azumamugi × Kanto Nakate Gold.

Source	df	Mean square	
		Heading date	Plant height
Year	1	9493.63**	70527.85**
Block (Year)	3	115.58	4519.78
Line	98	250.18**	577.09**
Line × Year	98	28.98	80.45

** Significant at P<0.01

Mapping QTLs: For each trait, the linkage of QTLs to molecular markers mapped in the RILs population was assessed by single marker analysis. Although single marker analysis can be useful for a quick look at the data, especially in case of having missing observations that could affect later analysis, however QTL mapping methods such as CIM are more robust and powerful than SM (Basten *et al*., 1999; Wang *et al*., 2004). Therfore, only the results from CIM (Table 2) are presented here.

Mapping QTLs for heading date: The CIM analysis in F_{13} generation detected seven QTLs on chromosomes 1H, 2H, 3H, 5H and 7H (Fig. 2A). A strong QTL on chromosome 5HL near to the *e07m25.3* marker explained the highest phenotypic variance (26%) with the largest LOD score (Table 2). The effect of AZ allele in this locus reduced heading date. The QTL was located on chromosome 1HL near to the *ABC261* marker had the highest additive effect on increasing heading date and explained 11 percent of total phenotypic variance with the considerable LOD score. The second QTL on chromosome 1HL with explaining about 10% phenotypic variance of heading date was located in interval of *e02m18.4-e06m18.10* markers. The QTLs were detected on chromosome 2H in the interval of *e11m19.3-ABG613* and *e13m31.7.1-e15m19.8.1* markers could totally explain 15% of heading date phenotypic variance. Both QTLs with allele from AZ parental line reduced heading date. The minor QTLs controlling heading date in interval of *e15m19.7-ABA001* markers on chromosome 3HS and *cMWG704-e11m1710.2* markers on chromosome 7HS showed the additive effect of AZ allele on increasing heading date.

Mapping QTLs for plant height: Results of CIM analysis indicated four QTLs controlling plant height (Fig. 2B). Of these, a major QTL located in the interval of *uzu-e06m30.10.1* markers on chromosome 3HL explained 52 percent of plant height phenotypic variance (Table 2). For this QTL allele inherited from AZ parent decreased plant height. Also three minor QTLs were identified near to the *ABC261*, *cMWG704* and *e12m2210.2* markers on chromosomes 1HL, 7HS and 7HL, respectively, could totally explained 19% of phenotypic variance. Allele of AZ parental line in the interval near to *ABC261* and *e12m2210.2* markers had positive effect on increasing plant height.

