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Linkage Map of SSR Markers and QTLs Detection for Heading Date of Iranian Rice Cultivars

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ABSTRACT

The construction of molecular maps and identification of genomic regions controlling quantitative traits have great significance for plant breeders. In this study, a genetic analysis of quantitative trait loci (QTLs) affecting the heading date of rice was performed using an F_2 population of a cross between two Iranian landrace cultivars, Domsephid and Gerdeh, comprising 192 plants. An approximately normal distribution was observed for the heading date in the F_2 population. A genetic linkage map with 88 informative microsatellite markers (SSR) was constructed, which covered 1367.9 cM of the rice genome with an average distance of 18 cM between markers. Single marker analysis (SMA) and interval mapping (IM) procedures were used to detect the QTLs controlling heading date and QTLs identified were further confirmed using composite interval mapping (CIM). Six significant QTLs (LOD≥3.0) were identified for the heading date, of which three major QTLs mapped on chromosomes 6 *(hd6)*, 7 *(hd7)* and 8 *(hd8)* had particularly high LOD scores and explained 23.5%, 19.8% and 20.5% of the total phenotypic variance, respectively. Three other minor QTLs detected for the heading date, located on chromosomes 1 *(hd1)*, 3 *(hd3)* and 11 *(hd11)*, accounted for 6.6%, 11.7% and 6.6% of the phenotypic variation, respectively. The additive effect of a single QTL ranged from 1.67 to 3.91 days. In the QTL *hd6*, alleles from Domsephid were responsible for reducing the heading date, while in the other five QTLs, alleles from Gerdeh caused a decrease in the heading date. The QTLs *hd1, hd3* and *hd8* showed over dominance effects for increasing the heading date, whereas the other three QTLs had partial to incomplete dominance effects for increasing (*hd7* and *hd11*) and reducing (*hd6*) the heading date.

Keywords: Heading date, Linkage map, Microsatellite markers, Rice, Quantitative trait loci.

INTRODUCTION

Most agronomic traits in rice have continuous phenotypic variation and are controlled by quantitative trait loci (QTLs). The identification and mapping of QTLs for such traits has great significance for rice breeders. Since the introduction of molecular markers and the development of high-density molecular linkage maps in rice (Causse *et al*., 1994; Chen *et al*., 1997; Temnykh *et al*., 2000; McCouch *et al*., 2002), many quantitative traits like the heading date has been studied and QTLs affecting this important trait have also been identified (Li *et al*., 1995; Lu *et al*., 1997; Lin *et al*., 1998; Maheswaran *et al*., 2000; Zhou *et al*., 2001; Brondani *et al*., 2002; Yu *et al*., 2002; Hittalmani *et al*., 2002).

Xiao *et al*. (1996), using recombinant inbred lines, mapped a major QTL for heading date on chromosome 8 and two minor QTLs on chromosomes 3 and 11, while Yano *et al*. (1997) using an F_2 population, detected two major QTLs on chromosomes 6 (*Hd1*) and 7 (*Hd2*) and other three minor QTLs on chromosomes 6, 7 and 8 (*Hd3, Hd4* and *Hd5,* respectively). Lin *et al*. (2000), using near isogenic lines, revealed that *Hd1, Hd2* and *Hd3* are involved in photoperiod sensitivity. Additional analysis using a large segregating

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population derived from advanced backcross progeny constructed a high-resolution linkage map of *Hd3* on the short arm of chromosome 6 and detected two tightly linked genes controlling the heading date in the *Hd3* region (Monna *et al*., 2002). He *et al*. (2001) identified a major QTL on chromosome 8 which explained 35% of the phenotypic variation, and a minor QTL on chromosome 12. Yamamoto *et al*. (2001) mapped four QTLs on chromosomes 3, 4, 6 and 8, of which two QTLs identified on chromosomes 6 and 8 had large effects on heading date. Septiningsih *et al*. (2003) detected the QTLs controlling days to heading using an advanced backcross population and found six QTLs with small effects on chromosomes 2 (two QTLs), 7 (two QTLs), 11 and 12.

The high-coincidence of QTLs identified for heading date on chromosomes 3, 6, 7 and 8 for rice varieties belonging to the Japonica and Indica subspecies aroused our interest in verifying as to whether the QTLs detected for Iranian rice varieties show similar tendencies. While many researchers have identified the QTLs in rice varieties apart from Rabiei *et al*. (2004), who found QTLs controlling grain size and shape, there is no other report on QTL mapping in Iranian rice cultivars.

