QTLs Involved in Plant Height, Peduncle Length and Heading Date of Wheat (*Triticum aestivum* L.)

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ABSTRACT

In order to locate the QTLs for plant height, peduncle length, and heading date, a set of 107 wheat doubled haploid (DH) lines derived from the cross Fukuho-komugi× Oligoculm was grown during the growing seasons of 2004 and 2005. A total of 36 QTLs were identified based on composite interval mapping (CIM) approach. All detected plant height QTL's were stable over the two years. QTLs located near *RhtD1* (chromosome 4D) and in the *Xta556-RhtB1* interval (chromosome 4B) accounted for, respectively, 40.1% and 28.9% of plant height variation in 2004 and 30.7% and 26.36% in 2005. The other two QTLs identified for plant height were located near *Xcfd53* and *Xwmc25a* loci on chromosome *2D*. The results of composite interval mapping indicated that all detected QTLs for peduncle length were coincident with plant height QTLs. Of the most important heading date QTLs, the only stable one over years was located in the *Xcfd53-Xbarc168* interval on chromosome *2D* and accounted for 34.05% and 31.9% of heading date variation in 2004 and 2005, respectively. The *Xbarc168-Xgwm484* interval (LOD> 8.3) carried the other important QTL for heading date in 2004. In general, based on expression of stable and major effect QTLs in present study, it is possible to increase efficiency of marker assisted selection for the traits in breeding programs.

Keywords: Doubled haploid, Heading date, Peduncle length, Plant height, QTL, Wheat.

INTRODUCTION

During the 1960s and 1970s, plant breeders substantially increased grain yield by developing dwarf varieties of wheat, a period known as the 'Green Revolution' (Newbury, 2003). Since the taller plants are usually late in flowering, understanding the genetic basis of plant height and heading date is of importance in breeding programs (Lin *et al.*, 1995).

There are many *Rht* (reduced height) genes identified for reduction of plant height in wheat, but only *Rht-B1b* (*Rht1*), *Rht-D1b* (*Rht2*) and *Rht8* have been used extensively in plant breeding (Worland, 1996; Worland *et al.*, 1998; Ellis, *et al.*, 2002). According to the studies conducted to determine the genetic control of heading date, all wheat chromosomes carry genes for this trait (Worland 1996); however, the most important genes affecting the heading date in wheat are *Vrn* (vernalization) and *Ppd*

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(photoperiod) located on homeologous groups 5 and 2, respectively. Also, it is reported that the *Eps* (earliness per se) genes on chromosomes *7B, 6B, 6D, 4D, 3A,* and *2D* are responsible for earliness in wheat (Law *et al*., 1975; Worland, 1996). Nevertheless, many studies have revealed that plant height and heading date are controlled by quantitative trait loci (QTL) in different crops and affected by environmental conditions (Zhang *et al*., 2009; Shindo *et al*., 2003; Börner *et al*., 2002; Rami *et al*., 1998; Sourdille *et al*., 2000; Xu *et al*., 2005; Toth *et al*., 2003; Rabiei, 2007; Rebetzke *et al*., 2001).

Bullrich *et al*. (2002) identified a major QTL on chromosome *1A* of wheat for heading date. Cadalen *et al*. (1998) proposed a model including the main effects of the loci from chromosomes *4B* and *4D* (Xfba1-4B, Xglk556-4B and Xfba211-4D) and the interaction effects between *Xfba393-1A* and *Xcdo1188-1B,* which explained about 50% of the plant height variation in a doubled-haploid (DH) population of wheat. Marza *et al*. (2006) identified 5 major QTLs for plant height in wheat on chromosomes *2BL, 2BS, 2DL, 4B* and *6A*, which accounted for, respectively, 16.7, 16.9, 12.3, 14.9 and 12.1% of its phenotypic variation in a recombinant inbred line (RIL) population. In another study, Shindo *et al*. (2003) found that *Xpsr135b, Xgdm132, Xgwm469, Xgwm428*, and *Xgwm234* markers were closely linked to the heading date QTLs. Studying the wheat cultivar *Suwon 92* for three years, Xu *et al*. (2005) reported a QTL about 41.2 cM proximal to the distal end of chromosome *2DS* which explained 40.5% of phenotypic variation of early heading. Sourdille *et al*. (2000) found a QTL affecting wheat heading date near locus *Xfbb121-2B* co-segregated with the gene *Ppd-B1* involving in photoperiod response. In a study by McCartney *et al*., (2005), the most effective QTL for wheat plant height was *QHt.crc-4D* located on chromosome *4D*, which contributed to 47.5% of the phenotypic variation. The markers near this QTL were *Xwmc617* and *Xwmc48*.