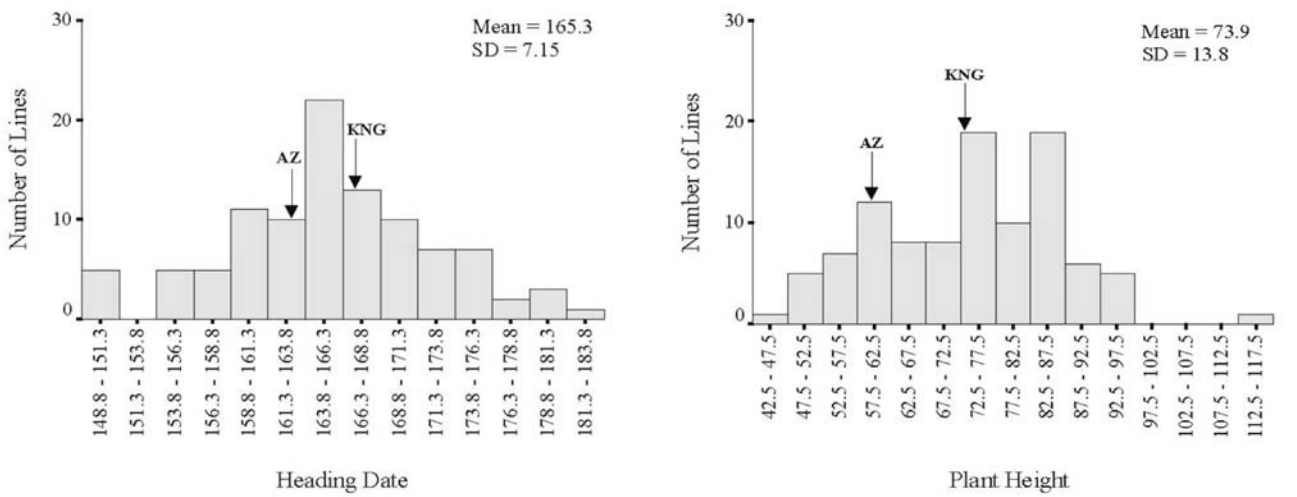

Figure 1. Frequency distribution of phenotypes for heading date and plant height in the RILs of Azumamugi × Kanto Nakate Gold cross based on means over years. Arrows indicate phenotypic values of AZ and KNG.

Table 2. The Chromosomal location, map interval, position of peak LOD, LOD score, additive effect and percent of explained variance by QTLs detected for heading date and plant height in the RILs derived from Azumamugi × Kanto Nakate Gold.

Trait	Chromosome	Interval	Position[a] (cM)	LOD[b] Score	Additive[c] Effect	R^{2} [d]
Heading date	1HL	*e02m18.4-e06m18.10*	99.21	10.27	2.45	0.09
	1HL	*ABC261-ABG055*	143.81	13.81	2.56	0.11
	2HS	*e13m31.7.1-e15m19.8.1*	60.61	9.14	-2.21	0.09
	2HL	*e11m19.3-ABG613*	125.31	8.24	-2.06	0.05
	3HS	*e15m19.7-ABA001*	49.91	8.38	1.69	0.05
	5HL	*e07m25.3-e12m199.1*	107.21	22.11	-3.93	0.26
	7HS	*cMWG704-e11m1710.2*	87.81	9.74	2.22	0.07
Plant height	1HL	*ABC261-ABG055*	144.81	3.92	2.52	0.03
	3HL	*uzu-e06m30.10.1*	65.61	30.08	-10.07	0.52
	7HS	*cMWG704-e11m1710.2*	86.81	7.87	-3.75	0.08
	7HL	*e12m2210.2-ABG608*	135.61	6.31	3.95	0.08

[a] Distance of peak LOD score position from the left side marker.
[b] Peak LOD score of significant marker interval.
[c] Additive effect of Azumamugi allele.
[d] Proportion of the phenotypic variance explained.

