Theor Appl Genet (2001) 102:1236–1242

Y. Zhou · W. Li · W. Wu · Q. Chen · D. Mao
A.J. Worland

Genetic dissection of heading time and its components in rice

Received: 1 June 2000 / Accepted: 16 October 2000

Abstract Heading time (HT, days from sowing to heading) is an important agronomic trait in rice. Physiologically, HT can be divided into two stages: vegetative growth time (VGT) and reproductive growth time (RGT). A number of studies for mapping QTLs conferring HT in rice have been reported, but none of them has tried to map HT-related QTLs based on their component traits (VGT and RGT). The present study aims to map HT-related QTLs in rice according not only to the performance of HT, but also the performances of VGT and RGT. A method based on an empirical equation of leaf age growth was developed to partition HT into VGT and RGT. An *indica/japonica* DH population and a corresponding RFLP map were constructed for the study. The methods of composite interval mapping and multiple-trait composite interval mapping were used to map QTLs. A total of 19 QTLs were mapped on all 12 rice chromosomes with the exception of chromosomes 1 and 4. Results showed that: (1) more QTLs could be detected by partitioning HT into VGT and RGT; (2) the genetic variation of HT was largely attributed to VGT; and (3) the two component stages were relatively independent in terms of QTL effects, suggesting that the ratio between VGT and RGT could be genetically adjusted without apparently altering HT.

Keywords Rice · Heading time · Vegetative growth time · Reproductive growth time · QTL

Communicated by P. Langridge

Y. Zhou · W. Li · W. Wu (✉) · Q. Chen · D. Mao
College of Crop Science, Fujian Agricultural University,
Fuzhou, Fujian, 350002, China
e-mail: wuwr@fjau.edu.cn or zjweiren@pub5.fz.fj.cn

A.J. Worland
Cereals Research Department, John Innes Centre,
Norwich, NR4 7UH, UK

Introduction

Heading time (HT, days from sowing to heading) is one of the most important agronomic traits in rice. Physiologically, HT can be divided into two developmental stages: vegetative growth time (VGT, days from sowing to panicle initiation) and reproductive growth time (RGT, days from panicle initiation to heading). VGT can be further divided into two parts: the basic vegetative phase (BVP) and the photoperiod sensitive phase (PSP) (Kakizaki 1938; Vergara et al. 1965). It has been thought that HT in rice is mainly determined by VGT (Vergara and Chang 1985).

Since the beginning of the 20th century, many studies have been carried out to investigate the genetic basis of HT in rice. It is now known that HT in rice is controlled by both major genes and minor genes. Since HT is composed of two different developmental stages, it is interesting, and also necessary, to study the two stages separately and make clear whether the two stages share a common genetic system or not. Up to now, however, all genetic studies have been focused on VGT only. Some major genes controlling VGT have been found. It was reported (Chang et al. 1969) that BVP is controlled by two or three *Ef* genes (*Ef-1*, *Ef-2*, *Ef-3*), while PSP is controlled by a series of genes including *Se-1*, *se-2*, *Se-3*, *Se-4*, *Se-5*, *Se-6*, *Se-7*, *E1*, *E2* and *E3*. Some of these genes have been located using morphological or isoenzymatic markers (Yokoo and Fujmaki 1971; Yokoo and Kikuchi 1992; Sato and Hayashi 1985; Poonyaritt et al. 1989; Okumoto et al. 1992; Mackill et al. 1993; Ohshima et al. 1993; Kinoshita 1995; Tsai 1995; Ichitani et al. 1998), but most of them remain unmapped. In recent years, with the help of molecular markers, a number of quantitative trait loci (QTLs) conferring HT have been mapped in rice (Li et al. 1995; Lin et al. 1995; Xiao et al. 1995, 1996; Lu et al. 1997; Yano et al. 1997; Lin et al. 1998; Sarma et al. 1998), some of them were even mapped to a fine scale (Yamamoto et al. 1998). But no work has been reported to specify the stage(s) (VGT or RGT or both) that a QTL is responsible for.

The fact that no genetic study has been conducted on RGT in rice may be largely due to the difficulty in determining the time of panicle initiation (i.e. the time of transition from vegetative growth to reproductive growth). In fact, all reported studies on VGT in rice were based on the hypothesis that RGT is a constant (usually considered to be 35 days), and therefore VGT could be estimated by subtracting 35 days from HT. However, studies have shown that RGT actually varies greatly among varieties in rice (Senanayake et al. 1994; Yin et al. 1997; Dung et al. 1998). Hence, taking RGT as a constant is not appropriate. To study the genetic basis of VGT and RGT, it is crucial to find a reasonable and convenient method for determining the time of panicle initiation.