In this study, a genetic analysis of QTLs governing the heading date of rice was carried out using an F_2 population derived from a cross between two Iranian landrace cultivars. Genetic analysis then followed to determine the number, chromosomal location, gene action and magnitude of effects of QTLs controlling heading date.

MATERIALS AND METHODS

Plant Materials and Field Experiments

Two Iranian landrace rice cultivars, Domsephid as the female parent and Gerdeh as the male parent, were crossed in 2001. Domsephid is a tall aromatic cultivar with long grains, low yield and a late heading date cultivated in Guilan Province of Iran, while Gerdeh is a semidwarf cultivar with short grains, relatively high yielding and with an early heading date cultivated in Azarbaijan Province of Iran. Both cultivars are basically landraces that have been cultivated by farmers over years and now carefully maintained along with other landraces for their genetic purity at the Rice Research Institute of Iran (RRII) at Rasht, Iran.

From this cross, approximately 40 F_1 hybrid plants were obtained. F_1 selfed seeds were collected from those F_1 plants and grown as an F_2 population. One hundred and ninety two F_2 plants, 20 replications of F_1 plants and the two parents, were raised in an experimental field with a spacing of 25×25 cm at the RRII. The heading date was measured as the days from sowing to emergence of the first panicle for each F_2 plant.

Construction of SSR Map

Genomic DNA was extracted from young and fresh leaves of F_2 plants and the two parents, as described by Dellaporta *et al*. (1983) with minor modifications. Based on the published rice SSR maps (Chen *et al*., 1997; Temnykh *et al*., 2000; McCouch *et al*., 2002), 88 informative SSR markers distributed throughout 12 chromosomes of rice were selected and scored on F_2 plants. SSR analysis was performed as described by Chen *et al*. (1997) and silver staining according to Panaud *et al*. (1996), with slight modifications. The software Mapmaker/EXP ver. 3.0 (Lander *et al*., 1987; Lincoln *et al*., 1993a) was used to construct the linkage map with a minimum threshold LOD score of 5.0 and a maximum recombination fraction of 0.3. The Kosambi map function (Kosambi, 1944) was employed to convert the recombination frequencies to marker distances in centiMorgan (cM), and the order of the markers was established using three-point analysis.

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QTL Identification

Segregation ratios at the marker loci for the three genotypic classes (homozygous Domsephid, heterozygous Domsephid/ Gerdeh, and homozygous Gerdeh) were compared with the expected ratios 1:2:1, based on Chi-square tests, and the skewedness of the marker loci were determined. The analysis of quantitative trait loci (QTLs) was performed using three analytical methods. Firstly, single marker analysis and interval mapping (Lander and Botstein, 1989) were used to identify the genomic regions affecting the heading date using Mapmaker/QTL ver. 1.1b (Lincoln *et al*., 1993b). Since the single marker analysis and the interval mapping is generally affected by two or more linked QTLs located on a chromosome, the composite interval mapping (Zeng, 1993 and 1994) was then used to confirm the identified QTLs using QTL Cartographer ver. 1.3 (Basten *et al*., 2001).

RESULTS AND DISCUSSION

Phenotypic Variation

The phenotypic distribution of heading dates in 192 F_2 plants is shown in Figure 1. An approximately normal distribution was observed for the heading dates. Some F_2 progenies showed extreme values, with values more than the higher parent (Domsephid) and less than the lower parent (Gerdeh), indicating a transgressive segregation for the heading date. The phenotypic value of the heading date was significantly different ($P<0.01$) between the two parents. The heading date for the female parent, Domsephid, was 99.19 ± 2.25 days, which was 18.7 days more than the male parent, Gerdeh. The mean value of heading dates in F_1 and F_2 progenies was closer to the higher parent Domsephid (95.45 ± 1.68 and 93.52 ± 7.27 for F_1 and F_2 plants, respectively).

Construction of Linkage Map

The linkage map consisting of 88 SSR markers was constructed, which covered 1367.9 cM of the 12 rice chromosomes with an average distance of 18.0 cM between marker loci. The chi-square tests of the observed frequencies of each marker locus in 192 F_2 plants indicated that deviations from the expected ratio of 1:2:1 were significant

