International Journal of Plant Production 3 (1), January 2009
ISSN: 1735-6814 (Print), 1735-8043 (Online)
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Identification of major and minor genes associated with heading date in an *indica* × *indica* cross of rice (*Oryza Sativa* L.)

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Received 06 June 2008; Accepted after revision 25 September 2008; Published online 15 January 2009

Abstract

In this study, quantitative trait loci (QTLs) controlling rice heading date were detected in a $F_{2:3}$ population derived from a cross between an *indica* rice variety, Tarom Mahalli, with early heading date, and an *indica* variety, Khazar, with late heading date. SSR linkage map was constructed using 74 polymorphic markers and 192 F_2 individuals and covered a total of 1231.50 cM of rice genome. QTL mapping of heading date was performed by simple and composite interval mapping. Three major genes (*hd1*, *hd4* and *hd9*) were identified on chromosomes 1, 4 and 9 and two minor genes (*hd2a* and *hd2b*) were mapped on chromosome 2. Major genes explained over 60% of total phenotypic variation and had negative additive effects for decreasing heading date. These results will be useful in marker-assisted breeding to improve rice genotype with early heading date.

Keywords: Rice; Quantitative trait loci (QTL), QTL mapping; Composite interval mapping (CIM); heading date; SSR

Introduction

In rice, heading date is a key determinant in adaptation to different cultivation areas and cropping seasons. Therefore, appropriate variation of heading date within the optimum range in a particular region is an important objective in rice breeding programs. Genetic diversity for heading date was detected in Iranian cultivars (Ahmadikhah et al., 2008). Heading date is controlled by many genetic factors and environmental conditions, many genetic studies have revealed that genes responsible for photoperiod sensitivity and for basic vegetative growth duration involved in the control of heading date in rice. However, the detailed genetic control mechanism for heading date still remains to be characterized (Yano and Sasaki, 1997). Recently, natural variation has become an efficient resource for the genetic and molecular analysis of complex traits in rice (Yano and Sasaki, 1997; Yano, 2001; Lin et al., 2003). In the last decade, the progress in development of DNA markers and the developments of high-density molecular marker linkage maps in rice made

quantitative trait locus (QTL) analysis possible to clarify the number and nature of the genes controlling flowering time in rice (Yano and Sasaki, 1997) and have provided a powerful tool for elucidating the genetic bases of quantitatively inherited traits, including most of the agriculturally important traits. Many genetic studies have focused on genetic bases of heading date to determine the chromosomal location of genes controlling heading date in rice. For heading date, at least nine chromosomal regions have been reported as showing significant effect in various rice populations (Lin et al., 1996; Yano et al., 1997; Lin et al., 1998; Yamamoto et al., 2000; Lin et al., 2002; Monna et al., 2002; Takahashi et al., 2001). In particular, 15 QTLs for heading date (*hd1-hd3a, hd3b-hd14*) have been identified by using several types of progeny derived from crosses between a *japonica* variety, Nipponbare and an *indica* variety, Kasalath (Yano et al., 1997; Lin et al., 1998; Yamamoto et al., 2000; Lin et al., 2002; Monna et al., 2002). Lin et al. (1996), based on RFLP map identified, major and minor genes controlling heading date. In Tesanai2/C.B. population, two major genes on chromosome 3(*hd3*), 8(*hd8*) and two minor genes on chromosome 12 (*hd12a* and *hd12b*) were mapped. In another population (Waijyin2/C.B.), two major genes linked on chromosome 6 (*hd6a* and *hd6b*) and one minor gene on chromosome 8(*hd8*) were mapped (Lin et al., 1996). Yano et al., (1997) performed a QTL analysis of heading date using several type of progeny derived from a single cross between rice cv. Nipponbare (*japonica*) and rice cv. Kasalath (*indica*) and identified 14 QTLs controlling flowering time in rice. Five QTLs, *hd1* through *hd5,* have been mapped based on analysis of the F_2 population. Lin et al. (1998) detected three QTLs, *hd7, hd8* and *hd11,* by using backcross progeny such as BC_1F_5 lines. Yamamoto et al. (1998) using advanced backcross progeny, precisely mapped a major QTL on chromosome 6 (*hd6*), together with other two minor QTLs conditioning the trait. Yano et al. (2000) located five QTLs (*hd3, hd6, hd7a, hd7b* and *hd7c*) on chromosome 3, 6 and 7 for heading date, which jointly explained 53% of the total variance of this trait. In another experiment, six QTLs on chromosome 3, 6, 7 and 11 were resolved for heading date, collectively accounting for 63% of the total phenotypic variation. The Zhenshan 97 allele at *hd6* caused late heading, whereas alleles from Zhenshan 97 at other QTLs resulted in early heading. Yano et al. (2000) and Kojima et al. (2002) defined a genomic region of 12 kb as a candidate for *hd1*, and functionally determined the gene of the *hd1* locus, which is allelic to *Se1* (photoperiod sensitive gene) and has high homology with CONSTANT, a gene for flowering time in Arabidopsis. *hd6, hd9, hd10, hd12, hd13* and *hd14*, were found when Yamamoto et al. (2000) and Lin et al. (2002) used advanced backcross progeny, such as BC_3F_2 or BC_4F_2. Yu et al. (2002) analyzed the genetic bases of heading date and plant height at both single locus and two locus levels, using a population of 243 $F_{2:3}$ families derived from a cross between two elite rice lines. Six QTLs detected for heading date; the sex QTLs for heading date collectively accounted for a much greater amount of phenotypic variation than the QTLs for plant height. Fine mapping of *hd4* and *hd5* and quantitative trait loci (QTLs) for heading date in rice, was performed by using advanced backcross progeny derived from a cross between a japonica rice variety, Nipponbare, and an *indica* variety, Kasalath (Lin et al., 2003). *hd4* was mapped between restriction fragment length polymorphism (RFLP) markers R46 and C39 in the proximal region of chromosome 7, and *hd5* was mapped between C166 and R902 on the short arm of chromosome 8; both QTLs were mapped as single Mendelian factors (Lin et al., 2003). Lin et al. (2003) detected interaction between

