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Quantitative trait loci for phyllochron and tillering in rice

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Abstract Morphogenetic processes in sequentially growing leaves and tiller buds are highly synchronized in rice (*Oryza sativa* L.). Consequently, the appearance of successive leaves in the main tiller acts as the 'pacemaker' for the whole shoot system development. The time interval between the appearance of successive leaves (days/leaf) in the main tiller is called the 'phyllochron'. The objectives of the investigation reported here were: (1) to identify quantitative trait loci (QTLs) that control rice phyllochron and (2) to understand the roles of phyllochron QTLs as an underlying developmental factor for rice tillering. For this purpose we developed a set of recombinant inbred lines derived from a cross between IR36 (*indica*) and Genjah Wangkal (tropical *japonica*). Composite interval mapping detected three phyllochron QTLs located on chromosomes 4, 10 and 11, where the presence of a Genjah Wangkal allele increased phyllochron. The largest QTL (on chromosome 4) was located on the genomic region syntenic to the vicinity of the maize *Teopod 2* mutation, while the QTL on chromosome 10 was close to the rice *plastochron 1* mutation. These three phyllochron QTLs failed to coincide with major tiller number QTLs. However, one tiller number QTL was associated with small LOD peaks for phyllochron and tiller-bud dormancy that were linked in coupling phase, suggesting that linked small effects of phyllochron and tiller-bud dormancy might result in a multiplicative effect on tiller number.

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Introduction

Morphogenetic processes in sequentially growing grass leaves and tiller buds are highly synchronized. In rice (*Oryza sativa* L.), for example, a tiller bud initiates at the appearance of the tiller's subtending leaf (i.e., the emergence of the tip of the leaf from the encircled sheath of the next lower leaf). The subsequent unfolding of successive leaves on the tiller is also synchronized with that on the mother tiller (for a review, see Nemoto et al. 1995). Such 'growth rules' result in the highly ordered and predictable patterns of their whole shoot development, where the appearance of successive leaves in the main tiller acts as the 'pacemaker' for the development of all daughter and granddaughter tillers (Mitchell 1953; Friend 1965; Hay and Kirby 1991). For this reason, the time interval between the appearance of successive grass leaves (days/leaf) in the main tiller, or the 'phyllochron' (Klepper et al. 1982), has successfully been used as a biological (i.e., not a chronological) time unit to quantify and model shoot system development (Haun 1973; McMaster et al. 1991; Moore and Moser 1995).

Rice shows an array of genetic variation in phyllochron, and this variation affects many aspects of the shoot system development through such a synchrony. For example, the *japonica* cultivar Aikawa 1 has the spontaneous *Ltn* mutation (Araki et al. 2003) that prolongs phyllochron. This long phyllochron (about 1.3-fold longer than that found in wild-type plants) results in a very slow increase in tiller number (Goto and Hoshikawa 1989). Long phyllochrons are also found in many low-tillering tropical *japonicas* (Goto and Hoshikawa 1989; Yin and Kropff 1996). Such tropical *japonicas* have been used as donors of the low-tillering habit in the 'New Plant Type' rice project at the International Rice Research Institute (IRRI), a breeding program for high-yield rice cultivars that relies

upon an ideotype with large panicles and few tillers (Khush 2000). However, nothing is known about: (1) the genetic factors responsible for their long phyllochron and (2) how such factors are integrated in their low tiller number.

The study reported here had two objectives. First, we aimed to identify quantitative trait loci (QTLs) that control phyllochron. To date, very little is known about the specific genetic factors involved in the naturally occurring variation of phyllochron, and such information would be useful in understanding how phyllochron is controlled genetically. Second, we aimed to clarify the role of phyllochron in determining tiller number. In rice, the potential tiller number is determined by phyllochron, while the actual tiller number is down-regulated by the dormancy of the tiller buds (Nemoto et al. 1995). Co-location of QTLs for these three traits (phyllochron, tiller dormancy, and tiller number) would be informative for understanding how phyllochron is integrated in rice tillering. To achieve these aims, we developed a set of recombinant inbred lines (RILs) from a cross between two rice cultivars—IR36, a high-tillering *indica* cultivar with a short phyllochron, and Genjah Wangkal, a low-tillering tropical *japonica* cultivar with a long phyllochron.