McCartney *et al*. (2005) also reported the coincidence of this QTL (*QHt.crc-4D*) with the QTL of *QMat.crc-4D* for time to maturity.

The objectives of the present study were to determine heritabilities, the QTLs and genetic control of plant height, peduncle, length, and heading date in a DH population in order to use in breeding programs of bread wheat.

MATERIAL AND METHODS

Field Experiments

A DH population consisting of 107 wheat lines was obtained from a cross between the Japanese cultivar Fukuho-komugi and the line Oligoculm (Atsmon and Jacobs, 1977) by means of wheat×maize crosses (Suenaga and Nakajima, 1993). Oligoculm harbors the GA-insensitive *Rht2* gene or a gene allelic to the *Rht2* locus while Fukuho-komugi carries the GA-insensitive *Rht1* gene (Suenaga and Nakajima, 1993). Both parents and DH lines (the population size included 107 lines as molecular marker data was available only for 107 DH lines) were evaluated under field conditions in a randomized complete block design with three replications in 2004 and 2005 at the Research Farm of Isfahan University of Technology (32° 32′ N, 51° 32′ E), Isfahan, Iran. The area has altitude of 1,630 m with temperate climate. Each experimental plot consisted of four 2-m rows spaced 20 cm. The seeds were treated with fungicide to control disease and 250 kg ha⁻¹ urea and 150 kg ha⁻¹ ammonium phosphate were applied to the plots. Also, weeds were controlled manually and a normal irrigation management was used. All genotypes were evaluated for plant height (cm), peduncle length (cm) and heading date (days from sowing to emergence of two thirds of the spikes from the leaves in 50% of plants in each plot). Plant height and peduncle length in each plot were recorded on 10 randomly selected plants in the center

rows of each plot and their average was used.

The data obtained from field evaluations in 2004 and 2005 were subjected to combined analysis of variance using the GLM procedure of SAS software (SAS Institute, 2000). Also, the heritability (h^2) of the traits was estimated according to the expected mean squares and the following equation (Kearsey and Pooni, 1996).

$$h^2 = \frac{\sigma_g^2}{\sigma_g^2 + \dfrac{\sigma_e^2}{r}} \qquad (1)$$

Since a DH population is completely homozygous, σ_g^2 (genotypic variance) would be equal to $2\sigma_A^2$ (additive variance) and therefore h^2 would show narrow-sense heritability.

Molecular Markers

Molecular marker data including 344 RAPD, SSR, RFLP and two morphological markers (glume colour and pubescence) were kindly provided by Suenaga *et al.* (2005). In addition, a series of AFLP (Vos *et al.,* 1995) primer combinations (PstI+ANN and MseI+CNN) were used to genotype the DH lines and their parents in the Biotechnology Laboratory at Isfahan University of Technology, Iran. Those AFLP primer combinations that amplified polymorphic bands between parents were used to genotype the DH population.

All newly detected AFLP markers along with the previously available 344 markers were subjected to JoinMap® 3.0 software (Van Ooijen and Voorrips, 2001) and non-informative co-segregating markers were excluded from the data set. Also, markers with high (*P*< 0.001) segregation distortion (distorted from 1:1 ratio for a DH population) (Kammaholz *et al*., 2001) were excluded from the molecular data based on the chi-square test. The marker data obtained from primary analyses by JoinMap® 3.0 (Van Ooijen and Voorrips, 2001) were used to construct linkage

groups by MAPMAKER/EXP 3.0b (Lander *et al.,* 1987). The assignment of markers to chromosomes was based on a LOD of 3.0. The genetic distances (cM) were calculated according to the Kosambi (1944) function.