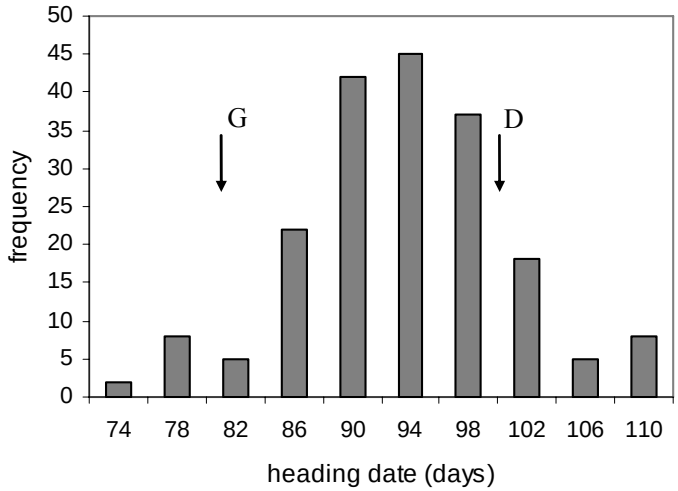

Figure 1. Phenotypic distribution of heading date in 192 F_2 progenies. D and G represent the phenotypic values of the parents Domsephid and Gerdeh, respectively.

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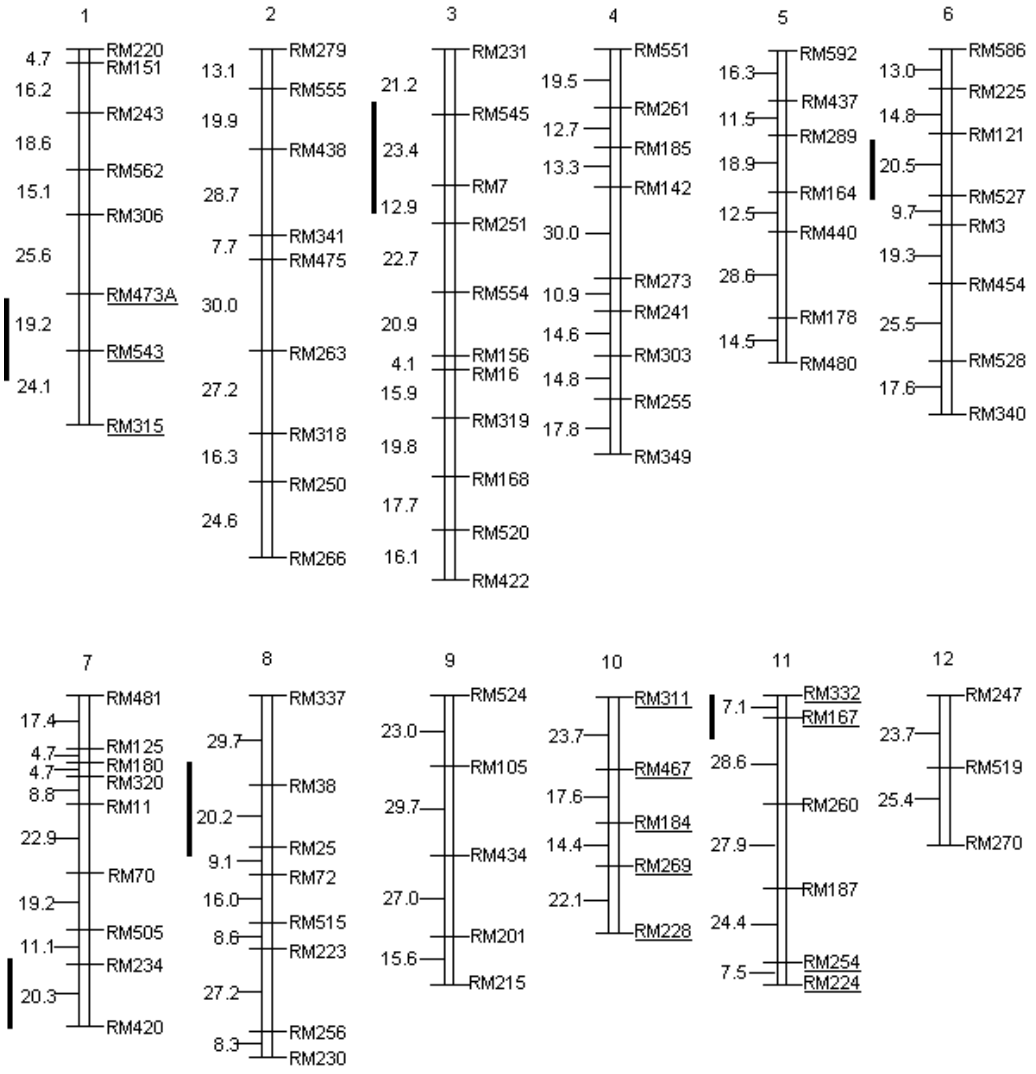

Figure 2. Linkage map of 88 SSR markers showing locations of QTL for heading date in the 192 F_2 individuals from the cross Domsephid/Gerdeh. Lengths of the vertical lines indicate a one-LOD support interval for the putative QTL. Kosambi values (cM) and markers are indicate left and right of the chromosomes, respectively. The underlined marker loci are skewed markers.