Materials and methods

Mapping population

RILs derived from a cross between IR36 and Genjah Wangkal (IRRI accession no. IRGC 35652) were used. IR36 is a high-tillering elite *indica* cultivar, while Genjah Wangkal is a tropical *japonica* landrace from Indonesia that has been used as a donor of low-tillering in the breeding of some 'New Plant Type' lines such as IR65598-112-2, a low-tillering 'New Plant Type' line that, like Genjah Wangkal, produces only a few (generally three to six) fertile tillers. The RILs were developed as single-seed descendants to the F_5 generation at the University of Tokyo. Panicles were bagged for each generation to avoid outcrossing. A total of 100 RILs were extracted in the F_5 generation, and the resultant F_6 seeds were used in this study.

Marker analysis

The DNA of the parents and the 100 F_5 plants was extracted from 3 g of fresh leaf tissue using the benzyl chloride method (Zhu and Zhu 1993). For restriction fragment length polymorphism (RFLP) analysis, DNA was digested with six restriction enzymes: *Bam*HI, *Bgl*II, *Dra*I, *Eco*RI,*Eco*RV, and *Hin*dIII. Southern blotting, hybridization, and detection using the ECL Direct Nucleic Acid Labeling and Detection kit (Amersham Pharmacia Biotech, Piscataway, N.J.) were performed as described by Kurata et al. (1994). The set of 192 RFLP landmarkers [Rice Genome Research Program (RGP): http://rgp.dna.affrc.go.jp] derived from the published RFLP linkage map (Kurata et al. 1994) was surveyed on the parents, and selected probes were mapped. Simple sequence repeat (SSR) markers (Chen et al. 1997; McCouch et al. 2002) were also mapped. PCR amplifications were performed as described on the RGP homepage (http://rgp.dna.affrc.go.jp) and by Chen et al. (1997). The amplified products of the mapping population were separated on either 3% agarose gels in 0.5× TBE buffer or 4% agarose gels in 1.0× TAE buffer and the patterns visualized using ethidium bromide.

Phenotypic evaluation

Phenotypic evaluation of the RILs (four plants each), along with their parents (24 plants each), was undertaken at the Tohoku University (38°16′N, 140°52′E) during the summer of 2003. The seeds were imbibed until the first leaf just started to emerge and then sown on August 4 in 3.2-l cylindrical plastic pots (one pot each for the RILs and six pots each for the parents) filled with 3 l clay soil containing 0.25 g ammonium sulfate, 0.50 g ammonium phosphate dibasic, and 0.25 g potassium sulfate. Following emergence, they were thinned to two seedlings per pot. Water was maintained about 3 cm above the soil level throughout the growth period. The experiment consisted of two replications.

We measured phyllochron, which is defined as the time interval between the appearance of a leaf (i.e., the emergence of the tip of the leaf from the encircled sheath of the next lower leaf) and the next leaf in the main tiller (Klepper et al. 1982). In the present study, the average duration of phyllochrons for the first seven leaves in the

Table 1 QTLs detected for phyllochron, tiller number, and tiller-bud dormancy with composite interval mapping

	Chromosome	Marker interval	LOD	Additive[a]	R^2 [b]	Significant LOD (P=0.05)[c]
Phyllochron	4	C891–RM3524	9.09	−0.19	0.32	3.17
	10	R1629–R2447	4.82	−0.12	0.14	
	11	R3202–C1350	3.89	−0.11	0.10	
Tiller number	2	R26–C424	7.57	0.70	0.23	3.06
	5	RM440–RM3870	4.45	−0.51	0.11	
	6	RM217–R2147	4.05	0.55	0.15	
	8	RM264–R1963	4.52	0.49	0.11	
Dormancy						
T2 tiller	2	RM166–C1445	3.30	8.86	0.11	3.11
	6	R2147–R2171	4.35	−10.70	0.16	
T2-p tiller	2	C424–C747	3.61	−6.98	0.13	2.65
T2-2 tiller	2	C424–C747	8.90	−19.55	0.28	4.13
	5	RM3870–C1018	4.33	12.68	0.12	
T3-p tiller	1	C86–C742	4.87	12.19	0.16	3.01
T3-1 tiller	2	C424–C747	7.44	−15.43	0.23	3.25
	5	RM3870–C1018	4.13	11.10	0.12	
T4-p tiller	1	C742–R117	3.93	11.06	0.11	3.44
	3	R3156–R2170	3.51	9.99	0.10	

[a]Additive effect of the IR36 allele
[b]Percentage of variance explained
[c]Significant LOD score for each trait at P=0.05 determined by the permutation test

main tiller was calculated as the number of days from the time of sowing to the appearance of the eighth leaf divided by seven.