hd5 and *hd1*, a key photo period sensitivity QTL, on the basis of an analysis of the F_2 population. Results of Lin et al. (2003) suggested that *hd5* is involved in photoperiod sensitivity and may act downstream or upstream of *hd1* in the same photoperiodic pathway. Fujini and sekiguchi et al. (2005) detected two QTLs controlling heading date on chromosome 6 and 7 using backcross inbred lines (BILs) derived from a cross between Hayamasari and Livorno. The most effective QTL, qDTH-7 on chromosome 7, accounted for 64.5% of total phenotypic variation.

The objective of the present research is to identify quantitative trait loci (QTLs) conferring genetic variation for heading date using a $F_{2:3}$ population derived from two *indica* variety Tarom Mahalli (TAM) and Khazar (KHZ) under natural field conditions in Iran.

Material and methods

A F_2 population of (192 individuals) was derived from a cross between rice cultivar Tarom Mahalli and Khazar. The parents and F_2 population was planted in Rice Research Institute of Iran (RRII) in paddy field during 2006. The seeds were harvested and stored at room temperature for 6 months. The seeds of $F_{2:3}$ populations, whose dormancy was broken, were used to evaluate heading date. 192 $F_{2:3}$ families were grown as spaced plants and induced to flowering under field condition at RRII. The plants were transplanted at a distance of 25 cm between plants on a row and the rows were 25 cm apart. The field management followed the normal agricultural practice. Only the 25 plants in the middle of each row were used for trait scoring. Days to heading was evaluated as number of days from seeding until heading. 192 plants of F_2 population were used to construct a linkage map. Leaves from the main stem of each F_2 plant were sampled, and genomic DNA was extracted according to Saghi Maroof et al. (1994). 365 SSR primer pairs which were appropriately distributed on 12 rice chromosomes were chosen according to Chen et al. (1997), Temnykh et al. (2000) and McCouch et al. (2002). These SSR primer pairs were surveyed based on their polymorphism between two parents, and the polymorphic primers were used to amplify the DNA of each plant of F_2 population. Polymerase Chain Reaction (PCR) was carried out in a total volume of 10 µL containing, 0.4 µL of each primer at a concentration of 5 µmol/L, 1.2 µL of each 2 mmol/L dNTP, 1.6 µL $MgCl_2$, 0.2 unit of *Taq polymerase* (5 U/µL), 1 µL of 10x PCR buffer for 1 PCR reaction and 2 ng of template DNA for 1 PCR reaction. PCR amplification was performed on a thermal cycler (*Biometra Uno II, Germany*) in biotechnology laboratory of Rice Research Institute of Iran. The amplification products were electrophoresed on 6% (w/v) polyacrylamide gels (38:2 acrylamide : bisacrylamide) and detected by silver staining as described by Basam et al. (1991) and Creste et al. (2001). SSR linkage map of F_2 population was constructed using *Map Manager QTXb17* software (Manly and Olson, 1999), and the genomic distance (in cM) was calculated from recombination value using Kosambi function (Kosambi, 1944). Using *Map manager QTbX17*, 12 linkage groups were constructed with a minimum LOD score 3.0. Simple Interval QTL mapping (SIM) related to heading date was conducted using the software *QTL cartographer v 2.5* software (Basten et al., 2001). A LOD score 2.5 was used to declare the presence of putative QTL in a genomic region and the percentage of total phenotypic variation and additive effects explained by each QTL for heading date