($P<0.05$) for 12 of 88 (13.64%) mapped markers. These skewed marker loci corresponded to four linked chromosomal regions on three different chromosomes (Figure 2). Comparison of the resulting linkage map and the maps of the Chen *et al*. (1997), Temnykh *et al*. (2000) and McCouch *et al*. (2002) showed that all markers were located in the expected order on the chromosomes.

QTL Mapping

Six QTLs (*hd1, hd3, hd6, hd7, hd8* and *hd11*) were mapped for their heading date on chromosomes 1, 3, 6, 7, 8 and 11 (Table 1 and Figure 2). Amongst these, three QTLs located on chromosomes 6 (*hd6*), 7 (*hd7*) and 8 (*hd8*) had particularly high LOD scores and explained 23.5%, 19.8% and 20.5% of the total phenotypic variation, re-

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Table 1. QTLs affecting heading date (HD) in the 192 F_2 plants derived from a cross between two Iranian rice cultivars Domsephid and Gerdeh.

QTL[a]	Interval	Pos. (cM)[b]	LOD[c]	R^{2d}	a[e]	d[f]	d/|a|[g]
hd1	RM473A-RM543	10	3.10	6.6	-2.08	2.33	1.12
hd3	RM545-RM7	8	3.48	11.7	-1.82	2.21	1.21
hd6	RM121-RM527	12	5.76	23.5	2.71	-1.06	-0.39
hd7	RM234-RM420	4	4.85	19.8	-1.67	1.12	0.67
hd8	RM38-RM25	10	5.13	20.5	-3.91	4.32	1.10
hd11	RM332-RM167	7	3.14	6.6	-2.45	1.76	0.72

[a] :QTLs are named by trait abbreviation plus chromosomal numbers.
[b] :QTL positions are measured as distance from left marker per interval.
[c]:Log_{10}-likelihood.
[d]:Percentage phenotypic variance explained.
[e]:Additive gene effect of putative QTL.
[f] :Dominance gene effect of putative QTL.
[g]:Degree of dominance.

spectively. The additive effect of a single QTL ranged from 1.67 to 3.91 days. Domsephid alleles at *hd6* (chromosome 6) caused a decrease in heading date, whereas in the other five putative QTLs, alleles from Gerdeh were responsible for a reduced heading date. There were QTLs (*hd1, hd3* and *hd8*) that showed overdominance effects (with d/a ratios of 1.12, 1.21 and 1.10, respectively) for an increased heading date, while the other three QTLs showed partial to incomplete dominance effects for increased (*hd7* and *hd11*) and reduced (*hd6*) heading date.

Gene Action and Effect of QTLs on Heading Date

For successful QTL mapping studies, large differences between parents for traits studied are the essential requirements. Likewise in this study, the female parent Domsephid and the male parent Gerdeh differed significantly in terms of heading date. The percentage of phenotypic variation explained by each QTL ranged from 6.6% to 23.5%, with an average of 14.78%. Among these six QTLs, three of them accounted for a phenotypic variation of more than 19.8% (Table 1). This showed that the heading date might be governed by two or three major QTLs that explained the large proportion of phenotypic variation and several minor QTLs each explaining a small proportion of phenotypic variance. Similar findings have been reported by several researchers who had also identified two or three major loci similar to *hd6, hd7* and/or *hd8* that control heading date. Yano *et al*. (1997) had detected two major QTLs for heading date on chromosomes 6 (linked to R1679 marker locus) and 7 (linked to C728 marker locus), and three other minor QTLs on chromosomes 6, 7 and 8. Among the QTLs that identified relatively large genetic effects in this study, *hd6* within the interval of RM121-RM527 should be the same locus as with the earlier studies (Yano *et al*., 1997; Lin *et al*., 1998; Maheswaran *et al*., 2000; Yamamoto *et al*., 2001). Further, the major locus mapped on chromosome 7 in this study (*hd7*) between RM234-RM420 interval could be the same locus reported in previous studies (Yano *et al*., 1997; Lin *et al*., 1998). Xiao *et al*. (1996) had detected a major QTL controlling the days to heading on chromosome 8 (linked to RZ562) that accounted for 51% of total phenotypic variance. Moreover, Lu *et al*. (1997), He *et al*.