The number of tillers that appeared (including the main tiller) was also measured for each plant 30 days after sowing (DAS). A growing tiller bud was considered to have appeared when the tip of its first leaf emerged from its subtending leaf.

We also assessed the frequency in which tiller buds in a specific nodal position became dormant for each of the 100 RILs. We examined the following tiller classes (a 30-day-old plant potentially has tillers in these nodal positions): (1) primary tillers (tillers formed directly on the nodes of the main tiller) on the first to fourth nodes of the main tiller (designated as T1, T2, T3 and T4 tillers); (2) secondary tillers (tillers formed on the nodes of the primary tillers) on the prophyll, the first and the second nodes of the T2 tillers (T2-p, T2-1 and T2-2 tillers); (3) secondary tillers on the prophyll and first nodes of the T3 tillers (T3-p and T3-1 tillers); (4) secondary tillers on the prophyll node of the T4 tillers (T4-p tiller). A check for dormancy was undertaken 35 DAS because the above tiller buds would have appeared by this date, if grown. A tiller bud was judged to be dormant if it failed to appear by this date.

We confined our investigation to relatively early stages of plant development for the following reasons. First, some early-maturing RILs started panicle formation shortly after these early stages. This asynchronous reproductive development poses a problem because reproductive development increases phyllochron dramatically in rice (Nemoto et al. 1995) and, consequently, might cause a discrepancy in evaluating the phyllochron. For consistency purposes and to eliminate the effect of reproductive development on phyllochron, we only used the first seven phyllochrons for phenotypic evaluation. Second, research on tiller-bud dormancy is time-consuming because all of the leaves have to be marked. In practice it became difficult to continue our investigation after 35 DAS owing to the exponential increase in the number of leaves.

Broad-sense heritability (h^2) was calculated from the estimates of genetic (σ^2_G), and residual (σ^2_E) variances derived from the expected mean squares of the analysis of variance were calculated as $h^2=\sigma^2_G/(\sigma^2_E+\sigma^2_E/\kappa)$, where κ was the number of replications.