Composite interval mapping (CIM) approach (Zeng, 1994; Jiang and Zeng 1995) was conducted by Windows QTL Cartographer 2.5 (Wang *et al.,* 2007). A forward-selection backward-elimination stepwise regression and model 6 was used to select co-factors for CIM. A 10 cM scan window was used for analysis and log of odds (LOD) statistic was computed in 2 cM walk speed. The significant threshold (LOD) values for detection of QTLs were determined based on a permutation test with 1000 random samples (Churchill and Doerge 1994: Doerge and Churchill 1996) and the related LOD plots were produced using Windows QTL Cartographer 2.5.

RESULTS

Field Experiments

The results of combined analysis of variance over years showed that the effect of year, genotype and genotype×year interaction were significant (Table 1). These results indicated the existence of genetic variation for the investigated traits and also different responses of genotypes to the environmental conditions in 2004 and 2005. The estimated heritabilities showed high degree of genetic determination for all evaluated traits (Table 1). The heritability for plant height was 99.0% in 2004 and 96.0% in 2005. However, these values for peduncle length and heading date were, respectively, 97.0% and 95.0% in 2004 and 94.0% and 94.0% in 2005. The parental genotype of Fukuho-komugi was taller than the Oligoculm in both years and plant height among the DH lines ranged from 47.3 to 120.2 cm in 2004 and 49.0 to 137 cm in 2005 (Table 2). The DH lines also showed extensive variation for peduncle length (Table 2).

Table 1. Combined analysis of variance over years and the estimated heritability for plant height, peduncle length and heading date.

Source of variation	DF	Mean squares		
		Plant height	Peduncle length	Heading date
Year	1	7733.9**	73.7**	7617.4**
Rep (Year)	4	17.0	14.9	99.0
Genotype	108	2140.5**	331.2**	100.9**
Genotype × Year	108	46.7**	8.9**	15.3**
Error	432	27.5	7.3	2.1
Heritability (%) 2004		99.0	97.0	95.0
2005		96.0	94.0	94.0

** Significant at 1% level of probability.

Table 2. Phenotypic values of Fukuho-komugi (F) and Oligo-culm (O) parental lines and the descriptive statistics in DH lines for plant height, peduncle length and heading date in 2004 and 2005.

| Trait	Year	Parents		DH lines				
		F	O	Min	Max	Mean	SD[b]	CV[c] (%)
Plant height (cm)	2004	90.3	88.1	47.3	120.2	86.2	17.7	20.6
	2005	95.3	93.6	49.0	137.0	93.0	20.6	22.1
	M[a]	92.8	90.9	48.6	128.0	89.6	19.0	21.2
Peduncle length (cm)	2004	36.0	36.6	18.5	54.0	35.8	7.8	21.9
	2005	32.6	36.5	19.0	52.3	35.1	7.3	20.9
	M	34.3	36.6	18.7	52.7	35.4	7.5	21.1
Heading date (day)	2004	142.6	153.3	135.0	159.6	149.3	5.3	3.5
	2005	151.6	157.6	151.0	164.3	156.1	3.1	2.0
	M	147.1	155.5	143.0	161.6	152.7	4.0	2.6

[a] Mean over years; [b] standard deviation of the mean, [c] coefficient of variation of the traits.

Evaluation of heading date showed that Fukuho-komugi was earlier in heading than Oligoculm (Table 2). The DH lines headed earlier in 2004 than 2005 and their range of heading date was 135 to 159.6 days in 2004 and 151 to 164.3 days in 2005. Distribution of phenotypic values for plant height, peduncle length and heading date (Figure 1) indicated that phenotypic variation for heading date in 2005 was less than 2004 and transgressive segregation occurred in DH lines for these traits.