This paper reports a study of mapping QTLs underlying HT, VGT and RGT in rice based on a method we have developed for indirectly estimating the time of panicle initiation according to the growth curve of leaf age.

Materials and methods

Population and RFLP map

A doubled-haploid (DH) population consisting of 111 lines was established by anther culture from a cross between an *indica* rice variety Gui-630 and a *japonica* rice variety Taiwanjing. Based on the DH population, a linkage map comprising 175 RFLP markers and covering a total length of 1,224.6 cM was constructed (Weng et al. 2000).

Data collection

Field experiment was conducted at Fujian Agricultural University, Fuzhou (26°05' N), China, in 1998. Seeds of all DH lines and their parents were sown in plastic trays on 5 April after pre-germinating under a constant temperature 30°C for 2 days. Seedlings were transplanted into the field on 25 April, with a spacing of 20 cm between plants and between rows. Twenty five seedlings of each line were planted in a square plot surrounded by a row of guard varieties on each side. Plants were grown under normal field management. Two replicates were used.

Ten plants from two inner rows in each plot were chosen for trait investigation. The number of developed leaves and the length of the developing leaf on the main-stem of each plant were recorded every 5–7 days, beginning from the 30th day (5 May) after sowing, until the end of leaf development. The final length of the developing leaf was measured after it had fully developed. The HT of each plant was recorded when its first panicle appeared. The HT of each line was represented by the mean value of individual plants.

Partitioning of HT into VGT and RGT

The leaf age (y) of a plant at a given observation time was calculated using the following formula:

$$y = \text{Number of developed leaves} + \frac{\text{Length of the developing leaf}}{\text{Final length of the developing leaf}}. \quad (1)$$

It was found that growth of the leaf age of each line (including the parental lines) showed a parabolic curve within the observation period (Fig. 1). Hence, an empirical non-linear model was used to fit the leaf-age growth of each line:

$$y = c + at^b, \quad (2)$$

where t is time (with an origin on 30 April, the 25th day after sowing), and a (> 0), b (> 0 and < 1) and c (> 0) are parameters. A method called the contraction-expansion algorithm (Gu et al. 1998) was used to fit model (2).

It has been observed in previous studies (Ling et al. 1980) that panicle initiation in rice is always at around the time of the 3.5 residual leaf age with a very small variation range (3.3–3.6), independent of genotype and environment. Based on this fact, the panicle initiation time (or VGT) of each line could reasonably be estimated from model (2) (Fig. 2) as:

$$\mathrm{VGT} = 25 + \left(\frac{y_F - 3.5 - c}{a}\right)^{\frac{1}{b}} \quad (3)$$

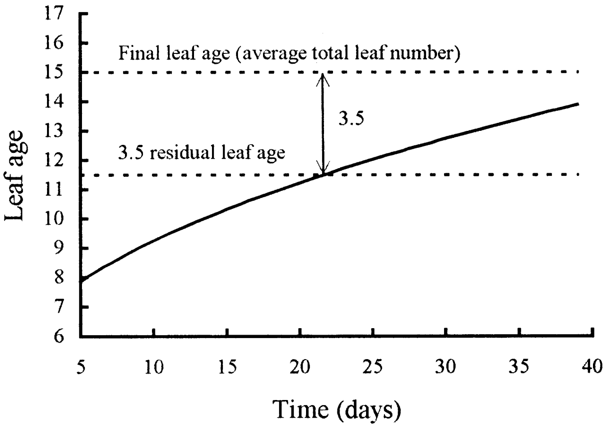

Fig. 2 Principle of determining 3.5 residual leaf age or the time of panicle initiation. Origin of time was set at the 25th day after sowing

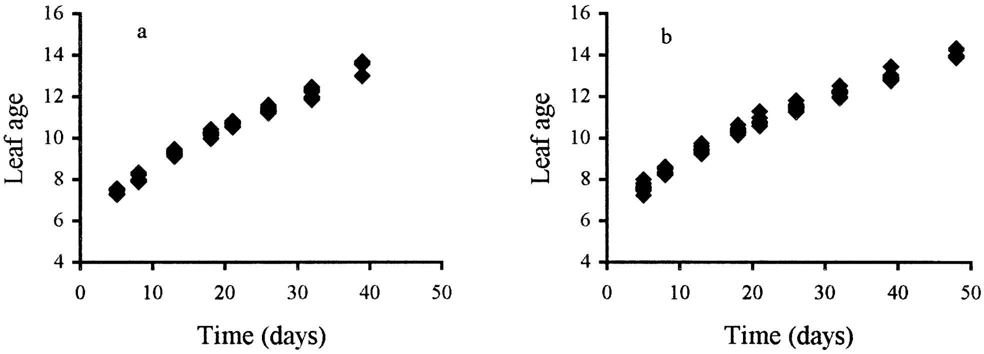

Fig. 1 Growth dynamics of leaf age in parental varieties Taiwanjing (**a**) and Gui-630 (**b**). Origin of time was set at the 25th day after sowing