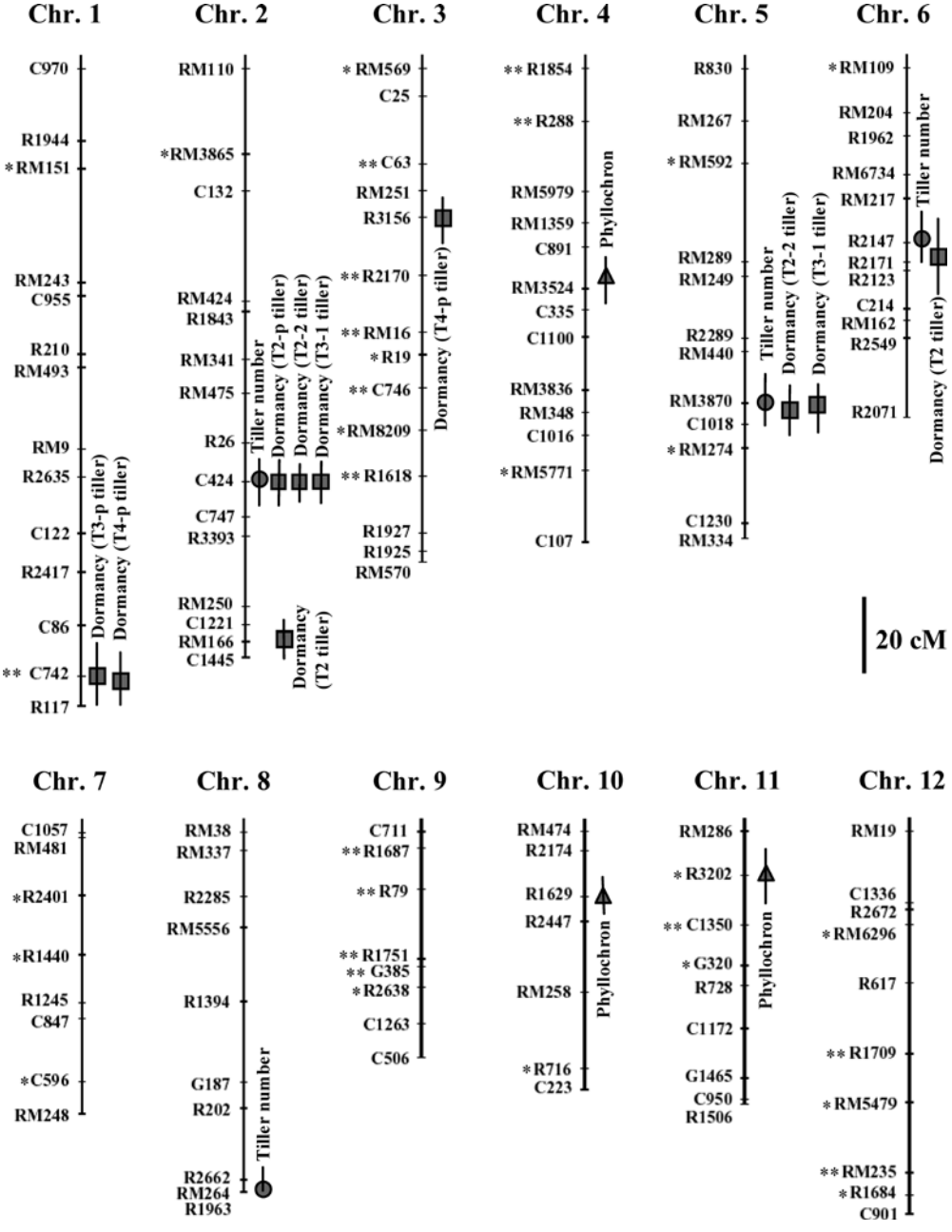

Fig. 1 Chromosomal location of QTLs for phyllochron, tiller number, and tiller-bud dormancy shown in Table 1. *Bars* to the *right* of the chromosomes indicate 1-LOD likelihood intervals, and *symbols* indicate the position of the peak LOD in the interval. *One asterisk* and *two asterisks*indicate segregation distortion significant at$P$=0.05 and 0.01, respectively

Map construction and QTL analysis

A linkage map was constructed using MAPMAKER/EXP ver. 3.0 (Lander et al. 1987). Composite interval mapping was performed using WindowsQTL CARTOGRAPHER 2.0 (Wang et al. 2001–2003). The experiment-wise LOD threshold significance level was determined by computing 1,000 permutations of each morphological character ($P<0.05$) as implemented by QTL CARTOGRAPHER. These permutations can account for non-normality in marker distribution and trait values. The levels of significance for QTL in this study are given in Table 1. Total percentage of variance explained by the detected QTLs was estimated by multiple regression analysis using the nearest marker of each QTL.

Results

Linkage map and marker segregation

Approximately 80% of the probes detected RFLPs. For monomorphic chromosomal regions, we applied SSR markers. Ultimately, we developed a map of 12 linkage groups consisting of 132 (83 RFLP and 49 SSR) markers that spanned 1,297 cM, with an average marker distance of 10.1 cM (Fig. 1). Of the 132 markers, 34 (26%), mainly located to chromosomes 3, 9 and 12, showed significant deviations ($P<0.05$) from the expected segregation ratios based on the Chi-square test. Among the 34 markers, 30 showed an excess of the IR36 homozygote. Only four markers (RM151, RM3865, RM592 and RM109 on chromosomes 1, 2, 5 and 6, respectively) showed an excess of the Genjah Wangkal homozygote. Among the published data on distortion in rice molecular maps, this pattern is most similar to that observed in IR34583 × Bulu Dalam (McCouch et al. 1988). The most severe distortion was found for marker R1709 on chromosome 12, which was strongly skewed in favor of the IR36 alleles (IR36 homozygote:heterozygote:Genjah Wangkal homozygote = 68:6:24).

Trait variation

In the 100 RILs and two parents, the eighth leaf began to appear 21–34 DAS. From these dates, the mean values of the first seven phyllochrons were calculated for each plant. The phyllochron for IR36 and Genjah Wangkal averaged 3.11 and 4.66 days per leaf, respectively (Fig. 2a). The frequency distribution of phyllochron of the RILs was approximately normal and within the range of the two parental values. The broad-sense heritability of phyllochron was high (0.91) and similar to that observed in barley, which was observed to have heritability values ranging from 0.71 to 0.91 (Dofing 1999).

