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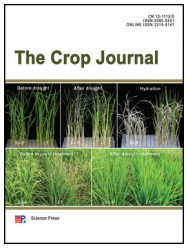

Minor-effect QTL for heading date detected in crosses between *indica* rice cultivar Teqing and near isogenic lines of IR24

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ABSTRACT

Identification of quantitative trait loci (QTL) having small effects on heading date (HD) is important for fine-tuning flowering time in rice (*Oryza sativa* L.). In this study, minor-effect QTL for HD were identified using five segregating rice populations, including a recombinant inbred line population derived from crosses between *indica* cultivar Teqing and near isogenic lines of IR24, and four populations derived from residual heterozygotes identified in the original population. HD data from these populations were obtained in multiple years or at two locations with different photoperiods. A total of 11 QTL were detected; they had small additive effects ranging from 0.21 to 1.63 days. The QTL were all detected in different populations, locations and/or years, having consistent allelic effects across experiments and a stable magnitude across years at the same location. These QTL, and other minor-effect QTL that have been cloned or fine-mapped, generally do not have strong photoperiod sensitivity, and thus can be used in a wide range of eco-geographical conditions. Seven of the 11 QTL were different from those that have been cloned or fine-mapped, providing new candidates for gene cloning and marker-assisted breeding. Allelic effects of QTL corresponding to those that had been cloned or fine-mapped, were much smaller in this study than previously reported. The results supported the assumption that qualitative and quantitative genes may be different alleles at the same loci, suggesting that it may be promising to identify minor-effect QTL from major heading date genes/QTL that have been cloned.

1. Introduction

Flowering is prerequisite for grain production in cereal crops. Timing of flowering is the key to maintaining an appropriate balance between full use of resources and avoidance of environmental stresses. High yield in rice (*Oryza sativa* L.) is associated with long growth duration in most growing areas [1–3]; however, early flowering is required for double-season

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cropping and for production in northernmost cultivation areas [4–6]. The wide range of variation in flowering time in rice is controlled by many quantitative trait loci (QTL) that vary greatly in magnitude of additive effects and in association with photoperiod sensitivity [7]. Large-effect QTL often have strong responses to photoperiod and play critical roles in eco-geographical adaptation [8–10]. Small-effect QTL generally adjust heading by several days without obvious photoperiod sensitivity, allowing flowering time to be fine-tuned for optimal use of the available temperature and light [11–13].

Over the past two decades, a complex gene network of regulation of flowering time in rice was unraveled whereby most pivotal genes are large-effect QTL isolated by map-based cloning [7]. In recent years, more attention has been given to QTL with relatively small effects. For example, two minor-effect QTL for flowering time were cloned [11,12], and three others were fine-mapped [13–15]. It was shown that minor-effect QTL also make important contributions to flowering regulation. Nevertheless, many more QTL with small effect were detected as large regions of statistical significance [16,17]. Further genetic analysis including fine-mapping, gene cloning, and functional characterization are necessary. Since minor-effect QTL may have inconsistent additive effects across different genetic backgrounds and environments, selection of reliable candidates for further study remains a challenge. In this regard, specific types of mapping populations could prove useful [16].

A primary mapping population of rice generally has wide phenotypic variation, but only a small number of QTL with relatively large effects are found [18–20]. A common way to detect QTL that failed to show significant effects in original populations has been the use of secondary populations in which previously detected major QTL are fixed [21–23]. The use of a population derived from a cross between two cultivars carrying the same allele at major locus could also facilitate the detection of minor QTL [24]. Presumably, a population derived from a cross between two cultivars of similar ecological adaption could be used to detect minor QTL for flowering time. In a previous study [25], we constructed a recombinant inbred line (RIL) population for which the male and female parents were middle-season *indica* rice cultivars with similar eco-geological adaptation. As expected, a small range of variation on flowering time was observed. This population and four others derived from its progenies were used in the present study that aimed to identify QTL having consistent small effects on flowering time. QTL analysis was firstly performed using the original RIL population, followed by two runs of validation with increasing homogeneity of the genetic background. A total of 11 QTL were detected. All were detected in different populations, locations and/or years and showed small and stable additive effects.

2. Materials and methods

2.1. Plant materials

Five mapping populations were used. The first was the TI population reported by Mei et al. [25], consisting of 204 RILs of Teqing/IRBB. The male parent IRBB included six near isogenic lines in the genetic background of IR24, among which IRBB52, IRBB59 and IRBB50 were parents of 122, 77 and two RILs, respectively, and IRBB51, IRBB54 and IRBB55 were each a parent of one RIL. Teqing (TQ) and IR24 are middle-season *indica* rice varieties and restorer lines of three-line hybrids grown in the middle-lower reaches of the Yangtze River valley.

The other four populations were derived from residual heterozygotes of the cross TQ/IRBB52 as described below and illustrated in Fig. 1. To verify QTL detected in the TI population and identify new QTL in a more homogenous background, two F_7 plants carrying a number of heterozygous segments were selected. They were selfed to produce two S_1 populations, Ti52-2 and Ti52-3 consisting of 251 and 250 plants, respectively. QTL were determined from data generated from the $S_{1:2}$ and $S_{1:3}$ families of each population. Two S_2 plants that were heterozygous for one or two QTL of interest but homozygous at other QTL regions were selected from the Ti52-2 population. They were selfed to produce two S_1 populations designated ZC9 and ZC12 and consisting of 203 and 241 plants, respectively. QTL were determined using S_1 plants and $S_{1:2}$ families of the two populations.

2.2. Field trials and phenotypic evaluation

Rice populations were grown in paddy fields at the experiment stations of the China National Rice Research Institute located at either Hangzhou in Zhejiang province or Lingshui in Hainan (Table 1). During the floral transition period the day length was longer than 13.5 h at Hangzhou and shorter than 12.5 h at Lingshui, corresponding to natural long-day (NLD) and short-day (NSD) conditions, respectively [26]. There was no replication of S_1 plants in the ZC9 and ZC12 populations. For other populations the experiments followed a randomized complete block design with two replications. In each replication, one line was grown as a single row of 12 plants. Seedlings at about 25 days post sowing were transplanted at a planting density of 16.7 cm × 26.7 cm in all the trials. Field management followed the normal agricultural practices.

Heading date (HD) was scored in all populations. For RILs which generally do not have within-line segregation, HD was recorded as days from sowing to the time when one or more panicles on 50% of the 12 plants had emerged from the leaf sheath. For $S_{1:2}$ and $S_{1:3}$ lines in which within-line segregation was expected, HD was recorded for each plant at first panicle emergence. In replicated trials, HD values of each line were averaged over the two replications and used for data analysis. In S_1 plant trials, HD data was recorded and analyzed on a single-plant basis.

2.3. DNA marker analysis

The linkage map for the TI population constructed previously consisted of 125 simple sequence repeat (SSR) and two sequence tagged site (STS) markers [25]. New markers were developed according to 50× whole genome re-sequencing of TQ, IRBB52 and five bulk samples of the TQ/IRBB progenies. Eight polymorphic markers, including four on chromosome 1,

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