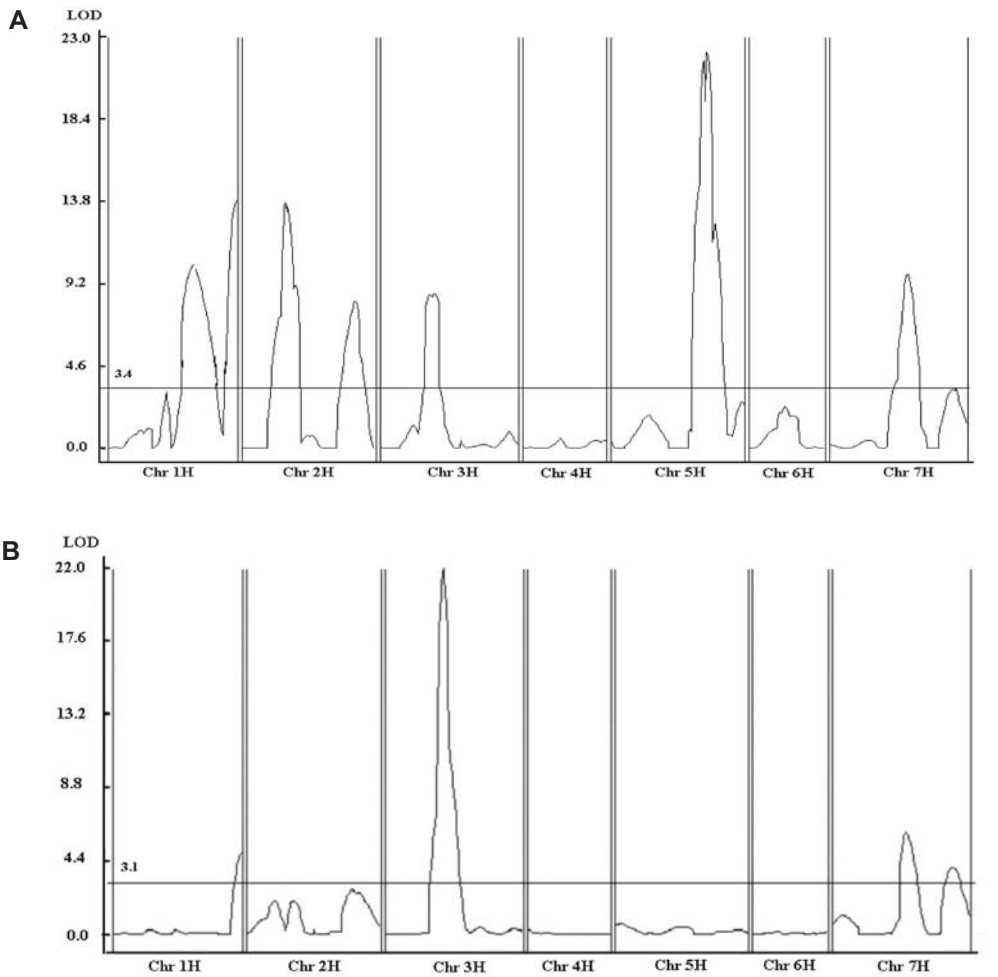

Figure 2. The Logarithm of odds (LOD) score plots of QTLs detected for (A) heading date and (B) plant height calculated by composite interval mapping in the RILs derived from Azumamugi × Kanto Nakate Gold based on means over years. LOD score profiles of chromosomes are shown in the order of 1H, 2H, 3H, 4H, 5H, 6H and 7H, oriented from short arm.

Correspondence between QTLs affecting heading date and plant height: We found a highly significant phenotypic correlation (r= 0.75) between heading date and plant height in this study. Some QTLs affecting heading date were associated with plant height QTLs (Table 2). Specifically, the two QTLs, close to the *ABC261* and *cMWG704* markers on chromosomes 1HL and 7HS, respectively, were overlapped. Also, by decreasing 1.0 LOD score from each side of the maximum value (Lander and Botestein, 1989), the QTLs controlling heading date and plant height in the interval of *e15m19.7-ABA001* and *uzu-e06m30.10.1* markers on chromosome 3H were mapped within overlapping 90% confidence intervals of each QTL LOD.

DISCUSSION

Heading date: In barley chromosome 1HL, the presence of the photoperiodic sensitive gene *Ppd-H$_2$* was reported at the position being 20.6 cM proximal to the *cMWG733* marker (Laurie *et al*., 1995). According to the barley consensus map in GrainGenes (*http://www.graingenes.org*), the *cMWG733* marker located approximately at a position 10 cM proximal to that of the *ABC261* marker and the QTL detected for heading date on chromosome 1HL near to the *e02m18.4* marker in this study was located at a position 35.59 cM proximal to *ABC261* marker. By decreasing 1.0 LOD score from each side of the maximum value (Lander and Botestein, 1989), the 90% confidence interval obtained for this QTL included the same position with the *Ppd-H$_2$* locus. Another QTL near to *ABC261* marker on this chromosome was identical with the QTL detected by Marqueez-Cedillo *et al*., 2001. This QTL could be identical with the early maturity gene *eam8* (Franckowiak, 1996) and detected by Takahashi and Yasuda (1970). Since the *eam8* locus is present in Japanese two-rowed barley, it is possible that Kanto Nakate Gold (two-rowed) harbors an allele, which confers sensitivity to long days (Sameri and Komatsuda, 2004).

According to integrated molecular and morphological/physiological marker maps (Kleinhofs, 2002 and 2004) in barley, the QTL located on chromosome 2HS near to *e13m31.7.1* marker had the same interval including the *Eam1* (Early maturity 1) or *Ppd-H1* locus. This QTL has been reported before by Hayes *et al*., 1993; Lauri *et al*., 1995 and Baum *et al*., 2003.