QTLs for Plant Height

According to the results of the permutation test, the LOD threshold was estimated as 3.2 for the data obtained in both years and the composite interval mapping detected four significant QTLs for plant height (Table 3). These QTLs were common over both years. The locus *RhtD1* was associated with a major QTL (LOD= 32.09) on chromosome *4D* in the first year of data analysis and this QTL explained 40.1% of the total variation of plant height. The additive effects for the QTL linked to *RhtD1* showed that alleles inherited from Oligoculm had a decreasing effect on plant height. The QTL located in the *Xta556-RhtB1* interval on chromosome *4B* (Figure 2a-b) accounted for 34% of plant height variation in both 2004 and 2005 (Table 3). The map positions of the other two major QTLs for plant height were near *Xcfd53* and *Xwmc25a* on chromosome *2D*. Except for the QTL on chromosome *4D*, Fukuho-komugi alleles showed decreasing
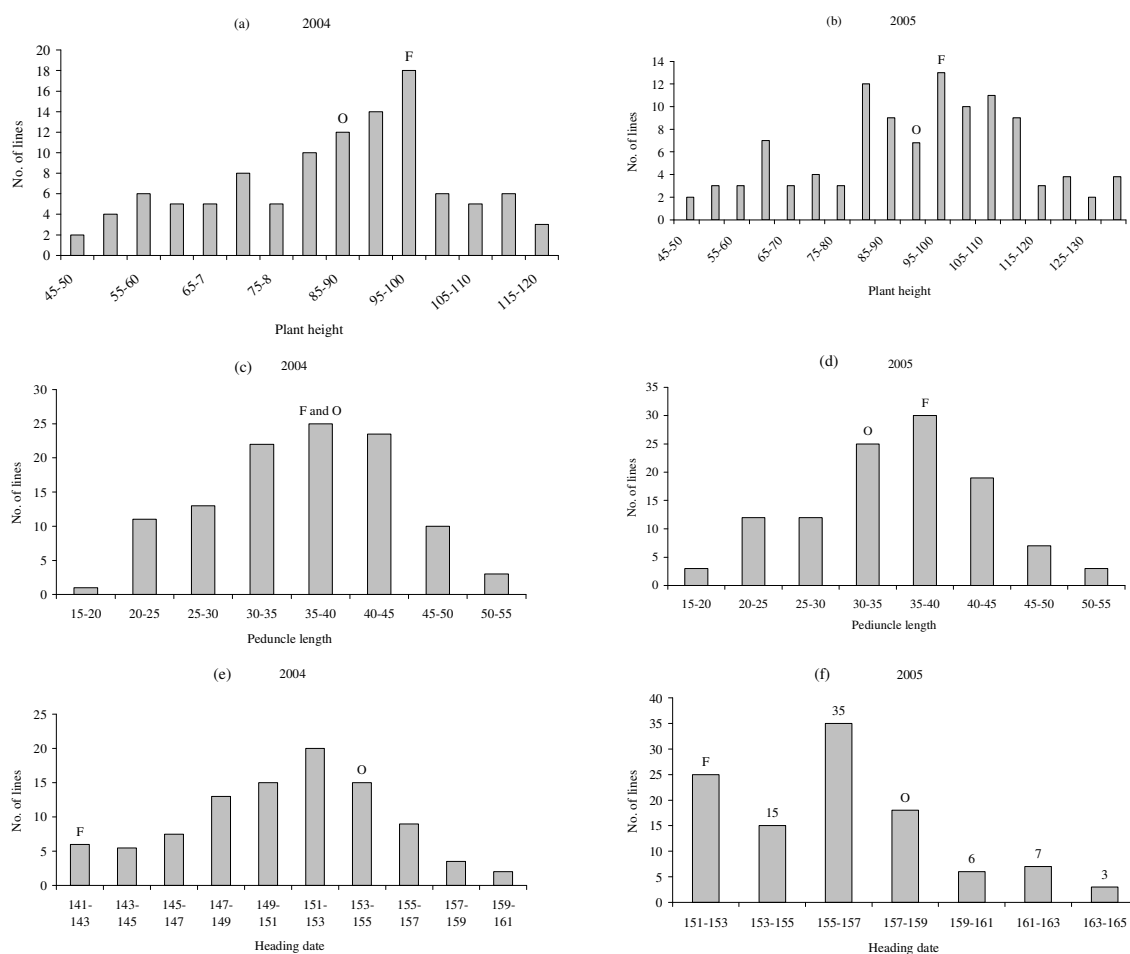
Figure 1. Frequency distribution of plant height (a and b), peduncle length (c and d) and heading date (e and f) recorded in 2004 and 2005 for parental genotypes (F and O denote Fukuho-komugi and Oligo-culm, respectively) and 107 DH lines of wheat.

effects on plant height of the DH lines in both years of evaluation. All markers linked to the four major QTLs detected in 2004 and 2005 were also significantly identified in combined data over the two years (Table 3).