were calculated. To identify additional QTLs that may have been masked by the larger QTLs, Composite Interval Mapping (CIM) was employed. Automatic cofactor selection using a forward/backward regression (forward $p<0.01$, backward $p<0.01$) was performed with *QTL cartographer v 2.5* software (Basten et al., 2001). Significance threshold for CIM were determined at 11.5, LR (LOD=2.5). Interaction between detected QTLs was identified by the use of *QTLMapper* based on a mixed model approach (Wang et al., 1999).

Result and discussion

Frequency distribution in the $F_{2:3}$ Tarom Mahalli × Khazar population for segregating phenotypic classes of heading date is shown in Figure 1. Values of skewness and kurtosis for heading date were less than 1.0, indicating their approximately normal distribution and thereby being suitable for QTL mapping. A linkage map based on F_2 population was constructed, which covered a total of 1231.50 cM with an average interval of 19.83 cM between two loci. The position of most SSR markers on chromosomes was identical with the previous reports (Figure 2).

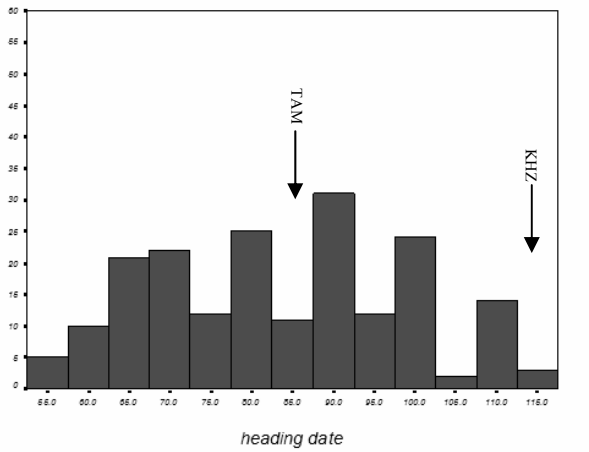

Figure 1. Frequency distribution of heading date (days from seeding until flowering) in $F_{2:3}$ families of Tarom Mahalli and Khazar population.

In this study, we analyzed the genetic basis of heading date using a population of 192 $F_{2:3}$ families derived from a cross between two Iranian rice cultivars. Up to now, several QTLs for heading date (*hd1-hd3a*, *hd3b-hd14*) have been identified by using several types of progeny derived from crosses between *japonica* varieties and *indica* varieties (Yano et al., 1997; Lin et al., 1998; Yamamoto et al., 1998; Yamamoto et al., 2000; Lin et al., 2000; Lin et al., 2002; Monna et al., 2002). Any knowledge of the genetic mechanism of heading date will be of benefit to rice breeders; on the other hand, the genetic information on the heading date of Iranian rice germplasm and *indica* × *indica* cross is limited. We identified QTLs related to heading date in a population caused from *indica* × *indica* crosses.