where y_F is the final leaf age (i.e. the average total number of leaves on the main-stem) of the line. Note that a constant 25 was added in (3) because the origin of time t in (2) was set at the 25th day after sowing. As HT = VGT + RGT, the RGT of each line can thus be estimated as:

$$\mathrm{RGT} = \mathrm{HT} - \mathrm{VGT}. \quad (4)$$

QTL mapping

To map QTLs, HT was analyzed with the method of composite interval mapping (CIM; Zeng 1994) based on least squares estimation (Wu et al. 1996), and VGT and RGT were jointly analyzed with the method of multiple-trait composite interval mapping (MCIM; Jiang and Zeng 1995) based on least squares estimation (Wu et al. 1999). Because the population was not large and there were more markers than lines, QTL mapping was performed on each chromosome separately (Wu et al. 1999). Four window sizes (0, 10, 15 and 20 cM) were tried for CIM and MCIM. Significance thresholds of the LOD score for CIM and MCIM were estimated by the method of permutation tests (Churchill and Doerge 1994) with 1,000 replicates. An overall or genome-wise significance level of 0.05 was used to declare putative QTLs.

Since QTL mapping was performed on each chromosome separately in CIM and MCIM, the effects of QTLs on other chromosomes were not statistically controlled. In a small sample, a correlation between unlinked QTLs may exist due to sampling error. This may possibly cause false positives (Wu et al. 1999). For this reason, after QTLs had been mapped by CIM and MCIM, they were re-evaluated with both univariate stepwise regression (for HT alone) and multivariate stepwise regression (for VGT and RGT jointly), using a significance level of 0.10 (Wu et al. 1999). Since HT is composed of VGT and RGT, QTLs controlling VGT and RGT may also be related to HT and vice versa. Hence, in both of the univariate and multivariate stepwise regression analyses, all mapped QTLs were taken as candidate regression variables. QTLs not significant in both stepwise regression analyses were considered to be false positives and therefore discarded. Effects of the remaining QTLs were then estimated by multiple regression and their contributions to phenotypic variation were indicated by a determination coefficient (R^2).

Path analysis

In order to investigate the relative contributions of VGT and RGT to the genetic variation of HT, both phenotypic and genetic path-analyses were performed. The genetic path-analysis was conducted using the genetic variances of and the genetic covariances between HT, VGT and RGT explained by the mapped QTLs. The QTL-explained genetic variance of a trait was estimated by the following formula (epistatic effects not considered, Wu et al. 1999):

$$\mathrm{var} = \sum_i a_i^2 + \sum_{i \neq j} \left(1 - 2r_{ij}\right) a_i a_j, \quad (7)$$

where a_i is the additive effect of the i^{th} QTL and r_{ij} is the recombination frequency between the i^{th} and j^{th} QTLs. We found that the effects of mapped QTLs on the three traits also followed the relationship of HT = VGT + RGT (see Table 1). Therefore, the QTL-explained genetic covariances between HT and VGT and between HT and RGT could be estimated with the following formulae, respectively:

$$\begin{aligned}\mathrm{cov}(\mathrm{HT},\mathrm{VGT}) &= \mathrm{cov}(\mathrm{VGT}+\mathrm{RGT},\mathrm{VGT}) \\ &= \mathrm{var}(\mathrm{VGT}) + \mathrm{cov}(\mathrm{VGT},\mathrm{RGT}) \quad (8)\end{aligned}$$

$$\begin{aligned}\mathrm{cov}(\mathrm{HT},\mathrm{RGT}) &= \mathrm{cov}(\mathrm{VGT}+\mathrm{RGT},\mathrm{RGT}) \\ &= \mathrm{var}(\mathrm{RGT}) + \mathrm{cov}(\mathrm{VGT},\mathrm{RGT}), \quad (9)\end{aligned}$$

where

$$\mathrm{cov}(\mathrm{VGT},\mathrm{RGT}) = [\mathrm{var}(\mathrm{HT}) - \mathrm{var}(\mathrm{VGT}) - (\mathrm{var}(\mathrm{RGT})]/2. \quad (10)$$

Results

Performances of HT, VGT and RGT

All lines (including parental varieties) showed a determination coefficient (R^2) greater than 95% (only one line's R^2 = 94.55%), with an average ± standard deviation of 98.33 ± 1.15%, when their leaf age growths were fitted with model (2), indicating that the fitting was successful. Therefore, using model (2) to partition HT into VGT and RGT should be feasible. All three traits showed an approximately symmetric continuous distribution. The parents Taiwanjing and Gui-630 had a quite similar HT (about 80 and 85 days, respectively), but the variation among DH lines was large, ranging from 79.7 to 110.0 days (mean ± standard deviation = 91.7 ± 7.9). A similar performance was observed in VGT and RGT. The differences between parents for VGT and RGT were only 2 and 3 days, while the variation ranges of the two traits among the DH lines were 44.2–73.2 (56.9 ± 6.4) and 28.0–46.2 (34.8 ± 3.6) days, respectively. These results suggest that all the traits, including RGT, displayed great transgressive segregation and genetic variation. Therefore, taking RGT as a constant (e.g. 35 days) as in previous studies is inappropriate. Similar results have also been reported before (Senanayake et al. 1994; Yin et al. 1997).