QTLs for Peduncle Length

The composite interval mapping identified four QTLs for peduncle length in 2004 which explained 97% of the variation of the trait (Table 3). Among wheat chromosomes, *4D, 4B* and *2D* made the largest contribution to the expression of peduncle length. The *RhtD1-Xgwm888b, RhtB1-Xgwm935b* and *Xwmc25a-Xgwm261* intervals and also *Xcfd53* locus were the most important genome regions associated with peduncle length variation (Table 3). The estimated LOD scores in the *RhtD1-Xgwm888b* interval were 30.32 and 27.73 in data set obtained in 2004 and 2005, respectively, indicating the existence of highly significant QTLs in this interval. The expression of this QTL was almost the same in 2005 (R^2= 41.6%) and 2004 (R^2= 44.0%). Coefficient of determination for another QTL (Figure 2c-d) on chromosome *4B* was 30.6% in 2004 and 28.3% in 2005. Chromosome *2D* carried two major QTLs for peduncle length that were
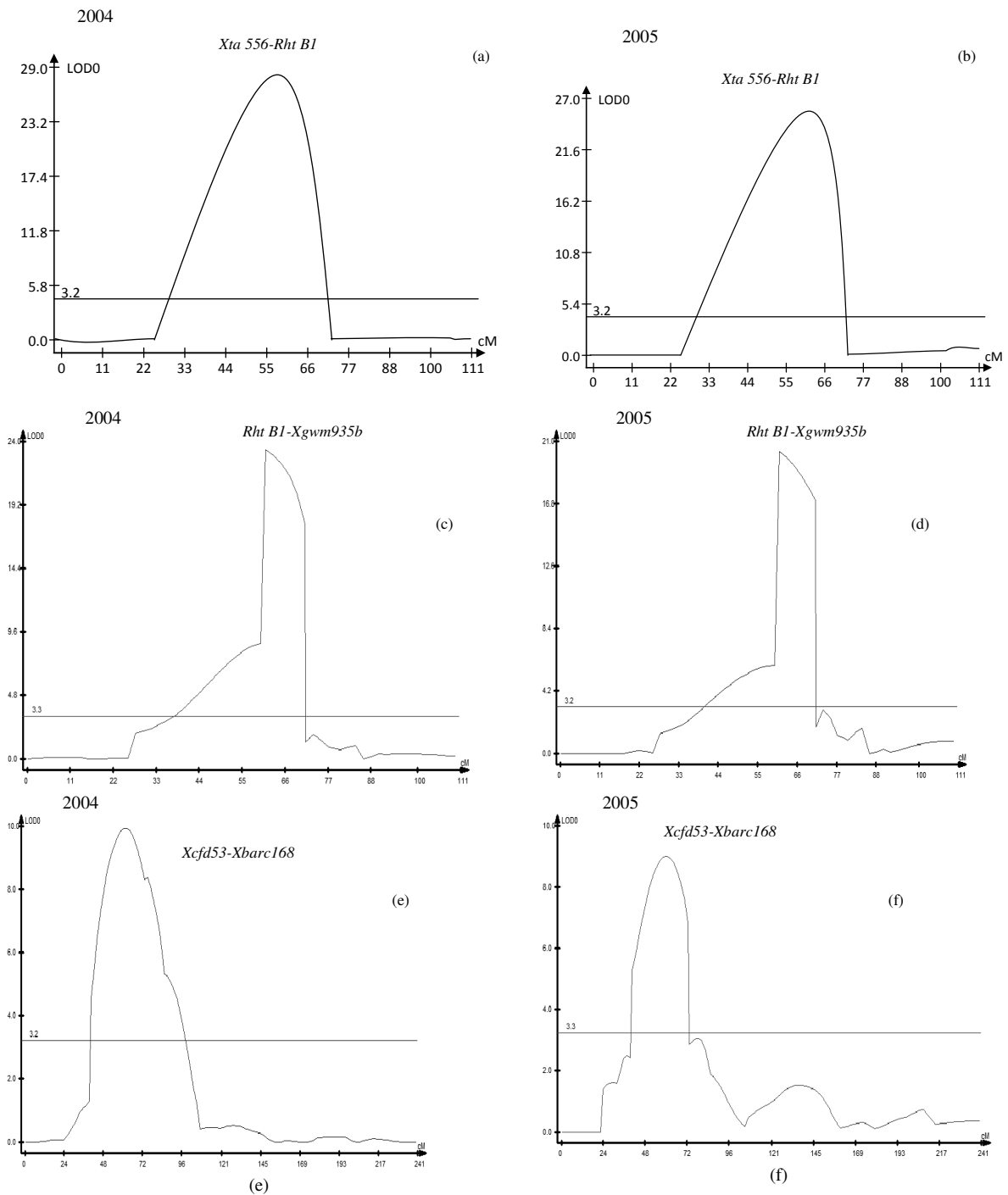
Figure 2. The LOD plot for a major QTL (marker interval is shown at peak of curve) of plant height (a and b) on chromosome 4B, peduncle length (c and d) on chromosome 4B and heading date (e and f) on chromosome 2D in 2004 and 2005. Horizontal and vertical axes represent the linkage group (cM) and LOD values, respectively.