The QTL on chromosome 7HS close to *cMWG704* marker might correspond to the *dsp1* (dense spike 1) locus. For QTL in the interval of *e15m19.7-ABA001* near to *uzu1 gene*, no QTL have been identified in other mapping populations. It was known that AZ carries the *uzu1* (semi brachytic) gene (Mano *et al*., 2001), so the intervals controlling heading date near to *uzu1* locus can be investigated in this population and AZ parent causes delay in heading date.

Plant height: A strong QTL for plant height was detected on chromosome 3HL near to the *uzu1* locus on which allele inherited from AZ parent causes plant height reduction. Since none of the parents carried the *uzu1* gene in the former studies, no QTL in this locus have been reported before. The *uzu1* gene has pleiotropic effects on several agronomic characters (Takahashi and Yamamoto, 1951). Even, a strong QTL for shoot differentiation has been found very close to the *uzu1* locus, in tissue culture (Mano and Komatsuda, 2002). Kuraishi (1974) reported the pleiotropic effect of the *uzu1* gene in reducing auxin hormone production. This may explain the effect of QTLs near to the *uzu1* gene on decreasing plant height. Marquez-Cedillo *et al*. (2001) and Teulat *et al*. (2001) reported two QTLs near the *uzu1* locus, but the *uzu1* gene coming from the Japanese cultivars (Takahashi and Yamamoto, 1951), so former QTLs may not be allelic with *uzu1*. The QTL detected for plant height at centromeric region on chromosome 7H, near to *cMWG704* marker could be identical with QTL reported by Hayes *et al*. (1993) and Tinker *et al*. (1996). The location of *cMWG704* marker was very close to the *dsp1* locus on chromosome 7H, the locus with decreasing effect on stem internodes (Franckowiak and Konishi, 1997). The QTLs near to *ABC261* marker on chromosome 1HL and *e12m22.10* marker on chromosome 7HL might be new loci for controlling plant height detected in this population.

Sameri and Komatsuda (2004) and Sameri *et al*. (2006) using the recombinant inbred lines of the cross between AZ and KNG cultivars and a field experiment conducted in Japan, reported three strong QTLs for heading date located on chromosomes 1HL, 2HS and 5HL near to the *ABC261, e13m31.7.1* and *e07m25.3* markers, respectively and a major QTL near to *uzu* marker for plant height. The results of present study confirmed the stable position of these QTLs identified across two environments and are more confident for marker assisted selection in this population. Three QTLs for heading date on chromosomes 2HL, 3HS and 7HS near to *e11m19.3*, *e15m19.7* and *cMWG704* markers, respectively and a QTL for plant height on chromosomes 1HL near to *ABC261* marker expressed in this study which were not detected in previous

report. Although the genomic position of a QTL is constant but the effect of a QTL may vary by environmental interaction and sampling variance (Tinker *et al*., 1996; Utz *et al*., 2000).

The results of present study revealed the correspondence between the QTLs affecting heading date and plant height in relation to *eam8*, *uzu1* and *dsp1* genes on chromosomes 1H, 3H and 7H, respectively. Marqueez-Cedillo *et al*. (2001) reported heading date QTLs on chromosome 3H and 5H, which had common flanking markers with plant height QTLs. Baum *et al*. (2003) also reported common flanking markers for plant height and heading date on chromosome 2H.

Major genes for earliness in barley have been shown to have pleiotropic effects on plant height (Kjær *et al*., 1991). However, it has been shown that major genes for height (i.e., the *denso* gene) have pleiotropic effects on heading date (Barua *et al*., 1993; Kjær *et al*., 1991). Comparative data support the possibility that independent closely linked genes, rather than a single gene, account for increased height and short day flowering, respectively (Lin *et al*., 1995).

It is important to determine to what extent QTL in one cross maybe equivalent to major genes in others, as this would allow close flanking markers for the major genes to be used to manipulate QTL in other crosses. This would increase the efficiency of marker assisted selection of QTL and the accuracy with which specific combination of QTL could be put together (Bezant *et al*., 1996; Pillen *et al*., 2003).

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