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(2001) and Yamamoto *et al*. (2001) had also found a QTL for days to heading on chromosome 8 which explained a large proportion of the phenotypic variation. The QTL mapped on chromosome 8 (interval RM38-RM25) in this study (*hd8*) is located in approximately the same region as a QTL for days to heading reported previously. Li *et al*. (1995) and Hittalmani *et al*. (2002) had identified a major QTL for the heading date on chromosome 3 (near to RG348). However, in this study, a minor QTL was detected on chromosome 3 (*hd3*) within the interval of RM545-RM7, which should be the same locus as that of the earlier mapped as major QTL. Two new minor QTLs i.e. *hd1* (interval RM473A-RM543) and *hd11* (interval RM332-RM167) that were mapped for the heading date in this study, may be loci unique to the Iranian parents studied. Nevertheless the QTL *hd11* detected in this study can be the same locus as compared with the minor QTL identified by Xiao *et al*. (1996) and Septiningsih *et al*. (2003).

The degree of dominance, which is presented as the ratio of dominance to additive effects (d/a), for three QTLs detected for heading date was overdominance towards an increased heading date and three QTLs were partial to incomplete dominance towards an increased heading date, except for *hd6* which exhibited a negative partial dominance for a reduced heading date (Table 1). These high levels of dominance can be related to the heterosis as observed in the F_1 hybrid. Several researchers such as Li *et al*. (1995) and Yu *et al*. (2002) have also reported partial dominance or overdominance effects for the QTLs controlling heading date.

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نقشه لینکاژی نشانگرهای SSR و شناسایی QTL های کنترل کننده تاریخ گلدهی در ارقام برنج ایرانی

ب. ربیعی

چکیده

تهیه نقشه های مولکولی و شناسایی نواحی ژنومی کنترل کننده صفات کمی (QTLs) اهمیت زیادی برای به نژادگران گیاهی دارد. در این مطالعه، تجزیه ژنتیکی QTLهای کنترل کننده تاریخ گلدهی با استفاده از ۱۹۲ گیاه F_2 حاصل از تلاقی دو رقم برنج ایرانی (دم سفید و گرده) انجام شد. توزیع فنوتیپی تاریخ گلدهی در جمعیت مورد مطالعه تقریباً نرمال بود. نقشه پیوستگی ژنتیکی ۸۸ نشانگر چند شکل ریز ماهواره (SSR) در جمعیت F_2 حاصل، ۱۳۶۷/۹ سانتی مورگان از کل ژنوم برنج را پوشش داد و فاصله متوسط نشانگرها از یکدیگر ۱۸ سانتی مورگان بود. برای شناسایی QTLها، ابتدا از دو روش تجزیه تک نشانگری (SM) و مکان یابی فاصله ای (IM) استفاده گردید و سپس برای تأیید QTLهای شناسایی شده از مکان یابی فاصله ای مرکب (CIM) استفاده شد. در مجموع، شش QTL (LOD≥3.0) برای تاریخ گلدهی شناسایی گردید که سه QTL بزرگ اثر بوده و با LOD نسبتاً بالا در روی کروموزوم های ۶ (*hd6*)، ۷ (*hd7*) و ۸ (*hd8*) مکان‌یابی شدند و به ترتیب ۲۳/۵٪، ۱۹/۸٪ و ۲۰/۵٪ تنوع فنوتیپی تاریخ گلدهی را کنترل کردند. سه QTL کوچک اثر دیگر در روی کروموزوم های ۱ (*hd1*)، ۳ (*hd3*) و ۱۱ (*hd11*) شناسایی شدند و به ترتیب ۶/۶٪، ۱۱/۷٪ و ۶/۶٪ از تنوع موجود در تاریخ گلدهی را توجیه کردند. اثر افزایشی QTLها از ۱/۶۷ تا ۳/۹۱ روز متغیر بود و به استثنای *hd6* که در آن الل های والد دم سفید موجب کاهش تاریخ گلدهی شدند، در پنج QTL دیگر الل های کاهش دهنده تاریخ گلدهی از والد گرده بودند. برآورد درجه غالبیت QTLها نشان داد که QTLهای *hd1*، *hd3* و *hd8* اثرات فوق غالبیت ژن ها را برای افزایش تاریخ گلدهی در بر داشتند، در حالی که سه QTL دیگر غالبیت جزئی تا ناقص ژن ها را برای افزایش (*hd7* و *hd11*) و کاهش (*hd6*) تاریخ گلدهی نشان دادند.

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