Since HT varied greatly among the lines, the temperature condition during panicle development of different lines might be varied. Hence, it would be necessary to examine whether temperature had a large effect on RGT. For this purpose, the mean value of the mean temperature per day during RGT (abbreviated as MTRGT) of each line was calculated. It was found that the variation of MTRGT among the lines was not large, with a difference only of about 4°C between the largest (29.14°C) and the smallest (25.15°C). Regression analysis showed that RGT was slightly positively correlated with MTRGT, but the determination coefficient was small (15.76%). So, although temperature might somewhat influence RGT, the effect was small and therefore might not significantly interfere with genetic analysis.

QTL mapping

A total of 19 QTLs were mapped on all 12 rice chromosomes with the exception of chromosomes 1 and 4 (Fig. 3). All of these QTLs were detected by MCIM (joint analysis of VGT and RGT), but only nine of them were detected by CIM (analysis of HT). This indicates that dividing HT into VGT and RGT could detect more QTLs related to HT. Seventeen of the mapped QTLs were significant in the subsequent multivariate stepwise regression analysis, but only 11 were significant in the univariate stepwise regression analysis. The two QTLs on chromosome 11 (QTL11a and QTL11b) were not significant in both of the stepwise regression ana-

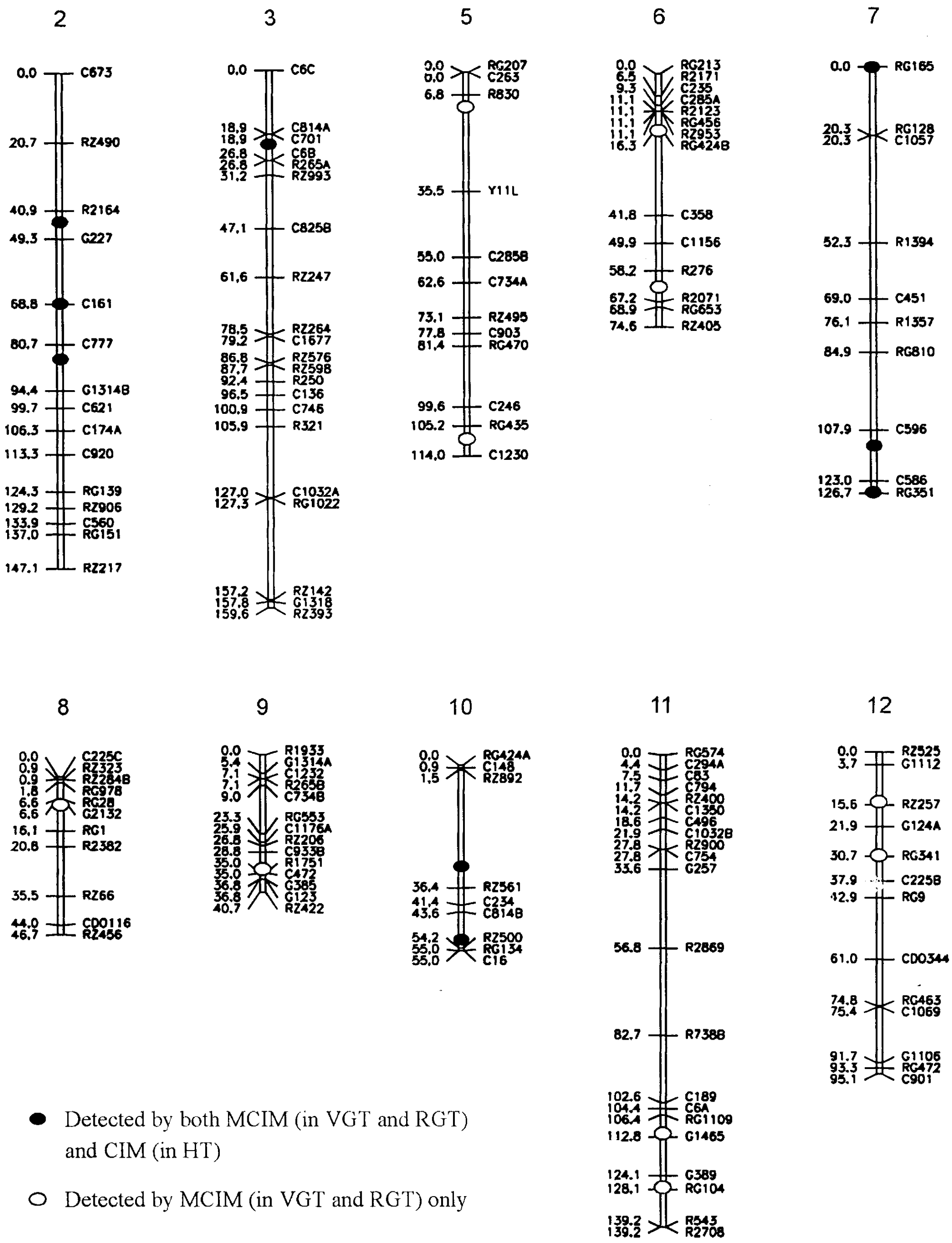

Fig. 3 Locations of QTLs conferring VGT, RGT and HT in rice. Names and positions of markers are listed on the right side and the left side of each chromosome. Positions of QTLs are indicated by *ovals*

lyses. They were, therefore, suspected of being false positives and were discarded. Effects of the remaining 17 QTLs on VGT, RGT and HT, and their relative contributions to the phenotypic variation (R^2) of the three traits, were then estimated by multiple regression (Table 1, Fig. 4).

It is seen from Fig. 4 that the relative importance of QTLs for a trait (indicated by R^2) varied greatly, with a range of 0.32%–6.34%, 0.17%–8.18% and 0.01%–8.40% in VGT, RGT and HT, respectively. In total, these QTLs explained about 2/3rds of the phenotypic variations of VGT, RGT and HT, respectively. If we take the R^2 of a QTL smaller than 1% as insignificant, and so neglect its