Table 3. Results of composite interval mapping analysis for detection of QTLs for plant height, peduncle length and heading in 2004 and 2005.

Trait/QTL	Year	Chr[a]	Position (cM)	Closest markers or interval[b]	LOD	R[2c] (%)	Additive effect
Plant height (cm)							
	2004	4D	0.01	*RhtD1*	32.09	40.1	11.78
		4B	59.61	*Xta556-RhtB1*	28.79	33.6	-10.76
		2D	48.21	*Xcfd53*	15.38	13.9	-6.83
		2D	35.41	*Xwmc25a-Xgwm261*	11.79	9.6	-5.61
	2005	4D	0.01	*RhtD1*	30.78	41.9	14.05
		4B	59.61	*Xta556-RhtB1*	26.36	33.2	-12.28
		2D	42.21	*Xcfd53*	9.46	8.1	-6.09
		2D	33.41	*Xwmc25a-Xgwm261*	8.57	7.0	-5.57
Peduncle length (cm)							
	2004	4D	2.01	*RhtD1-Xgwm888b*	30.32	44.0	5.38
		4B	60.91	*RhtB1-Xgwm935b*	23.41	30.6	-4.46
		2D	48.21	*Xcfd53*	11.78	12.8	-2.87
		2D	33.41	*Xwmc25a-Xgwm261*	10.83	9.6	-2.46
	2005	4D	2.01	*RhtD1-Xgwm888b*	27.73	41.6	4.88
		4B	60.91	*RhtB1-Xgwm935b*	20.37	28.3	-4.06
		2D	33.41	*Xwmc25a-Xgwm261*	8.92	8.3	-2.16
		2D	42.21	*Xcfd53*	7.06	7.4	-2.06
		4B	73.21	*Xgwm48.c-Xpsp303b*	2.98	2.4	-1.92
Heading date (Day)							
	2004	2D	62.21	*Xcfd53-Xbarc168*	9.94	34.0	-3.12
		2D	75.01	*Xbarc168-Xgwm484*	8.38	23.4	-2.61
		2B	140.51	*Xgwm55-Xctop2.510*	3.72	9.4	1.67
		2B	127.11	*Xwmc344-Xac14*	2.74	7.0	1.44
	2005	2D	60.21	*Xcfd53-Xbarc168*	9.02	31.9	-1.79
		3A1	84.41	*Xbcd1278a-Xgwm2*	2.28	7.8	-0.89
		2B	119.01	*Xwmc35-Xwmc344*	3.30	7.8	0.90
		2B	112.21	*Xgwm429-Xgwm148*	3.06	7.3	0.86
		2D	78.21	*Xgwm484-Xcfd43*	3.07	7.3	-0.94
		2D	37.31	*Xgwm261-Xcfd53*	2.50	5.8	-0.85

[a] Chr denotes the chromosomes; [b] Those common intervals or markers identified over years are bolded, [c] The explained phenotypic variation by each QTL.

common in both years. QTL analysis based on combined data over years indicated that, out of five detected QTLs, four were common with those identified based on the analysis of data in each year. However, the minor QTL located in the *Xgwm48.c-Xpsp303b* interval was not detected in data analysis of 2004 and 2005 experiments. The sign and magnitude of additive effects for all common detected QTLs were similar in

2004, 2005 and combined data analysis. Therefore, it seems that, except for the QTL located in the *RhtD1-Xgwm888b*, alleles inherited from Oligo-culm had increasing effects on peduncle length.