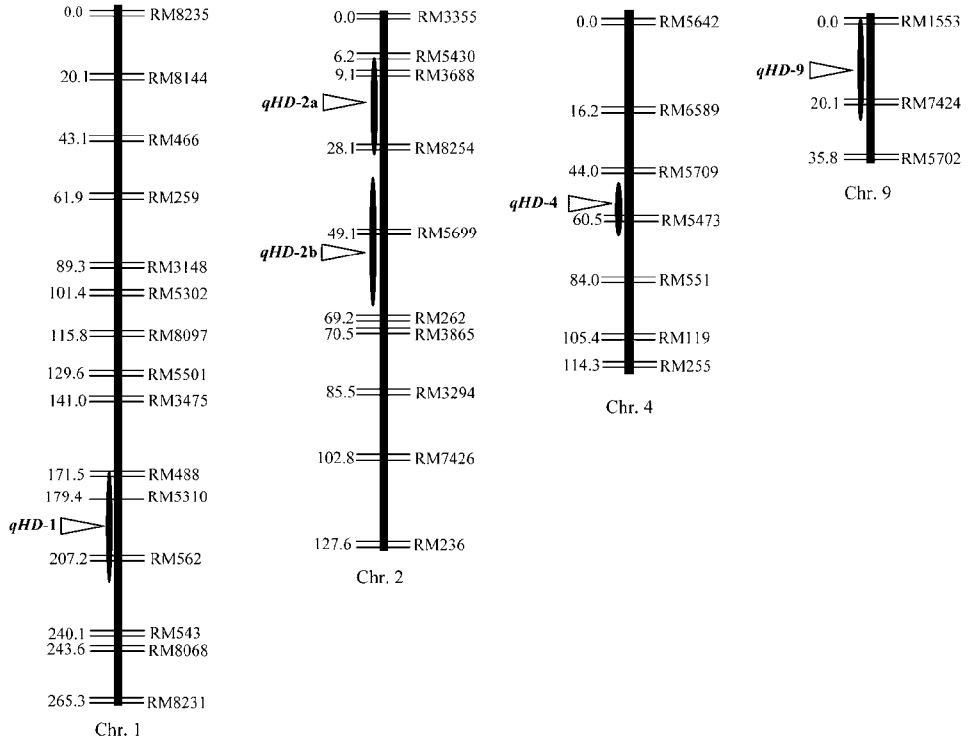

Figure 2. The position of QTLs for heading date in Tarom Mahalli × Khazar cross.

The heading date of different varieties performs differentially and is affected by different condition of light and temperature. In this study, one native population was constructed using two varieties of early season *indica* rice and lately season *indica* rice, and genes for heading date were mapped. Heading date of $F_{2:3}$ families showed a continuously variation and may be a quantitative trait. However, 3 major genes and some minor genes were mapped in Iranian rice population by interval mapping and composite interval mapping. This study thus demonstrated that heading date of rice was a qualitative-quantitative trait controlled by major and minor genes together.

Two QTLs were identified for heading date on chromosomes 2 and 9. These QTLs located in interval RM8254-RM262 (*hd2*) and RM1553-RM5702 (*hd9*), respectively. *hd2* and *hd9* showed negative effects on the heading date with an LR score of 12.31 and 11.24, respectively, explaining 6.9% and 8.28% of the total phenotypic variance, respectively. In these QTLs, alleles from TAM decreased heading date and also putative QTLs showed over dominance effect for heading date.

Five QTLs were mapped for heading date by CIM method. Two QTLs out of the five QTLs located on chromosomes 2. Amongst them, three QTLs with the largest effects were *hd1*, *hd4* and *hd9* that individually explained 20.13, 23.17 and 23.62% of the total phenotypic variation and had an additive effect of -1.29, -2.81 and -4.15 days, respectively.

In the case of four QTLs out of five QTLs the alleles for decreased heading date were from TAM whereas for other QTL, the alleles for increased heading date were from KHZ. All of the QTLs showed overdominance effects for decreased heading date.

Interval mapping analysis detected two QTLs (*hd2* and *hd9*) for heading date; collectively the QTLs for heading date accounted 14.97% of total phenotypic variation. Five QTLs (*hd2a*, *hd2b*, *hd1*, *hd4* and *hd9*) located on chromosomes 1, 2, 4 and 9 were detected for heading date by composite interval mapping, which joinly explained 95% of the total variation of this trait in this population. Yamamoto et al. (2000) and Lin et al. (2002) using advanced backcross progeny, such as BC_3F_2 or BC_4F_2 found a QTL (*hd9*) for heading date on chromosome 9. *hd9* wasn't detected by F_2 or BC_1F_5 population. Yu et al. (2002) mapped QTLs related to heading date in $F_{2:3}$ population. Five QTLs (*hd3*, *hd6*, *hd7a*, *hd7b* and *hd7c*) located on chromosome 3, 6 and 7 were detected for heading date in 1994 (Yu et al., 2002), which jointly explained 53% of the total variance of this trait in this population. In 1995 (Yu et al., 2002), six QTLs on chromosome 3, 6, 7 and 11 were resolved for heading date, collectively accounting for 63% of the total phenotypic variation. The Zhenshan 97 allele at *hd6* caused late heading, whereas alleles from Zhenshan 97 at other QTLs resulted in early heading (Yu et al., 2002). In our study, the Khazar allele at *hd2a* caused late heading, whereas alleles from Tarom Mahalli at other loci resulted in early heading.

Table 1. Putative QTLs for heading date in the $F_{2:3}$ populations derived from TAM × KHZ cross.