contribution, then we find from Fig. 4 that VGT was mainly controlled by 11 QTLs, namely, QTL7c, 2a, 7b, 10b, 8, 7a, 3, 2b, 9, 2c and 5a (listed in order from a larger R^2 to smaller R^2, as in what follows); RGT was mainly controlled by 12 QTLs, namely, QTL12b, 3, 12a, 7c, 6b, 7b, 5a, 6a, 5b, 2a, 7a and 8; and HT was mainly controlled by ten QTLs, namely, QTL7c, 3, 2a, 7b, 10b, 7a, 12a, 2b, 9 and 8.

It is interesting to note that QTL5a, 5b, 6a and 6b contributed almost nothing to HT (R^2 very close to zero; Fig. 4). The reason is that these QTLs had opposite effects on VGT and RGT (Table 1). Since a QTL's effects on the three traits also follows the relationship of HT =

Table 1 Mapped QTLs conferring vegetative growth time (VGT), reproductive growth time (RGT) and heading time (HT) in rice

QTL	Chromosome no.	Position (cM)	Additive effect [a]		
			VGT	RGT	HT
QTL2a	2	43	–2.056	–0.630	–2.686
QTL2b	2	69	1.610	0.529	2.139
QTL2c	2	85	–1.313	0.333	–0.980
QTL3	3	22	–1.395	–1.266	–2.661
QTL5a	5	10	–0.893	0.680	–0.213
QTL5b	5	109	–0.494	0.618	0.124
QTL6a	6	16	–0.789	0.592	–0.197
QTL6b	6	64	0.658	–0.906	–0.248
QTL7a	7	0	1.413	0.497	1.910
QTL7b	7	114	–2.989	–1.334	–4.323
QTL7c	7	127	3.214	1.319	4.533
QTL8	8	8	1.698	–0.499	1.199
QTL9	9	33	–0.905	–0.373	–1.278
QTL10a	10	30	0.739	0.269	1.008
QTL10b	10	51	2.148	0.586	2.734
QTL12a	12	15	–0.773	–1.444	–2.217
QTL12b	12	31	–0.849	1.782	0.933

[a] Effect of allele from Gui-630

VGT + RGT, the opposite effects of a QTL on VGT and RGT may be mutually offset, resulting in a smaller effect on HT (Table 1). Similar phenomena were found at QTL2c, 8 and 12b.

Relationship between VGT and RGT

Comparing VGT and RGT, we see that some QTLs, such as QTL3, QTL7c and QTL7b, showed significant contributions to both traits. However, in most of the cases, the relative importance of a QTL (indicated by R^2) for VGT and RGT was quite different. A typical example is QTL12a and 12b, which were among the most important QTLs for RGT, but unimportant for VGT. In fact, the linear correlation of R^2 between VGT and RGT was very small (= –0.066). This suggests that VGT and RGT are relatively independent in terms of QTL effects. This is consistent with the fact that both the phenotypic correlation and the genetic correlation attributed to the mapped QTLs between VGT and RGT were low (= 0.174 and 0.291, respectively).