QTLs for Heading Date

A highly significant QTL with LOD score of 9.94 (Figure 2e-f) was observed between *Xcfd53* and *Xbarc168* loci on chromosome *2D* and contributed to 34.0% and 31.9% of heading date variation in 2004 and 2005, respectively. For the *Xcfd53-Xbarc168* interval, the alleles derived from Fukuho-komugi had a decreasing effect on days to heading. Although QTLs identified on chromosomes *2D* and *2B* made the largest contribution to the expression of heading date, only expression of the QTL observed in the *Xcfd53-Xbarc168* interval was common over the years. Based on 2004 data set, the second significant QTL associated with heading date was located in the *Xbarc168-Xgwm484* interval, but this QTL was not located exactly at the same position in 2005 data analysis.

The QTL analysis using the data recorded in 2004 revealed that the most important genome regions of chromosome *2B* associated with heading date were the *Xgwm55-Xctop2.510* and *Xwmc344-Xac14* intervals that explained 9.4% and 7.0% of the heading date variation, respectively (Table 3). Although the QTL observed in *Xbcd1278a-Xgwm2* on 3A linkage group had no significant effect, it explained 7.8% of heading date variation in 2005. There were two QTLs on chromosome *2D* and *2B* for heading date, which were mapped in the *Xgwm484-Xcfd43* and *Xgwm261-Xcfd53* intervals. Composite interval mapping indicated that most of the QTLs identified based on single year data analysis were also detected in combined analysis of data over years (Table 3). The alleles derived from Fukuho-komugi parent had decreasing effect on days to heading for the most prominent QTLs located on chromosomes *2D* and *3A*.

DISCUSSION

Many authors have reported that plant height is genetically controlled by quantitative trait loci (QTL) (Börner *et al*., 1993; 1996; Cadalen *et al*., 1998; Marza *et al*., 2006; Huang *et al*., 2003, 2004). In the present study, the location of two highly significant QTLs of plant height was consistent with the expected location of *Rht1* and *Rht2*, the most prominent genes reported for plant height on chromosomes *4B* and *4D*, respectively (Worland, 1996). The QTL identified in the *Xwmc25a-Xgwm261* interval (on chromosome 2D) was mapped in the expected location of another height reducing gene, *Rht8*, which is known to be close to the *Xgwm261* locus (Worland, 1996; Ellis *et al*., 2002; Rebetzke *et al*., 2001). Although Ellis *et al*. (2007) showed that *Xgwm261* is not always associated with the *Rht8* dwarfing gene in wheat. Also, near *Xgwm261* locus, a QTL for stripe rust resistance was identified by Suenaga *et al*. (2003) using the same DH population evaluated in this study. The total phenotypic variation for plant height explained by QTLs were 97.2%, 90.2% and 96.5% based on the data of experiments in 2004, 2005 and the combined data over these years, respectively. Therefore, it can be concluded that the impact of environmental effects on the expression of plant height of this population was negligible.

The LOD scores indicated that QTLs for peduncle length located on chromosomes *4B, 4D* and *2D* were highly significant, using the combined data over years. But, the *Xgwm48.c-Xpsp303b* interval on chromosome *4B* carried a minor QTL which was only detected in the experiment conducted in 2005 and that based on combined data analysis. In the present study, most of the QTLs identified for length of peduncle were coincident with plant height QTLs that was in agreement with the results of Rebetzke *et al*. (2001). According to Borner *et al*. (2002), length of peduncle is of importance in disease escape and breeding

for resistance to head diseases, since, plants with shorter peduncles are more susceptible.