The distribution of tiller numbers showed a similar pattern (Fig. 2b). The two parental values averaged 11.50 (IR36) and 2.63 (Genjah Wangkal). The broad-sense heritability was low (0.34).

The distribution of tiller-bud dormancy varied across the nodal positions on which the tiller buds were formed. T1 tillers were completely dormant (i.e., showing 100% dormancy) in all RILs, while T2 tillers completely appeared (i.e., showing 0% dormancy) in more than half of the RILs (Fig. 3). T3 and T4 tillers completely appeared in all RILs. Tiller buds formed on the prophyll nodes of these primary tillers (T2-p, T3-p, and T4-p) showed a strong tendency for dormancy; these tillers were completely dormant in more than half of the RILs (Fig. 3). The other secondary tillers (T2-1, T2-2 and T3-1) tended to be weakly dormant; these tillers completely appeared in 30–60% of the RILs. IR36 showed very weak dormancy; the primary tillers completely (T3 and T4) or mostly (T2, with 8% of dormancy) appeared; the secondary tillers were partially dominant (48%, 4%, 44%, 4%, and 72% in T2-1, T2-2, T3-p, T3-1, and T4-p tillers, respectively) except for the T2-p tiller which was completely (100%) dormant. Genjah Wangkal showed strong dormancy; the T2, T3 and T4 tillers were partially dormant (68%, 11% and 25%, respectively); the secondary tillers were completely dormant (100%). The T1 tillers were completely dormant (100%) in both parents, as in the RILs.

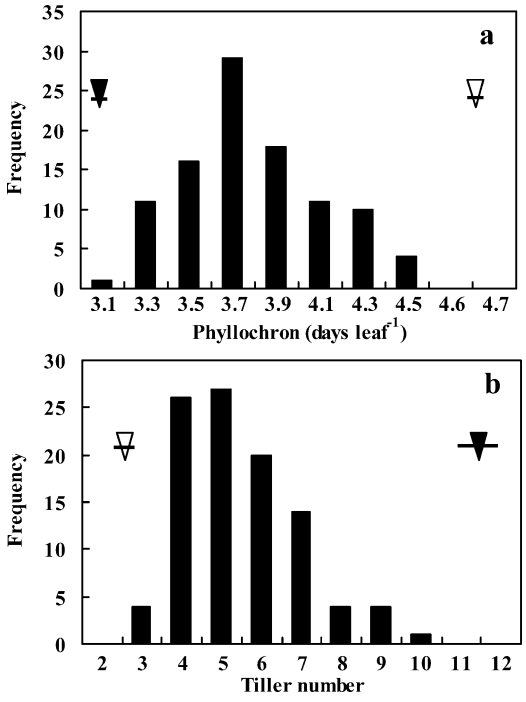

Fig. 2 Frequency distribution of 100 RILs for phyllochron (**a**) and tiller number (**b**). The values of phyllochron were 3.11±0.08 (n=24) and 4.66±0.10 (n=24) (days leaf^{-1}) for IR36 (*closed triangle* with standard deviation) and Genjah Wangkal (*open triangle* with standard deviation), respectively. Tiller number of IR36 and Genjah Wangkal was 11.5±1.7 (n=24) and 2.6±0.5 (n=24), respectively

QTLs for phyllochron

The analysis withQTL CARTOGRAPHER ver. 2.0 revealed three phyllochron QTLs located on chromosomes 4, 10, and 11 with LOD scores higher than 3.17 (Fig. 1, Table 1). The QTL on chromosome 4 had relatively large effects, explaining 32% of the total phenotypic variation. The

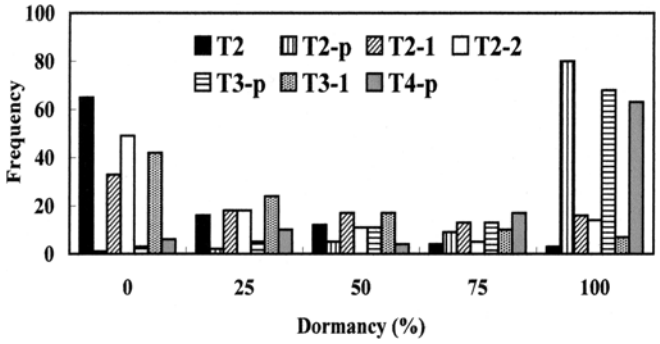

Fig. 3 Frequency distribution of tiller-bud dormancy (calculated as the percentage of tiller buds in dormancy) on the primary (T2) and secondary (T2-p, T2-1, T2-2, T3-p, T3-1 and T4-p) tillers of 100 RILs. For the parental values, see text

QTL on chromosomes 10 and 11 accounted for 14% and 10% of the phenotypic variation, respectively. Altogether, the three QTLs detected in this study explained 38% of the total phenotypic variation. At these QTLs, the presence of a Genjah Wangkal allele increased phyllochron (Table 1).