Contributions of VGT and RGT to HT

It is seen from Fig. 4 that the variation pattern of the QTL's relative importance (R^2) for HT was very similar to that of VGT (correlation = 0.861), but much less similar to that of RGT (correlation = 0.291). This is consistent with the result of path analysis. The direct phenotypic and genetic paths from VGT to HT were 0.816 and 0.797, respectively; while those from RGT to HT were 0.453 and 0.415, respectively. These results suggest that the genetic variation of HT should be largely attributed to VGT in rice.

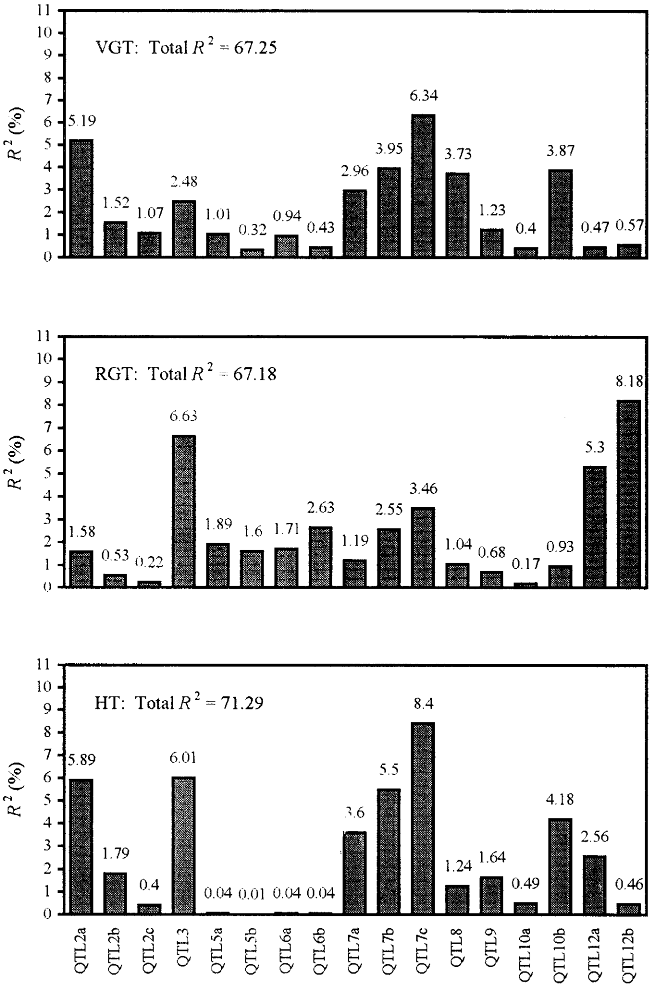

Fig. 4 Proportions of phenotypic variation (R^2) explained by QTLs for VGT, RGT and HT

Discussion

Importance of partitioning HT into VGT and RGT for QTL mapping

A number of studies for mapping QTLs conferring HT in rice have been reported (Li et al. 1995; Lin et al. 1995; Xiao et al. 1995, 1996; Lu et al. 1997; Yano et al. 1997; Lin et al. 1998; Sarma et al. 1998; Yamamoto et al. 1998). However, none of these have tried to map QTLs related to HT based on its component traits (VGT and RGT). In the present study, we developed an approach for indirectly estimating the time of panicle initiation so that HT could be divided into VGT and RGT. There are at least two advantages to partition HT for QTL mapping. First, QTL effects on VGT and HT can be distinguished. This may help us to better understand the genetic basis of HT and other related traits. Second, more QTLs related to HT can be detected, especially for those QTLs showing opposite effects on VGT and RGT.

Table 2 Possible allelism of QTLs conferring HT mapped in this study to those mapped in previous studies

Chromosome (arm) [a]	Common linked marker	QTL mapped		References
		This study	Previous studies	
3 (S)	RZ993	QTL3	*dth3*	Xiao et al. 1996
6 (S)	C235	QTL6a	*Hd-1*	Yano et al. 1997
			Hd-1	Yamamoto et al. 1998
			Hd1	Yamamoto et al. 2000
			Unnamed	Lin et al. 1998
7 (L)	C596	QTL7b	Unnamed	Lin et al. 1998
7 (L)	C586	QTL7c	*Hd-2*	Yano et al. 1997
			Hd-2	Yamamoto et al. 1998
8 (L)	RG978	QTL8	*QHd8a*	Li et al. 1995
			dth8	Xiao et al. 1996
			hd8	Lin et al. 1995
			hd-8	Lu et al. 1997
9 (L)	G123	QTL9	*FTLQ3*	Sarma et al. 1998
12 (?)	RG341	QTL12b	*hd12*	Lin et al. 1995