Variation in flowering time enables plants to optimize their use of resources available in the environments in which they grow (Laurie, 1997). Therefore, genes controlling flowering time have been investigated by many authors (Toth *et al*., 2003; Snape *et al*., 2001; Sarma *et al*., 2000; Zhang *et al*., 2009; Bullrich *et al*., 2002; Sourdille *et al*., 2000; Xu *et al*., 2005). The homologue group 2 of wheat showed the greatest contribution to the expression of heading date in the present study. Also, the composite interval mapping approach detected a major and highly significant QTL in the *Xcfd53-Xbarc168* interval on chromosome *2D* for this trait. The contribution of chromosome *2D* in the expression of heading time has been reported to be due to the presence of a photoperiodic responsive gene, *PpdD1,* (Worland, 1996). It is important to consider that this QTL (*Xcfd53-Xbarc168* interval) co-segregated with one of the QTLs observed for plant height. In this study, alleles derived from Oligoculm had a significant effect on reducing plant height and days to heading. Regarding the data analysis for heading date in 2004, there was another QTL identified close to *Xbarc168* locus that was not detected in 2005. The SSR marker *Xwmc35* is known to be located 17 cM distal to *Ppd-B1* (Worland, 1996). Also, the results of the present study showed that *Xwmc35* was close to a significant QTL for heading date that explained 7.8% and 10.7% of its variation based on the data of the second year and the pooled data analysis, respectively. Although the QTL close to *Xgwm261* had no significant effect on heading date, Sourdille *et al,* (2000) reported a major earliness QTL in the vicinity of *Xgwm261* marker.

In general, the results of the present study showed less influence of environmental effects on the expression of plant height compared with other traits, since all detected QTLs for plant height had stability over years. Based on the total explained phenotypic variation (over 90%) by plant height QTLs, it can be concluded that the size of population (107 DH lines) used in the present study was adequate for the detection of the most important genome regions of wheat involved in plant height variation. Some QTLs were significantly common for different traits. Therefore, focusing on the marker loci linked to the QTLs for simultaneous improvement of plant height and earliness will be more beneficial in wheat breeding programs.

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QTL های کنترل کننده ارتفاع بوته، طول پدانکل و سنبله‌دهی در گندم
(*Triticum aestivum* **L.**)

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چکیده

به منظور مکان‌یابی QTLهای ارتفاع بوته، طول پدانکل و سنبله‌دهی، از ۱۰۷ لاین هاپلوئید مضاعف (DH) گندم برگرفته از تلاقی Fukuho-komugi × Oligoculm در سال‌های ۱۳۸۲ و ۱۳۸۳ استفاده گردید. بر اساس روش مکان‌یابی فاصله‌ای مرکب (CIM) تعداد ۳۶ QTL شناسایی گردید. همه QTLهای شناسایی شده برای ارتفاع بوته در هر دو سال مشترک بودند. برای ارتفاع بوته، QTL نزدیک به *RhtD1* (روی کروموزوم ۴D) و QTL مکان یابی شده در فاصله نشانگری *Xta556-RhtB1* (کروموزوم ۴B) به ترتیب ۳۰/۷ و ۲۶/۳۶ درصد از تنوع این صفت را در سال های اول و دوم توجیه کردند. دو QTL بزرگ اثر دیگر برای ارتفاع بوته در نزدیکی نشانگرهای *Xcfd53* و *Xwmc25a* روی کروموزوم ۲D مکان‌یابی گردید. نتایج روش مکان‌یابی فاصله‌ای مرکب نشان داد که همه QTLهای طول پدانکل مطابق با QTLهای ارتفاع بوته بودند. از مهم‌ترین QTLهای مکان‌یابی شده برای سنبله‌دهی، تنها QTL (R^2 برابر ۳۴/۰ در سال اول و ۳۱/۹ در سال دوم) مشترک در ارزیابی‌های لاین‌ها در هر دو سال در فاصله نشانگری *Xcfd53-Xbarc168* روی کروموزوم ۲D قرار داشت که به ترتیب ۳۴/۰۵ و ۳۱/۹ درصد از تنوع این صفت را در سال‌های ۱۳۸۲ و ۱۳۸۳ توجیه کرد. در سال ۱۳۸۲ در فاصله نشانگری *Xbarc168-Xgwm484* (۸/۳ < LOD) یک QTL مهم دیگر برای سنبله‌دهی مکان‌یابی گردید. بطور کلی، با توجه به بروز QTL های بزرگ اثر و پایدار در هر دو سال، امکان استفاده از آنها و افزایش کارایی انتخاب در برنامه‌های انتخاب به کمک نشانگر برای به نژادی صفات مورد مطالعه وجود دارد.