QTLs for tiller number

For tiller number, four QTLs were detected on chromosomes 2, 5, 6, and 8 with LOD scores higher than 3.06 (Fig. 1, Table 1). Each QTL accounted for 11–23% of the phenotypic variation. Altogether, these four QTLs explained 44% of the total phenotypic variation. At these QTLs, the presence of an IR36 allele increased tiller number except for the QTL on chromosome 5 where the Genjah Wangkal allele increased tiller number (Table 1). Tiller or panicle number QTLs have repeatedly been reported for the QTL region on chromosome 2 (Ray et al. 1996; Li et al. 2000; Liao et al. 2001; Luo et al. 2001; Zhuang et al. 2002). Yan et al. (1998) reported a tiller number QTL for the QTL region on chromosome 8. These four tiller number QTLs failed to coincide with the phyllochron QTLs (Fig. 1).

QTLs for tiller-bud dormancy

Among the primary tillers, only the T2 tiller segregated for dormancy. In the T2 tiller, two QTLs were detected on chromosomes 2 and 6 (Fig. 1, Table 1). The Genjah Wangkal allele increased dormancy at the QTLs on chromosome 6, while the IR36 allele increased dormancy at the QTL on chromosome 2. The former QTL approximately coincided with a tiller number QTL (Fig. 1).

In the secondary tillers (T2-p, T2-2, T3-p, T3-1, and T4-p; no significant QTLs were detected in T2-1), four QTLs were detected on chromosomes 1, 2, 3 and 5, respectively (Fig. 1, Table 1). The QTL on chromosome 1 was detected in the T3-p and T4-p tillers, while the QTL on chromosome 2 was detected in the T2-p, T2-2, and T3-1 tillers. The QTL on chromosome 5 was detected in the T2-2 and T3-1 tillers. The QTL on chromosome 3 was detected in the T4-p tiller. The Genjah Wangkal allele increased dormancy at the QTL on chromosome 2, while the IR36 allele increased dormancy at the QTLs on chromosomes 1, 2, and 5 (Table 1). The QTLs on chromosomes 2 and 5 coincided with a tiller number QTL (Fig. 1).

Discussion

The first purpose of our study was to identify QTLs for rice phyllochron. We detected three phyllochron QTLs located on chromosomes 4, 10 and 11, respectively (Fig. 1). Individually, these QTLs accounted for up to 32% of the phenotypic variation (Table 1). Our preliminary analysis in an earlier year detected the same three QTLs (with LOD scores of 4.45, 3.12, and 4.32, respectively), which indicated that our results were consistent. This is the first report on QTLs for grass phyllochron. For these QTLs, two possible roles can be postulated. Firstly, these QTLs may directly control the initiation of leaf primordia at the shoot apex similarly to the maize *terminal ear 1* gene. The mutant phenotype and in situ expression pattern of the *terminal ear 1* gene suggest that this gene negatively controls leaf primordium initiation at the shoot apical meristem (Veit et al. 1998). However, none of the phyllochron QTL regions detected in our study are syntenic with the *terminal ear 1* region in the maize genome (the BNL5.37 region of maize chromosome 3, which is syntenic to the telomeric region of the long arm of rice chromosome 1) (Ahn and Tanksley 1993).