[a] S = short arm; L = long arm; ? = unknown

Consistency of QTLs for HT mapped in different studies

At least 32 QTLs for HT have been reported in rice. They are distributed over the whole rice genome except for chromosome 5. We may expect that some of these QTLs must be allelic. But, unfortunately, a comparison of QTLs mapped by different studies has been difficult because different sets of DNA probes were used in the different studies. Two sets of rice DNA probes have been commonly employed, one is from Cornell University (Causse et al. 1994) while the other is from the Rice Genome Research Program (RGP) of Japan (Harushima et al. 1998). In the present study, we used an RFLP map containing markers (probes) from both Cornell University and RGP (Weng et al. 2000). This allows us to compare our results with some previous studies, in which probes from either Cornell University or RGP were used. The comparison suggests that seven QTLs mapped in the present study appear to coincide with the QTLs for HT detected by earlier studies (Table 2), giving support to the existence of these QTLs.

Impact of mapping HT-related QTLs on rice breeding

Our research has indicated that VGT and RGT in rice are relatively independent in terms of QTL effects. This implies that it would be possible to adjust the ratio between VGT and RGT via genetic recombination without apparently altering HT. For example, according to the QTLs mapped in this study, it can be expected in theory that the ratio of VGT/RGT may vary from 1.10 to 2.20, equivalent to a variation range of about 11.5 days in VGT (or complementary for RGT), when HT is fixed at 70.0–70.1 days. This variation range is quite considerable. Hence, the structure of HT in rice is very flexible and there is wide freedom to re-mould it. Although it is still not clear how the ratio of VGT/RGT can affect the grain yield of rice at present, considering the fact that the two important yield components, the number of productive tillers and the number of spikelets per panicle, are built during VGT and RGT respectively, it is to be expected that there might be an optimal pattern(s) of the VGT-RGT ratio for the highest yield under a given length of HT in rice. This is worth further study.

Acknowledgements This work was supported in part by the High Technology Research and Development Program of China (Project 101-02-01-03), the Royal Society of UK, and the Rockefeller Foundation.

References

Causse MA, Fulton TM, Cho YG, Ahn SN, Chunwongse J, Wu K, Xiao J, Yu Z, Ronald PC, Harrington SE, Second G, McCouch SR, Tanksley SD (1994) Saturated molecular map of the rice genome based on an interspecific backcross population. Genetics 138: 1251–1274

Chang TT, Li CC, Vergara BS (1969) Component analysis of duration from seeding to heading in rice by the basic vegetative phase and the photoperiod sensitive phase. Euphytica 18: 79–91

Churchill GA, Doerge RW (1994) Empirical threshold values for quantitative trait mapping. Genetics 138: 963–971

Dung LV, Inukai T, Sano Y (1998) Dissection of a major QTL for photoperiod sensitivity in rice: its association with a gene expressed in an age-dependent manner. Theor Appl Genet 97: 714–720

Gu S, Hui D, Mo H (1998) The optimal fitting of the nonlinear equation with a contraction-expansion algorithm. Acta Agron Sinica 24: 513–519

Harushima Y, Yano M, Shomura A, Sato M, Shimano T, Kuboki Y, Yamamoto T, Lin SY, Antonio BA, Parco A, Kajiya H, Huang N, Yamamoto K, Nagamura Y, Kurata N, Khush G, Sasaki T (1998) A high-density rice genetic linkage map with 2275 markers using a single F_2 population. Genetics 148: 479–494

Ichitani K, O kumoto Y, Tanisaka M (1998) Genetic analysis of the rice cultivar kasalath with special reference to two photoperiod sensitivity loci, *E1* and *Se-1*. Breed Sci 48: 51–57

Jiang C, Zeng Z-B (1995) Multiple trait analysis of genetic mapping for quantitative trait loci. Genetics 140: 1111–1127

Kakizaki Y (1938) A concept of developmental physiology of rice and rice culture. Agric Hort 13: 7–14

Kinoshita T (1995) Report of the committee on gene symbolization, nomenclature and linkage group. Rice Genet Newslett 12: 9–153

Li Z, Pinson SRM, Stansel JW, Park WD (1995) Identification of quantitative trait loci (QTLs) for heading time and plant height in cultivated rice (*Oryza sativa L.*). Theor Appl Genet 91: 374–381

Lin HX, Qian HR, Zhuang JY, Lu J, Min SK, Xiong ZM, Huang N, Zheng KL (1995) RFLP mapping of quantitative trait loci in rice (*Oryza sativa L.*). Sci Agric Sinica 28: 1–7

Lin SY, Sasaki T, Yano M (1998) Mapping quantitative trait loci controlling seed dormancy and heading date in rice (*Oryza sativa* L.) using backcross inbred lines. Theor Appl Genet 96: 997–1003