QTL[a]	Chr.	Flanking Markers	position	Peak LR	a[b]	d[c]	Dpe[e]	PEV[d]
Interval Mapping								
hd2	2	RM8254-RM262	49.15	12.31	-1.96	7.33	TAM	6.69
hd9	9	RM1553-RM5702	12.01	11.24	-2.29	8.52	TAM	8.28
Composite Interval Mapping								
hd2a	2	RM5430-RM5699	9.10	10.53	0.12	4.98	KHZ	12.85
hd2b	2	RM8254-RM262	49.15	11.42	-2.04	6.98	TAM	11.17
hd1	1	RM448-RM543	195.44	16.29	-1.29	8.93	TAM	20.13
hd4	4	RM5709-RM551	60.5	9.86	-2.81	7.20	TAM	23.17
hd9	9	RM1553-RM5702	8	10.72	-4.15	8.46	TAM	23.62

[a]QTLs are named by abbreviations plus chromosomal number.
[b]Additive effect,
[c]Dominant effect,
[d]Percentage of total phenotypic variance explained by the QTL,
[e]Direction of phenotypic effect, TAM and KHZ indicate Tarommahalli (TAM) and Khazar (KHZ), respectively.

A test for interactions between marker loci for heading date identified a relatively small number of potential epistatic interactions between loci (Table 2). Five important digenic interactions out of all interaction detected affected on heading date (Table 2). All of these interactions showed small effects on heading date with R^2 ranging from 6.23 to 9.62%, with

an average R^2 of 8.25%. For two of these interactions, the two-locus parental genotypes were associated with increased heading date while, for the other three, the negative effects on the trait were contributed by the two-locus recombinants.

Table 2. Five important digenic epistatic loci affecting heading date in the TAM/KHZ $F_{2:3}$ population of rice

Loci (i)		Loci (j)		LR	A^a	R^{2b}
Chromosomes	Intervals	Chromosomes	Intervals			
1	RM8097-RM3475	2	RM8254-RM262	14.76	3.75	9.34
1	RM8097-RM3475	9	RM1553-RM5702	9.73	-1.08	7.55
4	RM5709-RM551	3	RM416-RM6832	10.82	-2.34	9.62
2	RM8254-RM262	5	RM421-RM480	9.52	2.57	6.23
7	RM5481-RM11	5	RM421-RM480	8.32	-2.99	8.53

[a]Additive . additive effect
[b]Variance explained by each pair of epistatic loci.

A number of QTLs for heading date have also been reported previously. Of the QTLs detected in this study with relatively large genetic effects (*hd1*, *hd4* and *hd9*), *hd1*, *hd4* may well correspond with the locus *hd1* and *hd4* for photoperiod response on chromosome 1 and 4 respectively (Yamamato et al., 1998). The QTL *hd2* is located in approximately the same region as a QTL (*hd2*) for flowering time reported previously (Yano et al., 1997). Additionally, the QTL *hd2* may also correspond with the E1 locus (*hd4*) suggested previously by Yano et al. (1997). However, the cloned QTL (*hd3*, QTL detected with a minor effect) was not detected in the present study. *hd3* was identified for flowering time in previously reports (Li et al., 1995; Xiao et al., 1996). It is possibly due to the specific germplasm used in our study which had an Iranian rice germplasm.

Although some of the heading date related QTLs identified through the study of progeny from crosses between Tarom Mahalli and Khazar have been analyzed at the molecular level (For example, *hd1*, *hd2a*, *hd2b*, *hd4* and *hd9* have been mapped by using an $F_{2:3}$ population in this study), these QTLs could not be characterized in detail because of the lack of appropriate advanced backcross progenies or NILs. Further genetic and molecular analysis of these QTLs may provide a clue to understanding the divergent features in the genetic control mechanisms of the photoperiodic response of heading in rice.

Some of QTLs (for example, *hd4* and *hd5* on choromosomes 7 and 8 respectively in study of Lin et al. 2003) was not detected in the present study. Precise localization of QTLs for heading date in Iranian rice population remained a problem due to less SSR markers used and low density linkage map and thus it is suggested that further study should be performed with more SSR markers and perpetual mapping population. Henceforth, it is necessary to analyze genes for heading date in other varieties using new molecular methods and to map different genes for heading date of rice. These studies will be useful in rice breeding and cloning of these genes.

Acknowledgment

The authors are grateful to prof. Abdolmajid Rezaei, Dr. Ali Moumeni, Ahmadreza Dardras, Mahnaz Katouzi and Ali Akbar Ebadi for their excellent assistance. We also thank

from Gorgan Univetrsity, Rice Research Institute of Iran and Isfahan University of Technology for their support.

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