The other possible role of these QTLs concerns ‘heterochrony’ (the change in relative timing of developmental events during the ontogenic process) (Gould 1982). In general, phyllochrons become progressively longer as the seedling grows from the juvenile to adult (Yin and Kropff 1996). This progressive increase in phyllochron is considered to be associated with the transition of the physiological status from juvenile to adult because all known grass heterochronic mutations that cause prolonged expression of the juvenile phase of plant development (maize *Teopod 1, Teopod 2, Teopod 3*, and rice *plastochron 1*) commonly shorten the phyllochron (Poethig 1988; Ahn et al. 2002). We found that the QTL near the marker RM3524 on chromosome 4 controls much of the variance for phyllochron (Table 1). Interestingly, this QTL region is in the syntenic region of the *Teopod 2* locus in maize chromosome 10 (Ahn and Tanksley 1993), which suggests that this QTL might be an allele of the rice *Teopod 2* gene (if any). Similarly, the QTL on chromosome 10 is located close to the *plastochron 1* locus, which maps at the middle of the marker intervals R1629–R2447 (Ahn et al. 2002). This suggests that the QTL might be an allele of the *plastochron 1*gene. It is worth considering that the primary role of these two QTLs might be to control the duration of the juvenile phase and that the variation in phyllochron might occur as a result of such a heterochrony.

The second purpose of our investigation was to understand the relevance of phyllochron QTLs to tillering. As mentioned, the appearances of leaves and tillers are highly synchronized in rice, and thus any potential tiller increase is determined by the phyllochron. On the other hand, actual tiller increase is down-regulated by tiller-bud dormancy (see Nemoto et al. 1995 for a review). In order to understand how phyllochron and tiller dormancy are integrated in the control of tiller number at the QTL level, we examined the co-location of QTLs for these three traits. Contrary to our expectations, none of these phyllochron QTLs coincided with the major tiller number QTLs (Fig. 1). In fact, the phyllochron QTL regions had only a small effect on tillering, whose peak LOD values for tiller number were at most 0.82 (e.g., the QTL on chromosome 10). It appeared that most of the tiller number QTLs actually control the dormancy of tiller buds—not the phyllochron—in our mapping population, because three of the four tiller number QTLs coincided with a tiller dormancy QTL (Fig. 1). This may arise from the fact that Genjah Wangkal has an extremely high ability to induce tiller-bud dormancy, which might mask the phyllochron-mediated variation in tiller number.

Nevertheless, phyllochron may be involved in some tiller number QTLs. In our study, the tiller number QTL on chromosome 8 did not coincide with either significant phyllochron or tiller dormancy QTLs (Fig. 1). Instead, this tiller number QTL was associated with small LOD peaks for both phyllochron (LOD = 1.18; additive effect = −0.071; R^2=0.042) and tiller dormancy (e.g., T2 tiller: LOD = 0.98; additive effect = −4.56; R^2=0.028), which were linked in coupling phase (i.e., this region on chromosome 8 had the same small effect on both traits) (Fig. 4). The peak for phyllochron is possibly allelic to *Ltn*, a gene controlling phyllochron that was recently located near marker RM264 (Araki et al. 2003). We suggest that the significant effect of this chromosomal region on tiller number may be a multiplicative effect of these two loci, because tiller number is mathematically a multiplicative function of underlying phyllochron and dormancy. These results suggest the complex nature of tiller number QTLs. The partitioning of tiller number under the categories of phyllochron and tiller dormancy would be an effective viewpoint for gaining a better understanding the genetic control of tiller number.

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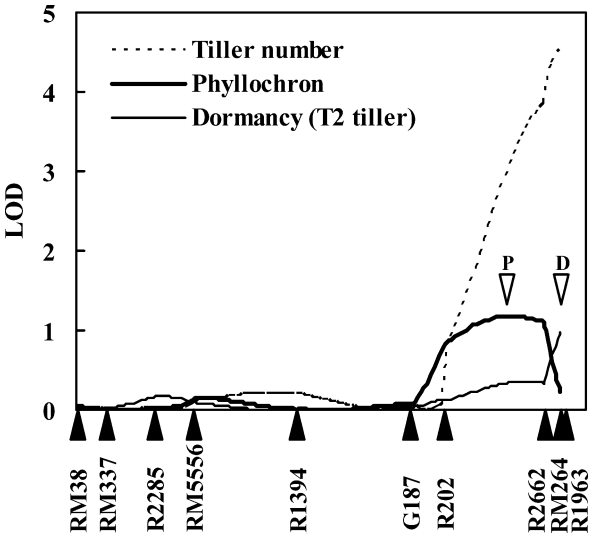

Fig. 4 LOD profiles of tiller number, phyllochron, and tiller (T2) bud dormancy QTLs along chromosome 8.*Arrowheads* indicated the position of peak LOD for phyllochron (*P*) and tiller-bud dormancy (*D*)

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