Ling QH, Cai JZ, Su ZF (1980) The practical value of using the ‘‘leaf index’’ and ‘‘leaf remainer’’ in determining the stages of panicle-differentiation in rice plants. Sci Agric Sinica 13: 1–11

Lu C, Shen L, Tan Z, Xu Y, He P, Chen Y, Zhu L (1997) Comparative mapping of QTLs for agronomic traits of rice across environments by using a doubled-haploid population. Theor Appl Genet 94: 145–150

Mackill DJ, Salam MA, Wang ZY, Tanksley SD (1993) A major photoperiod-sensitivity gene tagged with RFLP and isozyme markers in rice. Theor Appl Genet 85: 536–540

Ohshima I, Kikuchi F, Watanabe Y, Asahi C (1993) Genetic analysis of heading time in a cross between two *indica* varieties with inhibitor genes for photoperiod sensitivity. Japan J Breed 43: 101–106

Okumoto Y, Yoshimura A, Tanisaka T, Yamagata H (1992) Analysis of a rice variety Taichung 65 and its isogenic early heading lines for late-heading genes *E1, E2* and *E3*. Japan J Breed 42: 415–429

Poonyarit M, Mackill DJ, Vergara BS (1989) Genetics of photoperiod sensitivity and critical daylength in rice. Crop Sci 29: 647–652

Sarma RN, Gill BS, Sasaki T, Galiba G, Sutka J, Laurie DA, Snape JW (1998) Comparative mapping of the wheat chromosome 5 A *Vrn-A1* region with rice and its relationship to QTL for flowering time. Theor Appl Genet 97: 103–109

Sato YI, Hayashi K (1985) The genetic control of the basic vegetative phase in early maturing native rice varieties. Japan J Breed 35: 160–166

Senanayake N, Naylor Rel, Datta SKDE, Thomson WJ (1994) Variation in development of contrasting rice cultivars. J Agric Sci 123: 35–39

Tsai KH (1995) Multiple alleles detected at the *Ef-1* locus. Rice Genet Newslett 12: 204–206

Vergara BS, Chang TT (1985) The flowering response of the rice plant to photoperiod, 4th edn. IRRI, Manila, The Philippines

Vergara BS, Purranavhavung S, Lilis R (1965) Factors determining the growth duration of rice varieties. Phyton 22: 177–185

Weng Q, Wu W, Li W, Liu H, Tang D, Zhou Y, Zhang Q (2000) Construction of an RFLP linkage map of rice using DNA probes from two different sources. J Fujian Agric Univ 29: 129–133

Wu W, Li W, Lu H (1996) Composite interval mapping of quantitative trait loci based on least square estimation. J Fujian Agric Univ 25: 394–399

Wu W-R, Li W-M, Tang D-Z, Lu H-R, Worland AJ (1999) Time-related mapping of quantitative trait loci underlying tiller number in rice. Genetics 151: 297–303

Xiao J, Li J, Yuan L, Tanksley SD (1995) Dominance is the major genetic basis of heterosis in rice as revealed by QTL analysis using molecular markers. Genetics 140: 745–754

Xiao J, Li J, Yuan L, Tanksley SD (1996) Identification of QTLs affecting traits of agronomic importance in a recombinant inbred population derived from a subspecific rice cross. Theor Appl Genet 92: 230–244

Yamamoto T, Kuboki Y, Lin SY, Sasaki T, Yano M (1998) Fine mapping of quantitative trait loci Hd-1, Hd-2 and Hd-3, controlling heading time of rice, as single Mendelian factors. Theor Appl Genet 97: 37–44

Yamamoto T, Lin H, Sasaki T, Yano M (2000) Identification of heading date quantitative trait locus *Hd6* and characterization of its epistatic interactions with *Hd2* in rice using advanced backcross progeny. Genetics 154: 885–891

Yano M, Harushima Y, Nagamura Y, Kurata N, Minobe Y, Sasaki T (1997) Identification of quantitative traits loci controlling heading time of rice using a high-density linkage map. Theor Appl Genet 95: 1025–1032

Yin X Y, Kropff M F, Yalez M A (1997) Photoperiodically sensitive and insensitive phase of preflowering development in rice. Crop Sci 37: 182–190

Yokoo M, Fujimaki H (1971) Tight linkage of blast resistance with late maturing observed in different *indica* varieties of rice. Japan J Breed 21: 35–39

Yokoo M, Kikuchi F (1992) The *Lm* locus controlling photoperiod sensitivity in rice differs from the *E1* loci, *E2* loci and *E3* loci. Japan J Breed 42: 375–381

Zeng Z B (1994) Precision mapping of quantitative trait loci. Genetics 136: 1457—1468